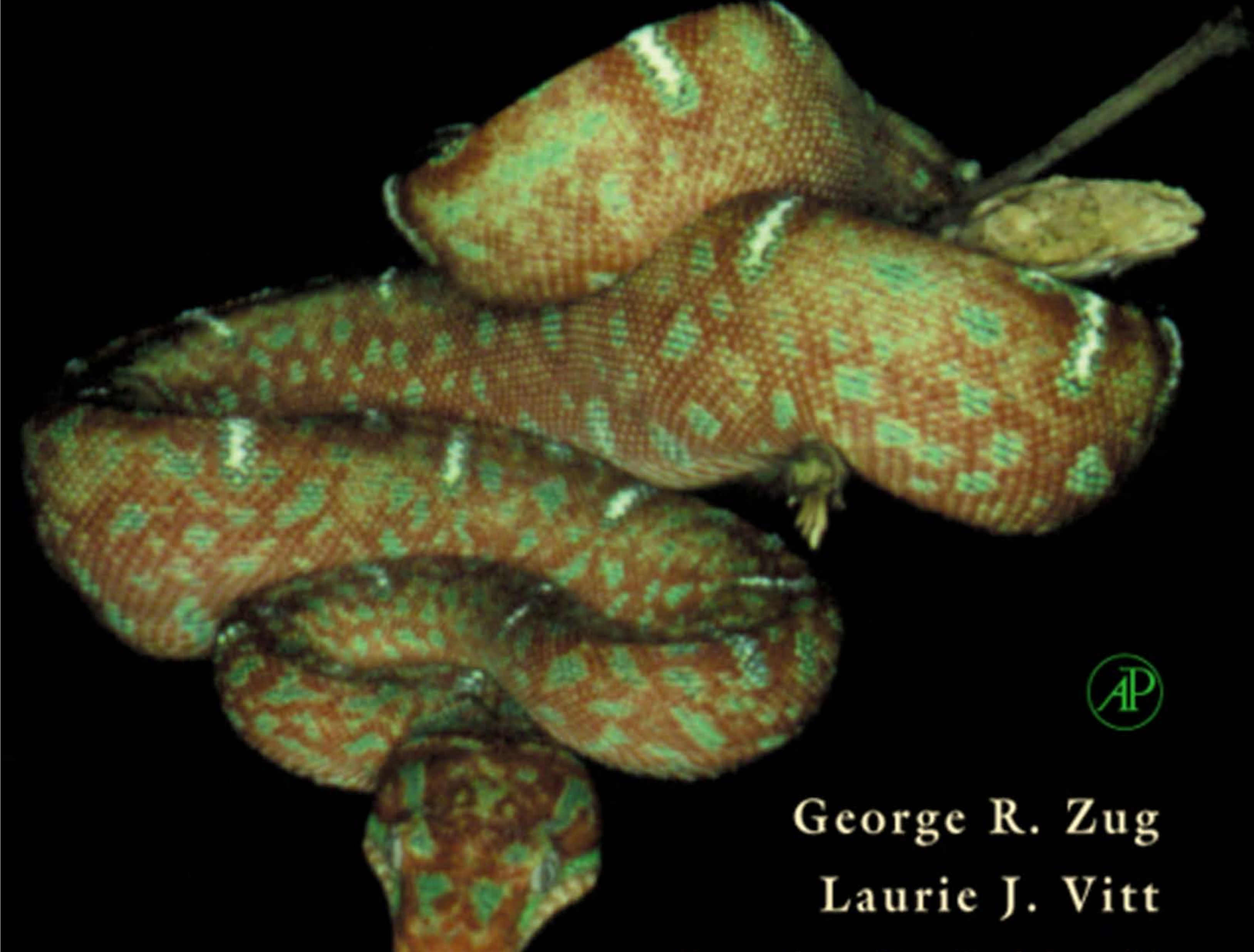
SECOND EDITION

Herpetology

An Introductory Biology of Amphibians and Reptiles



George R. Zug
Laurie J. Vitt
Janalee P. Caldwell

HERPETOLOGY

An Introductory Biology of Amphibians and Reptiles

Second Edition

HERPETOLOGY

An Introductory Biology of Amphibians and Reptiles

Second Edition

GEORGE R. ZUG

National Museum of Natural History
Smithsonian Institution
Washington, DC

LAURIE J. VITT

Sam Noble Oklahoma Museum of Natural History
and Department of Zoology
University of Oklahoma
Norman, Oklahoma

JANALEE P. CALDWELL

Sam Noble Oklahoma Museum of Natural History
and Department of Zoology
University of Oklahoma
Norman, Oklahoma

ACADEMIC PRESS
A Harcourt Science and Technology Company

San Diego San Francisco New York Boston London Sydney Tokyo

Academic Press
A Harcourt Science and Technology Company
525 B Street, Suite 1900, San Diego, California 9210-4495, USA
http://www.academicpress.com

Academic Press
Harcourt Place, 32 Jamestown Road, London NW1 7BY, UK
http://www.academicpress.com

Library of Congress Catalog Card Number: 00-111103

International Standard Book Number: 0-12-782622-X

PRINTED IN THE UNITED STATES OF AMERICA
01 02 03 04 05 06 WP 9 8 7 6 5 4 3 2 1

To colleagues, met and unmet, whose research stokes my continuing enthusiasm
for herpetology, and to past and present colleagues in the SI/NMNH Division of
Amphibian and Reptiles for camaraderie, assistance, and challenges.
G.R.Z.

To all who have been touched by a reptile or amphibian—
you understand why I do what I do!
L.J.V.

To all present and future students of herpetology, whose love and understanding of
amphibians and reptiles will be needed to ensure their continued existence in a
world of diminishing natural habitats.
J.P.C.

This Page Intentionally Left Blank

Contents

Part I

EVOLUTIONARY HISTORY

1 Tetrapod Relationships and Evolutionary Systematics

2 Anatomy of Amphibians and Reptiles

3 Evolution of Ancient and Modern Amphibians and Reptiles

Part II

REPRODUCTION AND LIFE HISTORIES

4 Modes of Reproduction and Parental Care

5 Reproductive Ecology and Life Histories

Part III

PHYSIOLOGICAL ECOLOGY

6 Water Balance and Gas Exchange

7 Thermoregulation, Performance, and Energetics

Part IV

BEHAVIORAL ECOLOGY

8 Spacing, Movements, and Orientation

9 Communication and Social Behavior

10 Foraging Ecology and Diets

11 Defense and Escape

Part V

POPULATION AND COMMUNITY ECOLOGY

12 Population Structure and Dynamics

13 Community and Geographical Ecology

14 Conservation Biology

Part VI

CLASSIFICATION AND DIVERSITY

15 Caecilians

16 Salamanders

17 Frogs

18 Turtles

19 Crocodylians

20 Tuataras and Lizards

21 Snakes

Preface

It is an admirable feature of herpetologists that they are able to cross the boundaries between different aspects of their subject, which remains, perhaps more than other branches of zoology, a single coherent discipline.

A. d'A. Bellairs and C. B. Cox, 1976

Those of us lucky enough to be herpetologists, whether professional or amateur, clearly recognize the value of all amphibians and reptiles. They not only are part of our own evolutionary history, but also are an integral part of our natural heritage; they, along with all other animal and plant species, constitute life on Earth. The excitement and enthusiasm that we all experience while observing and studying amphibians and reptiles have brought together a remarkable diversity of people, collectively known as herpetologists. The continued survival of the animals that have so deeply touched our lives depends on our ability to communicate what we know about them. We broadened our horizons writing this book; we hope reading it broadens yours.

Our goal in revising *Herpetology: An Introductory Biology of Amphibians and Reptiles* was twofold. First, we wished to update the text to include new concepts and interpretations of biology as they apply to herpetology and to provide the evolutionary and classificatory perspective of living amphibians and reptiles circa mid-1999. Second, we wished to improve the didactic scope of the text by introducing more concepts and associated examples and by demonstrating different interpretations and uncertainties. We have not attempted to be encyclopedic; thus, we have not included all concepts or all of the excellent studies that examine these concepts.

The first edition excluded literature citations from the text. We recognize their importance to the more advanced readers and their disruptive influence on the biologically and herpetologically novice reader. As a compromise, we have included citations in the text but have limited their numbers; we have included reference information at the end of each chapter for those desiring ready access to additional information. We include a brief glossary of terms and concepts that are not explained when first used in the text.

Classification and nomenclature are amidst major changes. New fossils, new techniques for obtaining and interpreting phylogenetic data, and the beginnings of a truly phylogenetic taxonomy and its associated nomenclature are changing amphibian and reptilian classification monthly. We have attempted to be as current as possible, and our classification sections reflect published interpretations through July 1999. Our classification contains a mix of the old and the new, perhaps befitting of these changing times. We have adopted the phylogenetic taxonomic concept of using a hierarchical arrangement to depict classificatory levels and have discontinued the use of higher-level labels (order, class, etc.). While we avoid the use of family and subfamily as labels in titles and classifications, we have found it convenient at times to use the familial and generic label within a textual discussion. There are numerous phylogenies for most groups of amphibians and reptiles, and these hypotheses result in different classifications—sometimes strikingly different. We have simply selected a single cladistic interpretation for each group or combined the results of two interpretations when a single cladistic analysis for all members of the group (clade) was not available. We discuss other interpretations and analyses, but not necessarily all available studies, to ensure that the reader is aware that other interpretations exist. We use Latinized familial and subfamilial group names for monophyletic groups and Anglicized or Latinized names in quotes for groups that are of uncertain monophyly. Some authors have not assigned family names to some species and groups of species that represent a sister taxon to another family; where Latinized familial names are available, we have used the available name or elevated a subfamilial name if that latter taxon includes the same set of species. For example, Ford and Cannatella (1993) recognized *Hemisus* as a potential sister taxon of Dendrobatidae or Microhylidae; hence, we use the available Hemisotidae. Distributions are an important component of an organism's biology; our maps show the natural (non-human dispersed) distribution as best as we were able to determine it.

Acknowledgments

The preparation of a book requires a cadre of helpful friends and colleagues. We are fortunate that many generous people have gone out of their way to provide information, reviews, illustrative materials, and suggestions. We thank all of you. We also renew our thank you to our colleagues who contributed to the first edition of this textbook and to those colleagues who used the book in their classes and offered suggestions for its improvement. We hope that your suggestions are evident.

The group of colleagues contributing directly to this revision has been equally large and generous with their time and materials. For reviewing portions of the book, we thank A. Bauer, P. Braziatis, R. I. Crombie, D. A. Croshaw, K. de Queiroz, R. D. Durtsche, C. H. Ernst, W. R. Heyer, J. Johnson, W. King, J. Lang, C. J. Leary, J. Legler, A. Leviton, J. Lovich, J. H. Malone, J. McGuire, S. B. Menke, D. Moll, R. L. Nydam, S. M. Reilly, S. C. Richter, E. D. Roth, S. S. Sartorius, S. Tilley, M. E. Walvoord, and A. Wynn. Good illustrations are essential teaching tools. We thank the organizations and individuals that have given freely of their materials. They are acknowledged in the figure legends where their illustrative materials are presented; however, we thank them here for their generosity. The illustrators and photographers are T. C. S. Avila-Pires, R. W. Barbour, R. D. Bartlett, D. Bauwens, W. R. Branch, A. Britton, E. D. Brodie, Jr., S. L. Collins, L. A. Coloma, P. do Amaral, E. G. Crespo, I. Das, C. K. Dodd, Jr., W. E. Duellman, C. H. Ernst, D. B. Fenolio, J. W. Gibbons, L. L. Grismer, W. Grossman, C. Haddad, W. Hödl, J. M. Howland, R. B. Huey, V. H. Hutchison, J. P. Jones, K.-H. Jungfer, D. R. Karns, M. Kearney, J. W. Lang, A. Lathrop, W. Leonard, E. Lindgren, M. A. Mares, C. Mattison, R. W. McDiarmid, P. A. Medica, R. Mendez, D. Moll, E. O. Moll, R. W. Murphy, K. Miyata, K. Nemuras, M. O'Shea, B. Palmer, E. R. Pianka, L. W. Porras, C. Raxworthy, R. P. Reynolds, S. J. Richards, G. H. Rodda, S. Ron, J. Rorabaugh, H. I. Rosenberg, C. A. Ross, R. Ruibal, A. P. Russell, P. Ryan, I. Sazima, C. Schwalbe, T. Schwaner, S. C. Secor, C. Strussmann, R. G. Tuck, Jr., M. J. Tyler, H. I. Uible, R. W. Van Devender, M. Vaira, J. Visser, G. Webb, R. Whitaker, M. Wilkinson, and S. Wilson. Numerous other herpetologists offered photographs that we were not able to select for inclusion and we thank them as well. Other colleagues have given us permission to use research or personally held copyrighted illustrations: J. D. Congdon, O. Cuellar, E. Gaffney, C. Gans, J. H. K. Pechmann, T. Rainwater, S. M. Reilly, R. Ruibal, R. A. Siegel, L. Trueb, and P. J. Wynne.

Organizations and journals permitting us to use their illustrative materials are Academic Press; American Association for the Advancement of Science; American Museum of Natural History; American Society of Ichthyologists and Herpetologists; American Society of Integrative Biology; Blackwell Science, Inc.; Cambridge University Press; Charles University Press; Chelonian Research Foundation; Cornell University Press; CRC Press, Inc.; Ecological Society of America; Elsevier Science, Ltd. (TREE); *Ethology Ecology & Evolution*; *Herpetological Natural History*; Harvard University Press; The Herpetologist's

League; Kluwer Academic Publishers; The McGraw-Hill Companies; Muséum National d'Historie Naturelle, Paris; Museum of Natural History, University of Kansas; Division of Amphibians and Reptiles, National Museum of Natural History; Smithsonian Institution; National Research Council of Canada; Princeton University Press; Savannah River Ecology Laboratory, University of Georgia; Selva; Smithsonian Institution Press; Society for the Study of Amphibians and Reptiles; Society for the Study of Evolution; Society of Systematic Biologists; Springer Verlag; University of Chicago Press; and John Wiley & Sons, Inc.

Part I

EVOLUTIONARY HISTORY

Chapter

1

Tetrapod Relationships and Evolutionary Systematics

Herpetology is the study of amphibians and reptiles, two distinct clades of vertebrates (Table 1.1). Both clades arose within the Tetrapoda (Greek for "four feet"), a clade of bony fish appearing first in the Paleozoic Era. Tetrapods are the fish that took the first "step" from fin to limb—from water to land—and one of their earliest divergent groups became the amphibians. Amphibians have successfully exploited humid (and even arid) environments in most areas of the world while remaining closely tied to water or moist microhabitats for propagation. Most amphibians experience rapid desiccation in dry environments, but some species have evolved modifications for existence in these habitats. In the Carboniferous, another divergent group of tetrapods, the anthracosaurs, appeared; they evolved modifications for

TABLE 1.1 A Hierarchical Classification of Vertebrates Demonstrating the Position of the Tetrapoda and Its Subgroups as Members of the Bony Fish Clade

- Vertebrata
  - Gnathostomata—jawed vertebrates
    - Osteichthyes (Teleostomi)—bony fishes
      - Actinopterygii—ray-finned fishes
        - Teleostei
      - Sarcopterygii—fleshy-finned fishes
        - Coelacanthiformes (Actinistia)—coelacanths
        - Dipnoi—lungfishes
        - Osteolepiformes—*Eusthenopteron* and relatives
        - Porolepiformes
        - Tetrapoda—tetrapods
          - Ichthyostegalia—*Ichthyostega* and relatives
          - Amphibia—amphibians
            - Colosteidae—*Greererpeton* and relatives
            - Temnospondyli—temnospondyls
              - Lissamphibia—extant amphibians
          - Anthracosauria—anthracosaurs
            - Amniota—amniotes
              - Reptilia (Sauropsida)—reptiles
              - Synapsida—synapsids

Note: The origin of the tetrapods among the sarcopterygians is presented as unresolved. Category titles are not assigned to the hierarchical ranks, and some ranks or nodes are absent. Alternate group names are in parentheses; these alternates are nearly equivalent but not identical in taxa content.

propagation on land in the absence of water, and, perhaps coincidentally, developed an effective skin barrier to reduce rapid and excessive water loss. Today, this group is represented by the reptiles (including birds) and mammals. The study of birds and mammals, formally called ornithology and mammalogy, respectively, are beyond the scope of this book.

If amphibians and reptiles (collectively, herps) are not each other's closest relatives, why has herpetology continued to study these two groups as a single scientific pursuit? In part, it is historical inertia—some would say tradition. In spite of the basic and early dichotomy of these clades, many aspects of the lives and biology of amphibians and reptiles are complementary and allow zoologists to study them together using the same or similar techniques. Current herpetologists show no evidence of fission, for there are too many shared interests. Further, the biological similarities of amphibians and reptiles and the ease of field and laboratory manipulation of many species have made them primary experimental or model animals for the study of ecology (e.g., tadpoles [Wilbur, 1997], *Cnemidophorus* [Wright and Vitt, 1993], *Trachemys scripta* [Gibbons, 1990]), behavior (e.g., *Physalaemus* [Ryan and Rand, 1995], *Anolis* [Jenssen and Nunez, 1998]), physiology (e.g., *Anolis* [Hertz et al., 1993]), developmental biology (e.g., *Xenopus* [Tinsley and Kobel, 1996], plethodontid salamanders [Wake and Hanken, 1996]), and evolutionary biology (e.g., *Anolis* [Roughgarden, 1995], *Lepidodactylus* [Radtkey et al., 1995]).

TABLE 1.2 A Hierarchical Classification for Living Amphibians and Reptiles

- Tetrapoda
  - Amphibia
    - Microsauria
    - Temnospondyli
      - Lissamphibia
        - Gymnophiona—caecilians
        - Caudata—salamanders
        - Anura—frogs
  - Anthracosauria
    - Amniota
      - Synapsida
      - Reptilia
        - Parareptilia
          - Testudines—turtles
        - Eureptilia
          - Diapsida
            - Sauria
              - Archosauria
                - Crocodylia—crocodylians
                - Aves—birds
              - Lepidosauria
                - Sphenodontida—tuataras
                - Squamata—lizards and snakes

Source: Gauthier et al. (1988a, 1989).

AMPHIBIANS AND REPTILES—EVOLUTIONARY HISTORY

Living amphibians consist of three clades: caecilians, salamanders, and frogs (Table 1.2). Detailed characterizations and taxonomy of the living amphibians and reptiles are given in Part VI. Caecilians superficially resemble earthworms (Fig. 1.1) and are formally labeled with the node-based name Gymnophiona (= "naked snake") and the stem-based name Apoda (= "without foot"). All extant caecilians lack limbs, are strongly annulated, and have bullet-shaped heads and tails. This morphology reflects the burrowing lifestyle of these tropical amphibians. The salamanders, labeled with the node-based name Caudata (= "having tail") and the stem-based name Urodela (= "tail visible"), have cylindrical bodies, long tails, distinct heads and necks, and well-developed limbs, although a few salamanders have greatly reduced limbs or even have lost the hindlimbs (Fig. 1.1). Salamanders are represented by many ecological types, including totally aquatic taxa, burrowing and terrestrial species, and arboreal species that live in epiphytes in the forest canopy. The frogs, given the node-based name Anura (= "without tail") and the stem-based name Salientia (= "jumping"), are unlike other vertebrates in having robust, tailless bodies with a continuous head and body and well-developed limbs (Fig. 1.1). The hindlimbs typically are nearly twice the length of the body, and their morphology reflects their bipedal jumping locomotion. Not all frogs jump or even hop; some taxa are totally aquatic and use a synchronous hindlimb kick for propulsion, whereas other species, including both terrestrial and arboreal forms, walk. Among amphibians, frogs are the most speciose and show the highest morphological, physiological, and ecological diversity and the broadest geographic occurrence.

The living reptiles consist of three clades: turtles, archosaurs, and lepidosaurs (Table 1.2). The turtles, called by the node-based name of Testudines (= "tortoises"), like frogs, cannot be mistaken for any other animal (Fig. 1.2). The body is encased within upper and lower bony shells (i.e., carapace and plastron,

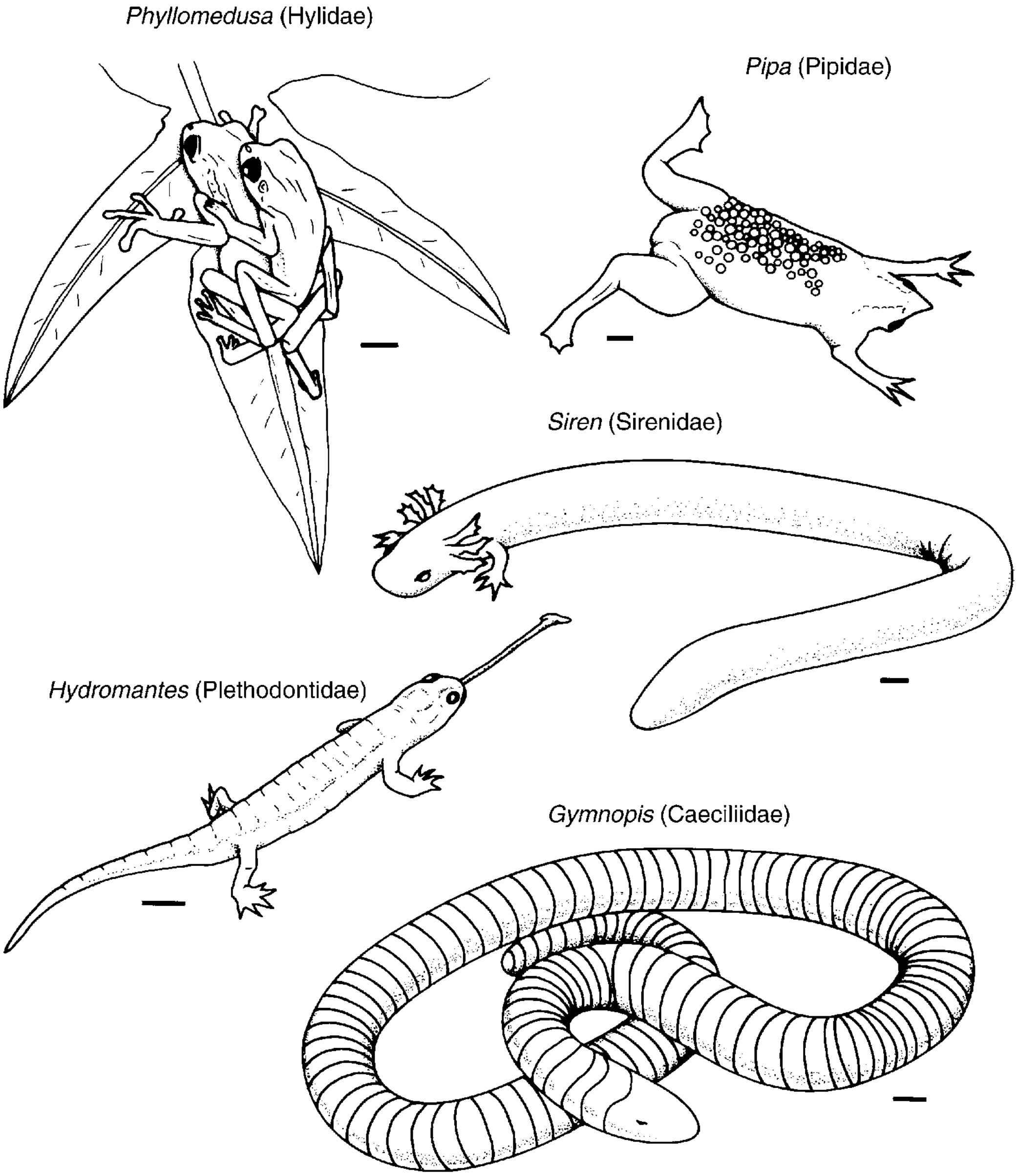


FIGURE 1.1 A sampling of adult body forms in living amphibians. Scale bar = 1 cm.

respectively). In some species, the two portions of the shell can close, fitting tightly together and completely protecting the limbs and head. Although turtles are only moderately speciose, they range from fully aquatic (except for egg deposition) to fully terrestrial, from pygmies to giants, and from herbivores to carnivores. Living archosaurs include the closely related crocodylians and birds. Although the archosaur origin of birds has been long recognized, only recently have biologists insisted on a classification accurately depicting evolutionary relationships, thereby promoting birds as reptiles. The crocodylians, called by the node-based name Crocodylia (Latin for "lizard"), are armored by thick epidermal plates underlain dorsally by bone. The elongate head, body, and tail dwarf the short, strong limbs. Crocodylians are a small group of predaceous, semiaquatic reptiles that swim with strong undulatory strokes of a powerful tail. The limbs also allow mobility on land, although terrestrial activities are usually limited to basking and nesting. The lepidosaurs include the tuataras, snakes, and lizards. The two species of tuataras, referred to by the node-based name Sphenodontida (= "wedge tooth") and the stem-based name Rhynchocephalia (= "nose or snout head"), are lizard-like but represent an early divergence within the lepidosaurian clade (Fig. 1.2); today, they occur only on islets off the coast of New Zealand.

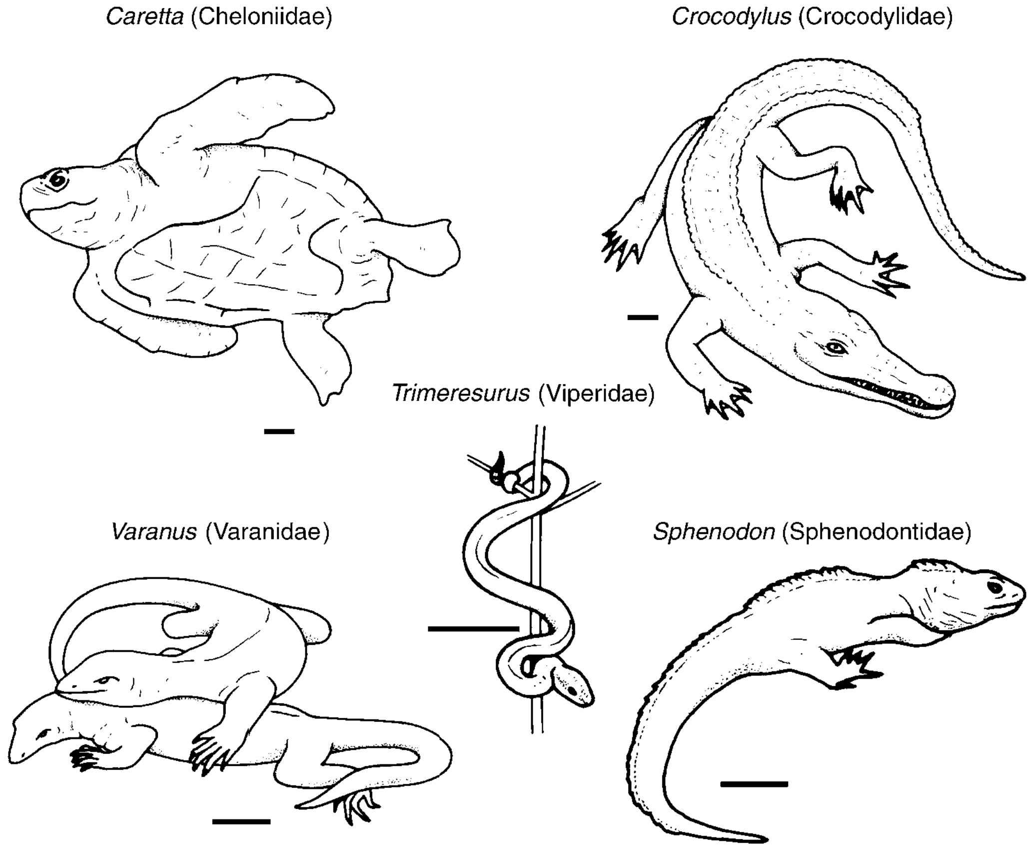


FIGURE 1.2 A sampling of adult body forms in living reptiles. Scale bar = 10 cm.

The node-based name Squamata (= "scaly") includes the lizards, snakes, and amphisbaenians. These groups are the most diverse and speciose of the living reptiles, occupying habitats ranging from tropical oceans to temperate mountaintops. They display a variety of body forms and sizes. Most taxa are terrestrial or arboreal, though many snakes are semiaquatic, spending much of their lives in or immediately adjacent to freshwater, or, less commonly, in estuaries and seawater. A few snakes are totally aquatic and some are even totally subterranean. Snakes, as you will discover in more detail later, are the most successful of several groups of limbless or reduced-limbed lizards.

Relationships among Vertebrates

Fish to Tetrapod

In the Middle Devonian (380–400 million years before present [mybp]) or perhaps earlier, a fish ancestor gave rise to the first tetrapods. Soon thereafter in a geological sense (30–40 mybp), the tetrapods split into two lineages, amphibians and anthracosaurs, which gave rise to extant tetrapods. Reptiles would soon evolve from one descendant lineage of the early anthracosaurs (at least that is one interpretation). These evolutionary events occurred in landscapes that appeared alien compared to the earth's present ones (Gensel and Andrews, 1987; Scott, 1980). Plants, like animals, were only beginning to radiate into terrestrial environments from a completely aquatic existence. The uplands were desert barrens of bare rock and soil. Plants grew only in valleys and along the coasts where water occurred in abundance.

The transition from fish to tetrapod occurred in water (Schmalhausen, 1968). The earliest tetrapods were highly aquatic creatures. They were no more adapted to survive on land than were their fish ancestors. An early proposition that tetrapods evolved from fish that used modified fins to escape from shrinking pools in drying river beds is no longer widely accepted. Although the issue will continue to be debated, limbs probably arose in an aquatic environment (Coates and Clack, 1995; Romer, 1966), perhaps for stalking prey in heavy vegetation, or perhaps as props to permit aerial respiration and movement in the shallow waters of marshes. Another unresolved controversy is whether tetrapods evolved in a marine/brackish or a freshwater environment (Thomson, 1980; Little 1990). The consensus favors a freshwater origin owing to tetrapod kidney structure and physiology and to the preponderance of early tetrapod fossils from nonmarine sediments. Some early amphibians have been found in marine sediments, and proponents of a marine origin interpret the kidney data to support a brackish environment (estuarine) for the transition from fish to tetrapod (Little, 1990).

Just as disagreement exists over the aqueous environment and the selective factors for the origin of tetrapods, controversy also exists over which of several groups of fishes are tetrapod ancestors. While there is little question that the ancestors were bony fish (Osteichthyes) and members of the fleshy-finned group (Sarcopterygii) rather than ray-finned fish (Actinopterygii), exactly which sarcopterygian group contains the ancestor remains controversial.

Whatever the driving force, one group of fishes began the transmutation from an entirely aquatic lifestyle to a terrestrial one. The early evolution began in water, and prototetrapods, like fish, were unable to survive on land. The gradual evolutionary changes affected most aspects of anatomy and physiology. Some structural changes were linked; others were not.

Terrestriality requires aerial respiration, but lungs appeared early in the evolution of bony fishes (Graham, 1997), long before any group of fishes displayed any other terrestrial adaptation. Indeed, lungs are the structural predecessors of swim bladders in the advanced fishes. Lungs may have developed as accessory respiratory structures for gaseous exchange in anoxic or low-oxygen waters. The lung structure of the fish-tetrapod ancestor and the earliest tetrapods is unknown. Presumably it was a ventral outpocketing off the pharynx, probably with a short trachea leading to either an elongated or a bilobed sac. The internal surface may have been only lightly vascularized, for cutaneous respiration was also possible. Respiration (i.e., ventilation) depended upon water pressure. The fish rose to the surface, gulped air, and dived (Fig. 1.3). With the head lower than the body, water pressure compressed the buccal cavity and forced the air rearward into the lungs, since water pressure was lower on the part of the body higher in the water column. Reverse airflow occurred as the fish surfaced head first. This mechanism is still used by most air-breathing fish for exhalation (Hughes, 1976; Graham, 1997). In early tetrapods, a buccal force pump replaced this passive pump mechanism. Air entered through the mouth with the floor depressed, the mouth closed, the floor contracted (elevated) and drove air into the lungs, and the glottis closed, holding the pulmonary air at supra-atmospheric pressure. Exhalation resulted from the elastic recoil of the body wall, driving air outward. Gills were present in the fish-tetrapod ancestor but presumably absent in adult ichthyostegalians, one of the earliest tetrapods. The loss of the gills may have occurred in a situation where aquatic respiration was negligible and closure of the gill openings improved the inhalation cycle.

Another set of adaptations for terrestriality involved the transformation of fins to limbs (Edwards, 1989; Schultze, 1991) (Fig. 1.4). The cause remains debatable, but fleshy fins seem a prerequisite. The fleshy fins of sarcoptyergian fish project outward from the body wall and contain internal skeletal and muscular elements that permit each to serve as a strut or prop. Since limbs evolved for locomotion in water, presumably initially for slow progression along the bottom, they were not built to support heavy loads because buoyancy reduced body weight. At first, the fin-limbs probably acted like oars, rowing the body forward with the fin tips pushing against the bottom. Minimal modifications of the fin-limb are necessary for bottom-walking in this manner. The next stage would involve bending of the fin-limb to allow the tip to make broader contact with the substrate. These bends or joints would be the sites of the future elbow/knee and wrist/ankle. As the flexibility of the joints increased, the limb segments developed increased mobility and their skeletal and muscular components lost the simple architecture of the fin elements. Perhaps at this stage, the fin rays were lost and replaced by short, robust digits, and the pectoral girdle lost its connection with the skull and allowed the head to be lifted while retaining a forward orientation as the limbs extended and retracted. The ichthyostegalians represent this stage. Their limb movements, although in water, must have matched the basic terrestrial walking pattern of extant salamanders, that is, the extension and retraction and rotation of the proximal segment, the rotation of middle segment (forearm and crus), and flexure of the distal segment (feet). As tetrapods became increasingly terrestrial and buoyancy no longer counteracted the pull of gravity, the vertebral column became a sturdier arch with stronger intervertebral links (muscular as well as skeletal). The limb girdles also became supportive—the pelvic girdle by a direct connection to the vertebral column and the pectoral girdle through a strong muscular sling connected to skin and vertebral column.

While in the water, the fluidity and resistance of water assisted in grasping and swallowing food. Once the tetrapod began to feed in shallow water or out of water, inertial feeding became important. The food item is stationary in inertial feeding, and the mouth/head of the tetrapod must move forward over the food. Several modifications of the skull may have been associated with this feeding behavior (Lauder and Gillis, 1997). With the independence of the pectoral girdle and skull, the skull could move left and right, and up and down on the occipital condyles—atlas articulation. The snout and jaws

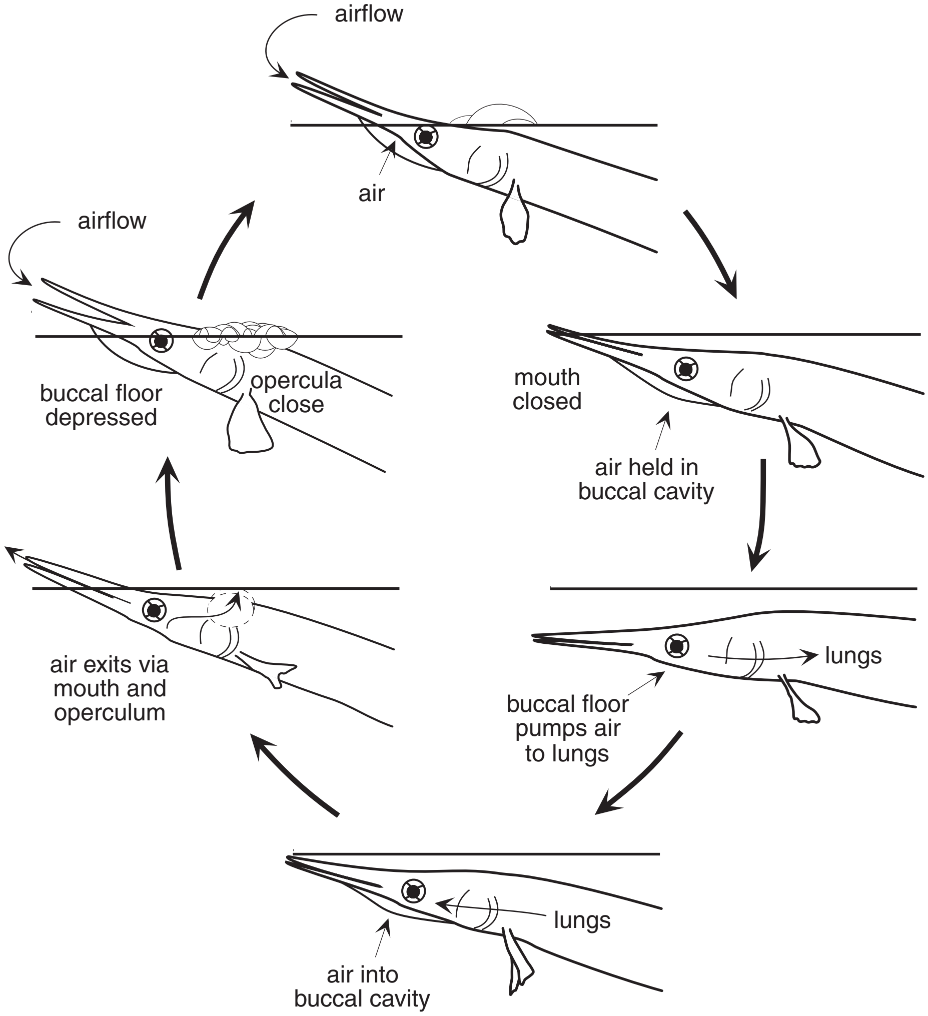


FIGURE 1.3 Air breathing cycle of the long-nosed gar (*Lepisosteus osseus*). As the gar approaches the surface at an angle, it drops its buccal floor and opens it glottis so air can escape from the lungs (bottom center, clockwise). By depressing the buccal floor, the gar flushes additional air from the opercular chamber. Once flushed, the gar extends it snout further out of the water, opens its mouth, depresses the buccal floor, thereby drawing air into the buccal cavity, and shuts the opercula. The mouth remains open and the floor is depressed further; then closing its mouth, the gar sinks below the surface. Air is pumped into the lungs by elevating the buccal floor. Adapted from Smatresk (1994).

elongated. The intracranial joint locked and the primary palate became a broader and solid bony plate.

As tetrapods became more terrestrial, the sense organs shifted from aquatic to aerial perception. Lateral line and electric organs function only in water and occur only in the aquatic phase of the life cycle or in aquatic species. Hearing and middle ear structures appeared (Fritzsch, 1990). The eyes evolved to sharpen their focus for aerial vision. The nasal passages became a dual channel, with air passages for respiration and portions of the surfaces modified for olfaction.

The skin of larval amphibians and fish is similar (Whitear, 1977). The epidermis is two to three layers thick and protected by a mucous coat secreted by numerous unicellular mucous cells. Adult amphibians have modifications that occurred during the transition from an aquatic to a terrestrial existence. The epidermis increased in thickness to five to seven layers; the basal two layers are composed of living cells and are equivalent to fish or larval epidermis. The external layers undergo keratinization and the mucoid cuticle persists between the basal and keratinized layers (Fox, 1985). Increased keratinization may have appeared as a protection against abrasion, since terrestrial habitats and the low body posture of the early tetrapods exposed the body to constant contact with the substrate and the

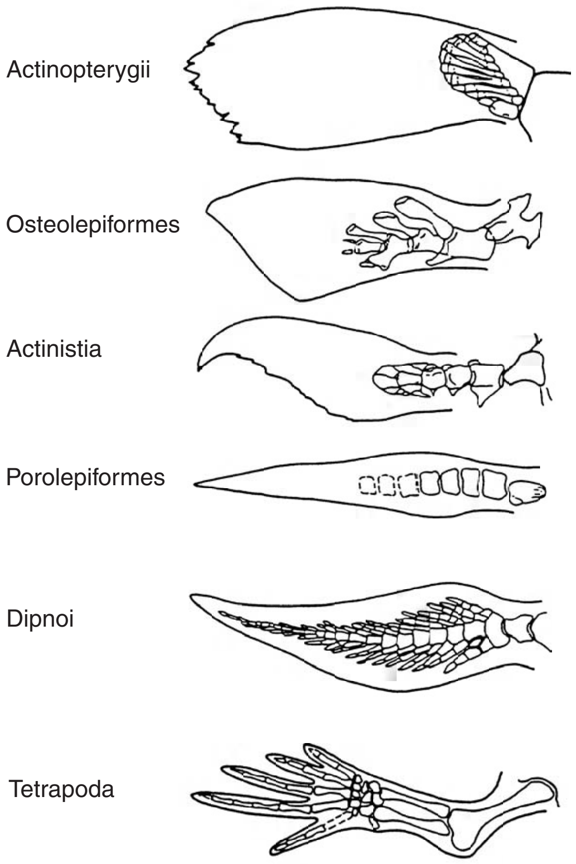


FIGURE 1.4 Fin and limb skeletons of some representative fishes and tetrapods. Top to bottom, ray-finned or actinopterygian fin, osteolepiform lobed fin, actinistian lobed fin, porolepiform lobed fin, lungfish or dipnoan lobed fin, and a tetrapod limb. Adapted from Schultze (1991).

probability of greater and frequent surface damage (Frolich, 1997).

The preceding changes represent the major anatomical alterations that occurred in the transition from fish to tetrapod (Schmalhausen, 1968). Many physiological modifications also occurred; some of these are described in Chapter 6. Some aspects, like reproduction, remained fishlike: external fertilization, eggs encased in gelatinous capsules, and larvae with gills. Metamorphosis from the aquatic larval to a semiaquatic adult stage was a new developmental feature.

Fish Ancestors and Early Tetrapods

The earliest tetrapods were terrestrial bony fish, that is, members of the sarcopterygian branch of the bony fish clade. With which early sarcopterygian group the tetrapods share an immediate common ancestor is debated. The debate has broadened in the last two decades because of: (1) the discovery of new "transitional" sarcopterygians that may be potential ancestors (e.g., Clack, 1998), (2) better specimens and/or preparations of already known transitional sarcopterygians (e.g., Vorobyeva and Schultze, 1991), and (3) different phyletic philosophies and analytical approaches (e.g., Eernisse and Kluge, 1993; Hedges et al., 1993; Hedges and Maxson, 1996; Panchen, 1991). Our review notes some, but not all, different interpretations and is unable to examine the complexities of the anatomy of the early sarcopterygians, the philosophies of different investigators, or even the diversity of the Devonian sarcopterygians.

A number of questions are embedded in the debate (Panchen and Smithson, 1988). Foremost, is the Tetrapoda monophyletic? The consensus answer is yes. Related and intertwined questions include the following: What is the sister group of living tetrapods? What are the closest living relatives of extant tetrapods to extinct ones? How are the major extant groups of tetrapods related? How are the early tetrapods related to one another and to the extant tetrapod groups? Answers to these questions will require an examination of the ancestry of, and divergence within, the Amniota, for example, mammals and reptiles, as well.

The Tetrapoda is considered monophyletic because of numerous unique (derived) traits shared by members of the group (Gauthier et al., 1988c, 1989). Extinct and extant members share a fenestra ovalis into the inner ear, a stapes, a sacrum, paired bones in the epipodial segment (forearm and crus) of the limbs, hinged joints between pro- and epipodial segments of limbs, digits on the end of limbs (i.e., dactyly), a cheek plate of the skull with seven or fewer bones, and several other skeletal features. As more transitional tetrapods are discovered, the characterization of Tetrapoda becomes increasingly difficult owing to transitional anatomy and an admixture of this anatomy among the different taxa. The emphasis for determining relationships is on the skeleton, because only skeletal characters are available in most fossils. The concept of multiple independent origins (i.e., diphyly or polyphyly) is still held by a diverse minority of zoologists and, most frequently, involves the independent origins of living salamanders or caecilians. These concepts have been reviewed and critically examined a number of times (see, for example, Hanken, 1986; Schultze, 1991).

Until the early 1980s, the Romerian concept of the rhipidistian crossopterygians as the ancestors of tetrapods held the consensus (Fig. 1.5). Now rhipidistians and crossopterygians are seldom-mentioned sarcopterygian groups because the monophyly of these groups is unlikely. Osteolepiform fishes, one component of both preceding taxa, are major contenders as the sister group of the tetrapod lineage (Fig. 1.5), but other taxa also have advocates.

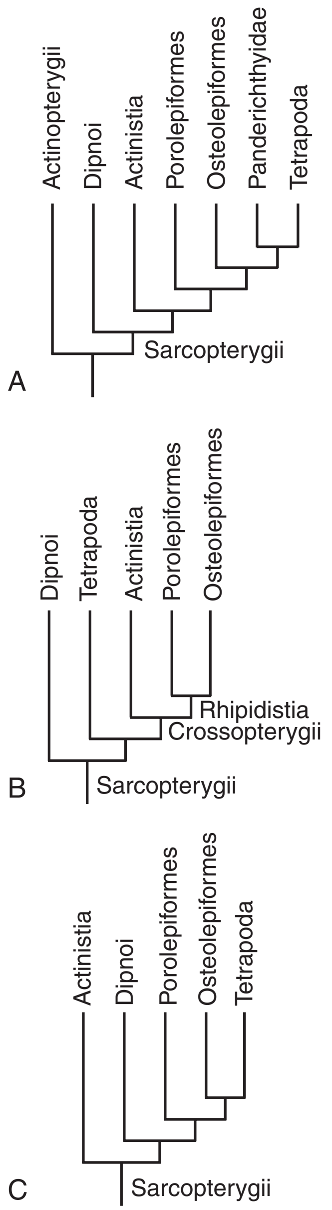


FIGURE 1.5 Origin of tetrapods from the perspective of different patterns of cladistic relationships. (A) Panderichthyid-tetrapod sister-group relationship; (B) classic crossopterygian–tetrapod sister-group relationship; and (C) osteolepiform-tetrapod sister-group relationship. After (A) Schultze (1991) and (B, C) Benton (1991).

One of the earliest tetrapods, *Ichthyostega*, appears much like the osteolepiform *Eusthenopteron* (Fig. 1.6), even though the former had legs and the latter fins. The structural similarity of this and other early tetrapods supports the osteolepiform–tetrapod hypothesis (Fig. 1.6); however, other similarities support other taxa as sister groups (Schultze, 1994). One factor contributing to the diversity of alternate interpretations is the difficulty in determining which shared features are derived and which are primitive; other difficulties include the determination of character homologies among diverse taxa. Nonetheless, several points now seem certain. *Ichthyostega* is not the ancestor of either amphibians or reptiles, although it is a member of the clade Ichthyostegalia, which is the sister group of the Tetrapoda and includes both amphibians and reptiles (Fig. 1.7). Nor is the extant coelacanth *Latimeria* the living ancestor of tetrapods; furthermore, the coelacanths (Actinista) are not the sister group of the tetrapods (Fig. 1.5). The Dipnoi or lungfishes are also contenders for the tetrapod sister-group title. This latter concept is based on skeletal traits; however, some structural similarities appear convergent rather than homologous. But more often than not, the question of tetrapod ancestry is asked with the emphasis on which living group of sarcopterygian fishes is the closest relative to living tetrapods. This viewpoint is prevalent in molecular studies because their samples can come only from living animals. Studies using a variety of molecular approaches and different genes and DNA sequences do not provide an unequivocal answer, although the majority indicate that the lungfishes are the closest relative. This relatedness does not equal a sister-group relationship because extinct taxa are absent from the analysis (e.g., Hedges et al., 1993b; but see Schultze, 1994). The molecular data provide a measure of *relative* phylogenetic relatedness, and aside from the absence of extinct lineages in these analyses, there are problems associated with the great age of the fish–tetrapod divergence. The real contenders for common ancestry are among the extinct sarcopterygians (Schultze, 1994), including "older" contenders such as the osteolepiforms and porolepiforms and newly discovered contenders such as *Elginerpeton* and *Panderichthys* (Fig. 1.6).

Evolution of Early Anamniotes

Ancient Amphibians

The ancestor issue cannot be unequivocally resolved because of the discovery of new transitional taxa. New taxa (e.g., *Elginerpeton*; Ahlberg, 1995) or more complete, better prepared specimens of older taxa (e.g., *Panderichthys*) can significantly alter the results of phylogenetic analyses and the interpretation of sister-group relationships. This aspect has altered the tetrapod debate this decade (Ahlberg and Milner, 1994; Carroll, 1995). If *Panderichthys* is not an osteolepiform then it may be the sister group of the tetrapods. *Elginerpeton* possesses a mixture of fish and tetrapod characters, and how we interpret a taxon becomes a semantic issue. For example, if *Elginerpeton* is considered a fish, then it becomes the sister group of the tetrapods, and if it is a tetrapod, it is then the likely sister group to all subsequent tetrapods;

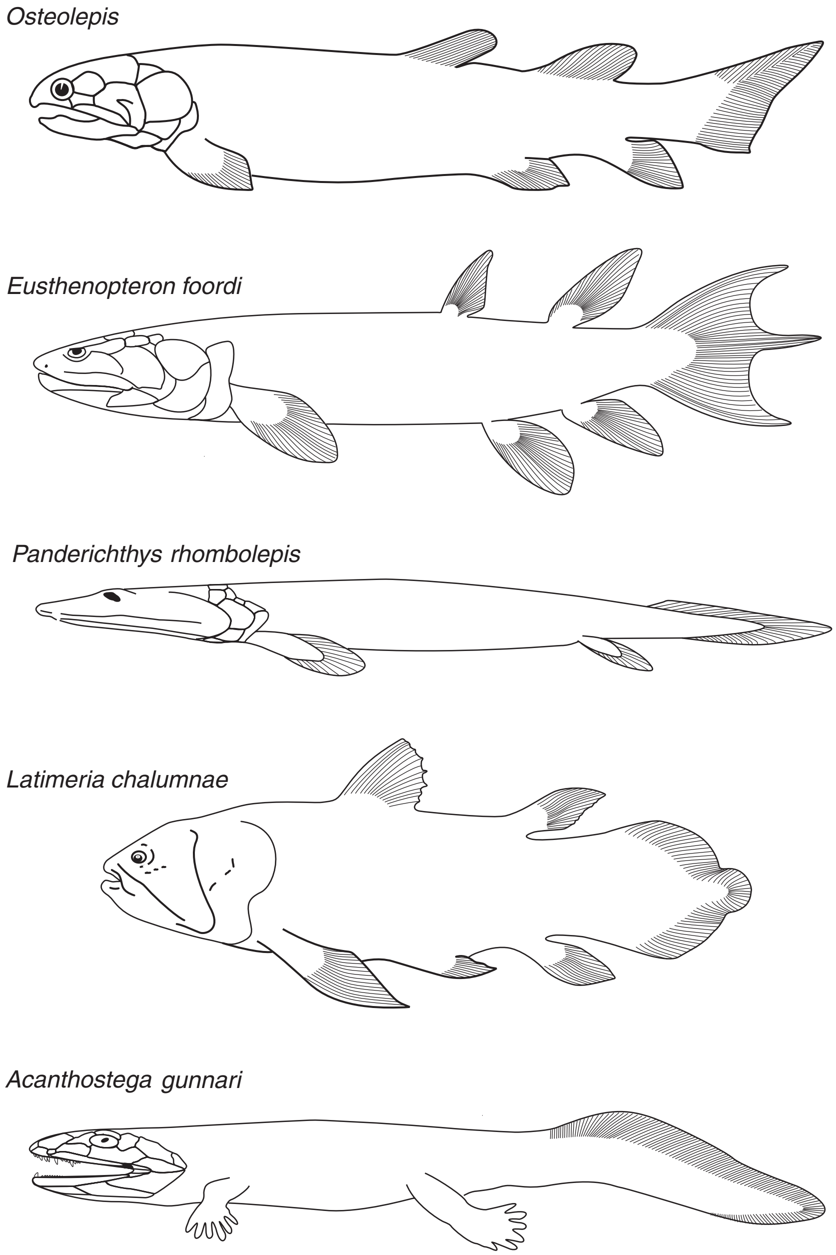


FIGURE 1.6 Body form in some sarcopterygian fishes and early tetrapods. Top to bottom, an osteolepiform *Osteolepis*, *Eusthenopteron foordi*, *Panderichthys rhombolepis*, the extant coelacanth *Latimeria chalumnae*, and the tetrapod *Acanthostega gunnari*. Adapted from Gregory (1951) and Coates and Clack (1995).

the labeling and not the cladistic estimation has changed. Other fossil taxa (*Obruchevichthys*, *Metaxygnathus*) share this mixture of characters with *Elginerpeton*, and all are considered stem-tetrapods, that is, early tetrapods but not amphibians.

Then, who and what are the Amphibia? Again, there are multiple answers or interpretations. The monophyly of the living amphibians, the Lissamphibia (caecilians, frogs, and salamanders), seems highly probable, and they are the members of the temnospondyl clade (Fig. 1.7). The assignment of extinct taxa to the Temnospondyli is more controversial (see Trueb and Cloutier, 1991a, for a review of the diverse opinions). *Edops* (Fig. 1.8) and relatives, *Eryops* and relatives, trimerorhachoids, and a diverse assortment of taxa labeled dissorophoids compose the major groups of extinct temnospondyls

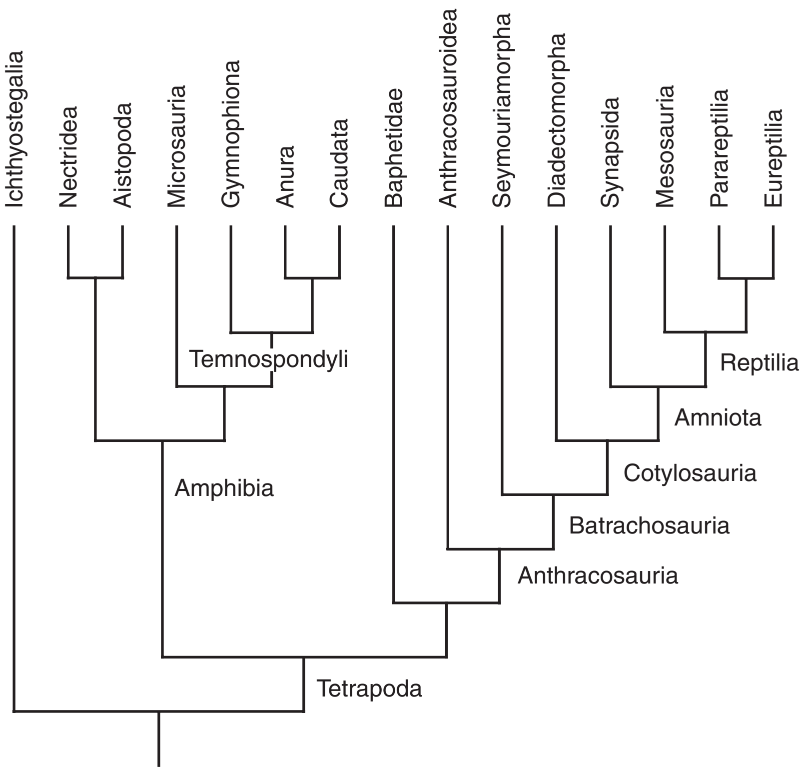


FIGURE 1.7 A branching diagram of the evolution within the Tetrapoda, based on sister-group relationships. The diagram has no time axis, and each name represents a formal clade-group name. After Clack (1998), Gauthier et al. (1988a,b, 1989), and Lombard and Sumida (1992); a strikingly different pattern is suggested by Laurin and Reisz (1997).

(Trueb and Cloutier, 1991b). Aistopods, baphetids (= Loxommatidae), microsaurs, and nectrides have been identified as amphibians, although their relationships remain controversial. We accept the proposed sister-group relationship between temnospondyls and microsaurs, and between aistopods and nectrides (Fig. 1.7); the latter clade is the sister group of the former clade, and together these four taxa encompass the Amphibia. The baphetids are not amphibians; presumably they are an early offshoot of the early protoamniotes and possibly the sister group of the anthracosaurs (Clack, 1998). Details on the appearance and presumed lifestyles of these extinct groups are in Chapter 3. All these groups may have had their origins in the Early Carboniferous, and only a few lineages survived and prospered into the Permian. As an aside, the lepospondyls and labyrinthodonts were once widely recognized groups of extinct amphibians. The members of the lepospondyls (= Aistopoda + Microsauria + Nectridea) shared features associated with small body size and aquatic behavior, but not features of phylogenetic relatedness that would support the monophyly of lepospondyls. The labyrinthodonts encompassed phylogenetically unrelated taxa united by shared primitive (ancestral) characters. Thus, the groups were polyphyletic and their use has been largely discontinued.

Defining Amphibia by its members, it is possible to identify unique characters shared by this group. These characters are surprisingly few (Panchen and Smithson, 1988): (1) the articular surface of the atlas (cervical vertebra) is convex; (2) the exoccipital bones have a suture articulation to the dermal roofing bones; and (3) the hand (manus) has four digits and the foot (pes) five digits. Other features commonly used to characterize amphibians apply specifically to the lissamphibians, although some of them may apply to all Amphibia but are untestable because they are soft anatomical structures that have left no fossil record.

Modern Amphibians—The Lissamphibia

The living amphibians are generally thought to share a common ancestor and hence to represent a monophyletic group. Numerous patterns of relationship have been proposed, but only three patterns continue to have time-tested evidence and advocates. The proposed patterns

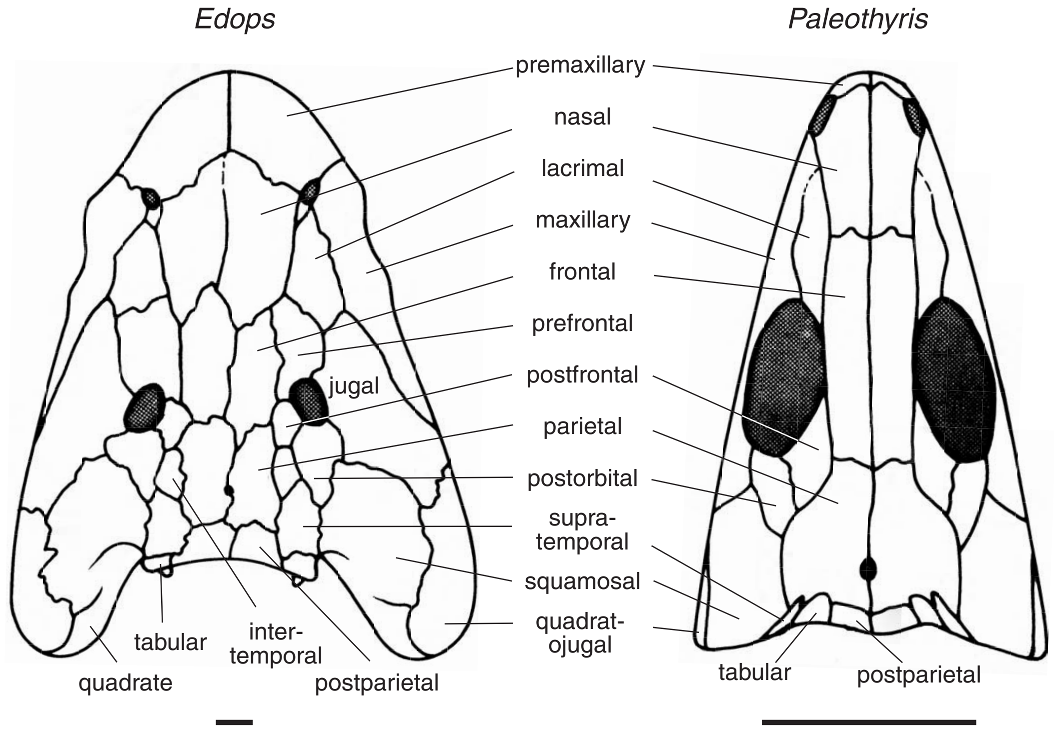


FIGURE 1.8 Comparison of the skulls of an early amphibian *Edops* and an early reptile *Paleothyris.* Scale bar = 1 cm. Reproduced, with permission, from Museum of Comparative Zoology, Harvard University.

are: (1) frogs arose from a different ancestor than salamanders and caecilians; (2) frogs and salamanders are a sister group and caecilians are a sister group to their clade; (3) caecilians and salamanders are a sister group, and frogs are a sister group to their clade. Carroll (1988, 1997, and elsewhere) has long been a proponent for the polyphyly of the lissamphibians, advocating the ancestry of salamanders and caecilians among the microsaurs, and that of the frogs in the temnospondyls. However, the preponderance of evidence argues for monophyly and probably a dissorophid ancestry (Trueb and Cloutier, 1991b). The uncertainty derives from the long time gap between the potential temnospondyl ancestors in the Upper Carboniferous and the occurrence of all three groups in the Early to Middle Jurassic. These Jurassic forms show the major characteristics of their extant descendants but few traits of ancient amphibians. Only the Lower Triassic frog *Triadobatrachus massinoti* from Madagascar shows a possible link to the dissorophid temnospondyls. *T. massinoti* shares with them a large lacuna in the squamosal bone that may have housed a tympanum. Neither salamanders nor caecilians have tympana, although they have greatly reduced middle ears, suggesting the loss of the outer ear structures.

A number of other unique traits argue strongly for the monophyly of the Lissamphibia (Bolt, 1991; Trueb and Cloutier, 1991b). All share a reliance on cutaneous respiration, a pair of sensory papillae in the inner ear, two sound transmission channels in the inner ear, specialized visual cells in the retina, pedicellate teeth, the presence of two types of skin glands, and several other unique traits.

Three structures, gills, lungs, and skin, serve as respiratory surfaces in lissamphibians; two of them frequently function simultaneously. Aquatic amphibians, particularly larvae, use gills; terrestrial forms use lungs. In both air and water, the skin plays a major role in transfer of oxygen and carbon dioxide. One group of terrestrial amphibians, the plethodontid salamanders, has lost their lungs, and some aquatic taxa also have lost lungs or have greatly reduced ones; these amphibians rely entirely on cutaneous respiration. All lunged species use a force-pump mechanism for moving air in and out of the lungs. Two types of skin glands are present in all living amphibians: mucous and granular (poison) glands. The mucous glands continuously secrete mucopolysaccharides which keep the skin surface moist for cutaneous respiration. Although the structure of the poison glands is identical in all amphibians, the toxicity of the diverse secretions produced is highly variable, ranging from barely irritating to lethal to predators.

The auditory system of amphibians has one channel that is common to all tetrapods, the stapes-basilar papilla channel. The other channel, opercular-amphibian papilla, allows the reception of low-frequency sounds (>1000 Hz). The possession of two types of receptors may not seem peculiar for frogs because they are vocal animals. For the largely mute salamanders, a dual hearing system seems peculiar and redundant. Salamanders and frogs have green rods in the retina; these structures are presumably absent in the degenerate-eyed caecilians. Green rods are found only in amphibians, and their particular function is as yet unknown.

The teeth of modern amphibians are two-part structures: an elongate base (pedicel) is anchored in the jaw bone and a crown protrudes above the gum. Each tooth is usually constricted where the crown attaches to the pedicel. As the crowns wear down, they break free at the constriction and are replaced by a new crown emerging from within the pedicel. Only a few living amphibians lack pedicellate teeth. In the extinct amphibians, pedicellate teeth occur only in a few dissorophids (Bolt, 1991; Carroll, 1988).

Living amphibians possess other unique traits. All have fat bodies that develop from the germinal ridge of the embryo and retain an association with the gonads in adults. Frogs and salamanders are the only vertebrates able to raise and lower their eyes. The bony orbit of all amphibians opens into the roof of the mouth, with a special muscle stretched across this opening which elevates the eye. The ribs of amphibians do not encircle the body.

This large number of unique similarities argues strongly for the shared ancestry of the living amphibian groups. Whether salamanders and frogs or salamanders and caecilians are sister groups remains unresolved; different data sets and analyses support one or the other of these pairs, but not a frog-caecilian sister relationship.

Evolution of Early Amniotes

Early Tetrapods and Terrestriality

Fully terrestrial tetrapods presumably arose in the Early to Middle Mississippian period (360–340 mybp, Lower Carboniferous). Uncertainty arises because few tetrapod fossils are known from this period. Tetrapod fossils appear with high diversity in the Late Mississippian and Early Pennsylvanian (340–320 mybp). The diversity includes the first radiation of the amphibians and the appearance of the anthracosaurs and the earliest amniotes. This interval saw the transformation of the biota from shallow-water and waterside forms to increasingly abundant and diverse terrestrial forms. Unlike the largely barren landscape of the Late Devonian during the transition from fish to tetrapod, Carboniferous forests were widespread, composed of trees 10 m and larger, probably with dense understories. Plant communities were beginning to move into upland areas. With increasing plant diversity and terrestriality, invertebrates and vertebrates were also evolving terrestrial residents.

The evolution of terrestrial forms required modifications in anatomy, physiology, behavior, and a host of other characteristics. True terrestriality required major reorganizations of lifestyle and life processes. The attention of zoologists has focused on the reproductive and developmental aspects of this reorganization or adaptation to life on land, specifically the shifts from eggs that required water or moisture for deposition to those that could withstand dry conditions and from free-living embryos to direct development on land. Other adaptations also were required. Movement and support under the influence of gravity on land demanded adjustments in the musculoskeletal system (Sumida, 1997). Feeding in air required behavioral and morphological shifts (Lauder and Gillis, 1997), as did the use of different prey and plant materials for food (Hotton et al., 1997). Gravity, friction, abrasion, and evaporation obligated modification of the integument for protection and support (Frolich, 1997) and of internal mechanisms to regulate water gain and loss (Martin and Nagy, 1997). Modification was not confined to the preceding anatomical and physiological systems. These changes did not occur synchronously—some were linked and others were not, and some required little modification because of exaptation ("preadaptation") and others required major reorganization. The diversity of changes is reflected in the diversity of Lower Carboniferous amphibians and anthracosaurs.

Amphibians remained associated with aquatic habitats and took occasional evolutionary ventures toward full terrestriality. Though many of these ventures were successful in terms of high abundance or diversity and geologic longevity, amphibians remained tied to moisture. This addiction to water (to a greater or lesser extent) is not a maladapted or a "low evolutionary" state, and, conversely, terrestriality is not a higher or more successful state. Each state is simply a different adaptative zone that gives amphibious and terrestrial organisms different options for living and reproducing.

As amphibians diversified in association with aquatic habitats, the anthracosaurs and their descendants became increasingly terrestrial in all phases of their life (Fig. 1.7; Table 1.3). The most successful terrestrial group, defining success by having descendants still living today, was the clade comprising the amniotes (Amniota).

Full terrestriality required that organisms have the ability to reproduce and develop in the absence of water. The evolution of the amniotic egg, which could be deposited on land and resisted dehydration, occurred at this time. (See Chapter 2 for anatomical details; note that many reptilian eggs still must absorb moisture to

TABLE 1.3 A Hierarchical Classification of Anthracosaur Descendants

- Tetrapoda
  - Amphibia
  - Anthracosauria
    - Anthracosauroidea
    - Batrachosauria
      - Seymouriamorpha
      - Cotylosauria
        - Diadectomorpha
        - Amniota
          - Synapsida
          - Reptilia

Note: This classification derives from the sister-group relationships displayed in Figure 1.7. Because of the hierarchical arrangement, a reptile or mammal is an anthracosaur, although paleontologists commonly use anthracosaur to refer to the extinct tetrapod groups that are not Amphibia and not yet Amniota.

complete development.) The amniotic egg did not appear *de novo* but in a series of steps, each increasing the embryo's survivorship on land (Packard and Packard, 1980; Packard and Seymour, 1997); in addition, the amniotic egg with its protective extraembryonic membranes was not necessarily the first step. The evolution of a closed (shelled) egg presumably was the first terrestrial "egg-step," and it had to have been preceded by internal fertilization, an exaptation that permitted the evolutionary shift from aquatic to terrestrial development.

Internal fertilization is not a prerequisite for direct development, nor does direct development free the parents from seeking an aquatic or permanently moist site for egg deposition. Among extant amphibians, internal fertilization predominates in caecilians and salamanders, but only a few anurans with direct development have internal fertilization. When an egg is encased in a protective envelope, the encasing process must be done inside the female's reproductive tract, and if sperm is to reach the egg/ovum surface, the sperm must be placed within the female's reproductive tract as well. Sperm delivery and fertilization must precede egg encasement.

Internal fertilization has arisen independently numerous times within lissamphibians (Goin, 1960; Packard and Kilgore, 1968); hence, it was an easy evolutionary hurdle for the protoamniote anthracosaurs to overcome. The evolution of a shelled egg presented a greater challenge, and its explanation requires a speculative scenario because it left no traces in the fossil record. The common scenario suggests that naked amniotic eggs with direct development were laid first in moist areas (e.g., Packard and Packard, 1980). Selection to reduce predation by microorganisms drove the replacement of gelatinous capsules by the deposition of an increasingly thicker calcareous shell and the shift of egg-laying to drier sites. Recent modification of this hypothesis has placed more emphasis on the development of the fibrous envelope precursor to the shell and the supportive role of such an envelope for a large-yolked egg (Packard and Seymour, 1997). Other scenarios, such as the "private pool" theory, have directed attention to the development of the extraembryonic membranes and their encapsulation of the egg or embryo (Benton, 1991). Each hypothesis has a facet that reflects an aspect of the actual evolutionary history, but none provides a full explanation. We cannot determine from this distance and without actual evidence whether the amniotic membranes evolved in embryos held within the female's oviduct or whether they evolved in externally shed eggs. Either explanation is equally parsimonious from available information on extant vertebrates (Fig. 1.9). Similarly, we cannot determine when and how the sarcopterygian's gelatinous envelope was replaced by a fibrous envelope, although a fibrous "shell" likely preceded a calcareous one because calcium crystals are deposited in a fibrous matrix in all living reptiles (Packard and Packard, 1988).

Juveniles and adults also required a protective envelope because of the desiccative effect of terrestrial life. Changes in skin structure are invisible in the fossil record, but the skin of present-day amphibians suggests that the initial evolutionary steps were an increase in skin thickness by adding more cell layers and keratinization of the external-most layer(s). Keratinization of skin effectively reduces frictional damage and the penetration of foreign objects, but appears to be ineffectual in reducing water loss. The amniotes and presumably their antecedents evolved increased skin thickness and keratinized layers, making the skin increasingly impermeable. Early modifications of the integument were also driven by its increased role in the support of internal organs to compensate for the loss of buoyancy and compression of water. These changes occurred in deep dermal layers and involved altering fiber direction and layering (Frolich, 1997).

As the skin became increasingly impermeable, cutaneous respiration would have become less effective and pulmonary respiration more so. Lungs probably changed in several ways. The first modifications were probably an increase in size and internal partitioning (Perry, 1998). The latter is commonly associated with increased vascularization. Once again, these modifications apparently occurred in the protoamniotes. When and where they occurred can be partially identified by examining rib structure and the appearance of a complete rib cage.

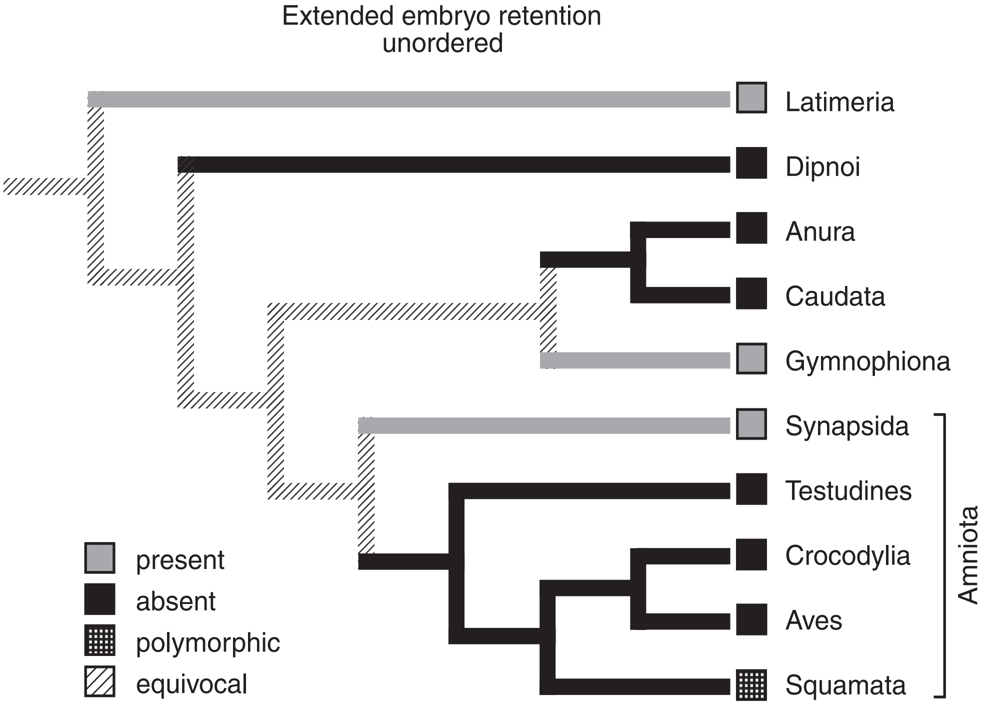


FIGURE 1.9 Distribution of the occurrence of viviparity in extant tetrapod groups. This distribution of egg retention based on extant species does not permit the identification of the condition in basal amniotes. The origin of terrestrial amniotic eggs as an intermediate stage is equally parsimonious with the evolution of amniotic eggs within the oviduct to facilitate extended egg retention. After Laurin and Reisz (1997).

A rib cage (thoracic basket) signals the use of a thoracic respiratory pump for ventilation of the lungs. The rib cage appears incomplete in most anthracosaurs and seymouriamorphs (Carroll, 1988), so those groups probably were still largely dependent on the buccal force pump. The rib cage of diadectomorphs extends further ventrally; although it still appears incomplete, this condition may mark the transition from buccal to thoracic ventilation.

Anthracosaurs and early amniotes lacked otic notches, denoting the absence of eardrums. Although not deaf, they were certainly insensitive to high-frequency sounds. It is doubtful that their olfactory sense was as limited. Well-developed nasal passages in fossils and the presence of highly developed olfactory organs in living reptiles indicate that this sense was well developed in the earliest amniotes. Nasal passages contained conchae, which may have aided in the reduction of water loss. Eyes were also likely well developed at this stage, for vision is extremely important in foraging and avoiding predators in an aerial environment.

Locomotory and postural changes for a terrestrial life are reflected in numerous changes in the postcranial skeleton (Sumida, 1997). Vertebral structure changed to produce a more robust supporting arch. The pleurocentrum became the main component of the vertebral body, displacing the intercentrum forward and upward. Neural arches became broader, zygapophyses tilted, and regionalization of neural spine height occurred, yielding differential regional flexibility with an overall strengthening of the vertebral column. Modification of the two anterior-most cervical vertebrae (atlas–axis complex) stabilized lateral head movement during walking and running. Modifications in the limb and girdle skeletons are not as evident in the early anthracosaurs as those appearing in later amniotes. The humerus remained a robust polyhedral element that had a screwlike articulation with the glenoid fossa. The shoulder or pectoral girdle lost dermal bone elements but remained large. The iliosacral articulation was variable and depended upon the size and robustness of the species, although two sacral ribs usually attached to each ilium. Hindlimbs commonly were larger and sturdier, demonstrating their increasing role in propulsion.

The skull became more compact and tightly linked, although it was still massive in many anthracosaurs and early amniotes (Fig. 1.8). A major trend was the reduction of the otic capsule in early tetrapods, without the concurrent development of structural struts; thus, the skull roof and braincase became weakly linked. Different strengthening mechanisms appeared in different lineages (Carroll, 1988). The diadectomorphs and reptiles shared the unique development of a large supraoccipital bone to link the braincase and skull roof. The cheek to braincase solidification occurred in three general patterns within the amniotes. The anapsids developed a strong attachment of the parietal (skull roof) to the squamosal (cheek) along with a broad and rigid supraoccipital attachment. In the diapsids, the opisthotic extended laterally to link the braincase to the cheek. A lateral expansion of the opisthotic also occurred in the synapsids but in a different manner.

The robust stapes with its broad foot plate was a critical strut in the strengthening of the skull. This role as a supportive strut precluded its function as an impedance matching system (Carroll, 1988; also see the discussion of ears in Chapter 2). Later, the opisthotic became the supportive unit, and the stapes (columella) became smaller and took on its auditory role. This change occurred independently in several reptilian lineages; although the results are the same, the evolutionary route to the middle ear of turtles differed from that of the archosaurs and lepidosaurs. The synapsids followed an entirely different route and evolved the unique three-element middle ear seen today in mammals.

Early Amniotes

The Amniota derives its name from the possession of an amniotic egg. Other anthracosaurs may have had amniotic eggs, although they are not classified as amniotes. A fossil taxon cannot be identified as an amniote or anamniote by structure of its egg, because few fossil eggs of anthracosaurs have been found. Further, no eggs have been found in association with an adult's skeleton or with a fossil embryo showing extraembryonic membranes. Bony traits must be used to determine which taxa are amniotes and which ones are not, and there is no unanimity in which bony traits define an amniote. Indeed, amniotes are commonly defined by content; for example, Amniota is the most recent common ancestor of mammals and reptiles and all of their descendants (Gauthier et al., 1988b).

Unquestionably, anthracosaurs are the ancestral stock that gave rise to the amniotes (Figs. 1.7 and 1.10). They possess features present in amniotes but not in Paleozoic or later amphibians. Anthracosaurs and amniotes share such features as a multipartite atlas-axis complex in which the pleurocentral element provides the major support. Both possess five-toed forefeet with a phalangeal formula of 2,3,4,5,3 and a single, large pleurocentrum for each vertebra. These traits are also present in the seymouriamorphs and diadectomorphs.

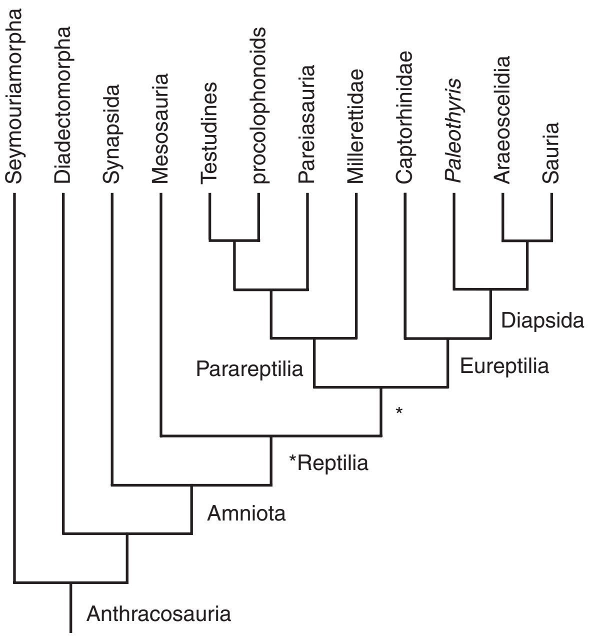


FIGURE 1.10 A branching diagram of the evolution of basal Amniota and early reptiles, based on sister-group relationships. The diagram has no time axis, and each capitalized name represents a formal clade-group name. *Opinion varies on whether the mesosaurs are members of the Reptilia clade or the sister group of Reptilia. If the latter hypothesis is accepted, the Mesosauria and Reptilia compose the Sauropsida. After Gauthier et al. (1989), Laurin and Reisz (1995), and Lee (1997); a strikingly different pattern is suggested by deBraga and Rieppel (1997).

The seymouriamorphs compose an early divergent group of anthracosaurs, although their fossil history does not begin until the Late Pennsylvanian. These small tetrapods, sometimes incorrectly called amphibians, may be a sister group to diadectomorphs or to the protoamniote taxa (Fig. 1.8). They probably had external development and required water for reproduction. Significantly, neither the seymouriamorphs nor the diadectomorphs are amniotes (Fig. 1.10).

The diadectomorphs shared a number of specialized (derived) features with early amniotes—traits that are not present in their predecessors (Gauthier et al., 1988c). For example, both groups lost temporal notches from their skulls, have a fully differentiated atlas-axis complex with fusion of the two centra in adults, and possess a pair of sacral vertebrae. They share a large, platelike supraoccipital bone and a number of small cranial bones (supratemporal, tabulars, and postparietals) that are lost in advanced reptiles. The stapes of both were stout bones with large footplates, and apparently eardrums (tympana) were absent (Carroll, 1988). These latter features do not suggest that they were deaf, but that their hearing was confined to low frequencies, probably less than 1000 Hz, much like modern-day snakes and other reptiles without eardrums. Possibly their development included preamniotic changes, such as partitioning of the fertilized egg into embryonic and extraembryonic regions, or even a full amniotic state.

The first amniote fossils are from the Middle Pennsylvanian (Carroll, 1991), but they are not primitive amniotes in the sense of displaying numerous transitional traits. These first amniotes are *Archaeothyris* (a synapsid), *Hylonomus* (a reptile), and *Paleothyris* (a reptile; Fig. 1.8); already the divergence of the synapsids and reptilian stocks was evident. The Synapsida is the clade represented today by mammals; they are commonly called the mammal-like reptiles, an inappropriate and misleading name. The pelycosaurs were the first major radiation of synapsids and perhaps gave rise to the ancestor of the Therapsida, the lineage leading to modern mammals.

Divergence among the basal reptiles apparently occurred soon after the origin of the synapsids, and again because of the absence of early forms and the later appearance of highly derived reptilian clades, there is uncertainty and controversy about the early evolutionary history of the reptiles. The Mesosauria of the Lower Permian are considered a sister group to all other reptiles or a sister group to all other parareptiles (Fig. 1.10). Mesosaurs were specialized marine predators, and their specializations have provided few clues to their relationships to other early reptiles.

Controversy surrounds the origin of turtles and whether the Parareptilia is paraphyletic or monophyletic. Recent discoveries and better preparation of old and new fossils have led to a redefinition of the Parareptilia and to its recognition as a clade including the millerettids, pareiasaurs, procolophonoids, and turtles (Reisz and Laurin, 1991; Laurin and Reisz, 1995). The latter two taxa are considered to be sister groups; however, another interpretation recognizes pareiasaurs and turtles as sister groups (Lee, 1993, 1995, 1997). A strikingly different interpretation considers the turtles as diapsids and further suggests a moderately close relationship to lepidosaurs (Rieppel and deBraga, 1996; deBraga and Rieppel, 1997). Molecular data seemingly support the diapsid relationship by yielding a turtle-archosaur (crocodylian + bird) sister-group relationship (Zardoya and Meyer, 1998) or a turtle-crocodylian one (Hedges and Poling, 1999). These data support the idea that turtles are more closely related to other living reptiles than to living mammals, but they do not provide information on the early history of reptile evolution. As noted earlier in the discussion of fish-tetrapod relationships, molecular data yield a simple phylogeny of living taxa. The relationships of the extinct taxa and their sequence of divergence add complexity to a phylogeny and a different relationship pattern (e.g., compare Lee, 1995, and Laurin and Reisz, 1995). Another difficulty with such molecular studies is that few taxa are used. As new taxa are added to the analysis, the proposed relationships can change greatly.

Prior to the preceding studies, turtles were considered a sister group to the captorhinids, and these two taxa were the main members of the Anapsida, the presumed sister group of the Diapsida (e.g., Carroll, 1988; Gauthier et al., 1989; Gaffney, 1980). The parareptiles were considered to be paraphyletic. In spite of the different placement of turtles, the preceding studies (i.e., Laurin and Reisz, 1995; Lee, 1996; deBraga and Rieppel, 1997) agree on the monophyly of the parareptiles and the sister-group relationship of captorhinids to all other eureptiles (Fig. 1.10). *Paleothyris* (Fig. 1.8) is one of the oldest eureptiles, although already structurally derived from, and the potential sister group to, all diapsid reptiles.

Radiation of Diapsids

Diapsida is a diverse clade of reptiles. It has a long taxonomic history and its member content is generally accepted with only minor controversy, excluding the current disagreement about inclusion of turtles. Modern diapsids include lizards, snakes, birds, and crocodylians; extinct diapsids include dinosaurs, pterosaurs, ichthyosaurs, and many other familiar extinct taxa. The stem-based name Diapsida is derived from the presence of a pair of fenestrae in the temporal region of the skull; diapsids are also diagnosed by a suborbital fenestra, an occipital condyle lacking an exocciptal component, and a ridged-grooved tibioastragalar joint (Gauthier et al., 1988c).

The earliest known divergence yielded the araeoscelidians, a short-lived group, and the saurians (Fig. 1.11, Table 1.4). The araeoscelidians were small (about 40 cm total length) diapsids of the Late Carboniferous and were an evolutionary dead end. In contrast, the saurian lineage gave rise to all subsequent diapsid reptiles. Members of the Sauria share over a dozen unique osteological features (Gauthier et al., 1988c), including a reduced lacrimal with nasal-maxillary contact, no caniniform maxillary teeth, an interclavicle with distinct lateral processes, and a short, stout fifth metatarsal.

The Euryapsida apparently arose from an early split in the Sauria clade (Fig. 1.11). They comprise a diverse group of mainly aquatic (marine) reptiles, ranging from the fishlike ichthyosaurs to the walruslike placodonts and the "sea-serpent" plesiosaurs. Individually these taxa and collectively the Euryapsida have had a long history of uncertainty in their position within the phylogeny of reptiles. Only since the late 1980s has their diapsid affinity gained a consensus among zoologists, although there remain different interpretations about basal relationships. For example, are they a sister group of the

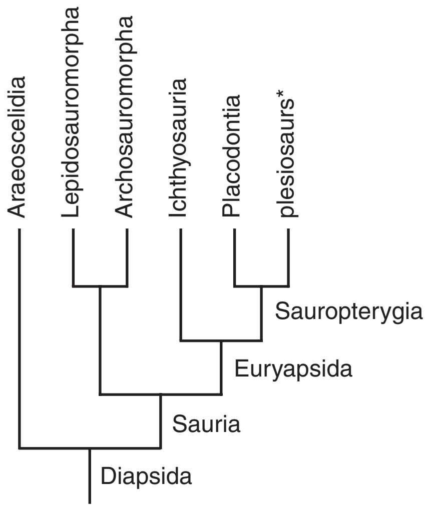


FIGURE 1.11 A branching diagram of the evolution of basal reptile clades, based on sister-group relationships. The diagram has no time axis, and each capitalized name represents a formal clade-group name. *Plesiosaurs is used as a vernacular name and is equivalent to Storr's (1993) Nothosauriformes. After M. Caldwell (1996) and Gauthier et al. (1989).

lepidosauromorphs or a sister group of the lepidosauromorph-archosauromorph clade? Is the Ichthyosauria a basal divergence of the euryapsids or perhaps not an euryapsid (M. Caldwell, 1996; Callaway, 1997; Rieppel, 1993; Storrs, 1993)? The monophyletic clade interpretation rests on sharing six or more derived characters, such as a lacrimal bone entering the external nares, an anterior shift of the pineal foramen, and clavicles lying anteroventral to the interclavicle.

Two clades, the Archosauromorpha and the Lepidosauromorpha, compose the other lineages of the Sauria (Fig. 1.11). Both clades have living representatives, crocodylians and birds in the former and tuataras and squamates (lizards and snakes) in the latter, and both clades have had high diversity in the deep past, although the dinosaurs focus attention on the diversity within archosauromorphs, specifically on the archosaurs. However, the Archosauria had earlier relatives (e.g., rhynchosaurs, protorosaurs, and proterosuchids; Fig. 1.12), and furthermore, the archosaurs are much more than just dinosaurs. The archosaurs encompass two main lineages, the Crocodylotarsi (or Crurotarsia) and the Ornithodira; they share a rotary cruruotarsal ankle, an antorbital fenestra, no ectepicondylar groove or foramen on the humerus, a fourth trochanter on the femur, and other traits (Benton and Clark, 1988; Evans et al., 1988). Aside from the two main groups, archosaurs include some early divergent taxa, for example, Erythrosuchidae, *Doswellia*, and *Euparkeria*. These taxa appear to have been carnivores and ranged in size from the 0.5–m *Euparkeria* to the 5–m erythrosuchid *Vjushkovia*. These basal lineages were relatively short lived. The Ornithodira and Crocodylotarsi radiated broadly and have modern-day representatives.

TABLE 1.4 A Hierarchical Classification of the Early Reptilia

- Amniota
  - Synapsida
  - Reptilia
    - Parareptilia
      - Millerettidae
      - Unnamed
        - Pareiasauria
        - Unnamed
          - procolophonoids
          - Testudines
    - Eureptilia
      - Captorhinidae
      - Unnamed
        - *Paleothyris*
        - Diapsida
          - Araeoscelidia
          - Sauria
            - Archosauromorpha
              - Archosauria
                - Pseudosuchia
                    - Crocodylia
                  - Ornithodira
                    - Aves
            - Lepidosauromorpha
              - Lepidosauria
                - Sphendontida
                - Squamata

Note: This classification derives from the sister-group relationships displayed in Figures 1.10 and 1.11.

The Ornithodira includes the Pterosauria and Dinosauria (Fig. 1.12). The pterosaurs were an early and successful divergence from the lineage leading to the dinosaurs. The leathery-winged pterosaurs seemingly never attained the diversity of modern birds or bats but were a constant aerial presence over tropical seashores from the Late Triassic to the end of the Cretaceous. The dinosaurs attained a diversity that was unequaled by any other Mesozoic group of tetrapods. Their size and diversity fan our imaginations; nonetheless, there were numerous other successful reptile groups (e.g., phytosaurs, prestosuchians), and some of these were just as fantastic as the ornithischian and saurischian dinosaurs.

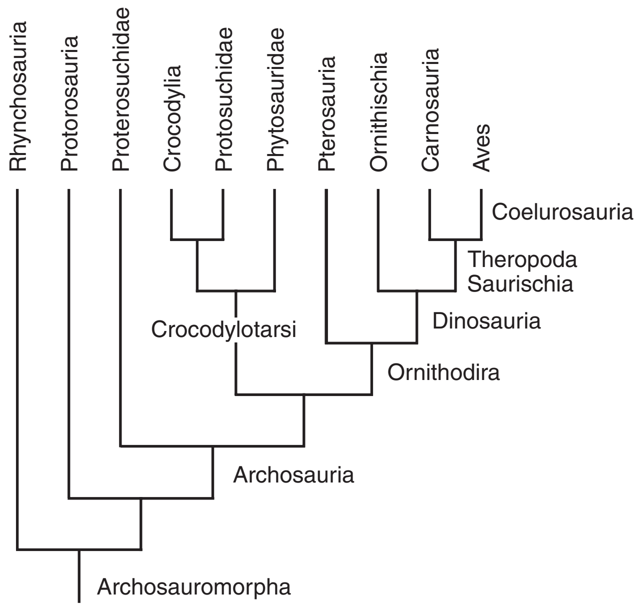


FIGURE 1.12 A branching diagram of the evolution within the Archosauromorpha, based on sister-group relationships. The diagram has no time axis; numerous clades and branching events are excluded; and each capitalized name represents a formal clade-group name. After Benton and Clark (1988), Gauthier et al. (1989), and Gower and Wilkinson (1996).

Dinosaur evolution is well studied (see Benton, 1997b; Farlow and Brett-Surman, 1997) and outside the province of herpetology but relevant to the evolution of the living reptiles. Birds (Aves) are feathered reptiles, and *Archaeopteryx* is a well-known "missing link" that has a mixture of reptilian and avian characteristics. Although no one would argue that *Archaeopteryx* is not a bird, a controversy exists over the origin of birds (Witmer, 1991). The current consensus places the origin of birds among the theropod dinosaurs (Fig. 1.12; Ostrom, 1991); however, three other hypotheses have current advocates, although all hypotheses place the origin of birds within the Archosauria. The theropod dinosaur hypothesis has the weight of cladistic evidence in its support (e.g., Gauthier, 1986). The other proposed bird ancestors are an early crocodyliform (e.g., Martin, 1991), among the basal ornithodiran archosaurs (Tarsitano and Hecht, 1980), and *Megalanocosaurus*, another basal archosaur taxon (Feduccia and Wild, 1993). Although these latter interpretations represent minority positions, the cladistic near-relatives (birdlike theropods) of birds occur much later (<25 mybp) in the geological record than *Archaeopteryx*.

Crocodylotarsi, the other major clade of archosaurs, has an abundance of taxa and a broad radiation in the Mesozoic and Early Tertiary. The Crocodylia, a crown group including the most recent common ancestor of the extant Alligatoridae, Crocodylidae, and *Gavialis* and its descendants, remains a successful group but shows only one aspect of crocodylotarsian radiation. The earliest radiations in the middle and Late Triassic included phytosaurs, aetosaurs, and rauisuchids. The phytosaurs were long-snouted crocodylian-like reptiles, and the position of their nostrils on a hump in front of the eyes suggests a similar aquatic ambush behavior on terrestrial prey. The aetosaurs were armored terrestrial herbivores, and the rauisuchids were terrestrial predators that developed an erect, vertical limb posture and reduced their dermal armor. Another lineage, the Crocodyliformes, which include the later-appearing Crocodylia, also appeared in the Middle Triassic and yielded the diversity of Jurassic and Cretaceous taxa (Clark, 1994). The crocodyliforms had members that were small wolflike, large bipedal tyrannosaurus-like, giant marine crocodylian-like, and a variety of other body forms.

The Lepidosauromorpha, the archosauromorph's sister group, consists of several basal groups and the lepidosaurs (Fig. 1.13). All share derived traits such as a lateral ridge of the quadrate supporting a large tympanum, no cleithrum in the pectoral girdle, an ectepicondylar foramen rather than a groove in the humerus, and a large medial centrale in the forefoot. The earliest known and basal group is the Younginiformes from the Upper Permian and Lower Triassic. They were aquatic, and the adaptation to an aquatic life is a recurrent theme in the evolution and radiation of lepidosauromorphs. Another basal group with a highly specialized lifestyle was the

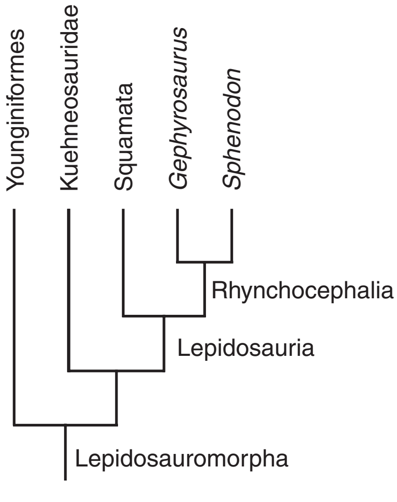


FIGURE 1.13 A branching diagram of the evolution within the Lepidosauromorpha, based on sister-group relationships. The diagram has no time axis; numerous clades and branching events are excluded; and each capitalized name represents a formal clade-group name. After Gauthier et al. (1989) and Rieppel (1994); M. Caldwell (1996) and deBraga and Rieppel (1997) provide different interpretations of lepidosauromorph relationships.

Kuehneosauridae. They had elongate thoracic ribs that probably supported an airfoil membrane and permitted them to glide from tree to tree or to the ground, as in the extant gliding lizards *Draco*. The kuehneosaurids are the sister group to the Lepidosauria. The Lepidosauria is a strongly supported clade with a wealth of derived features that are shared (Rieppel, 1994). Some of these features are teeth attached loosely to the tooth-bearing bones, fusion of the pelvic bones late in development, hooked fifth metatarsals, and paired copulatory organs (hemipenes; rudimentary in *Sphenodon*). Of the two sister groups within the Lepidosauria, only two species of tuataras (sphenodontidans) survive. The Sphenodontida has acrodont dentition and a premaxillary enameled beak. It was moderately diverse and abundant in the Late Triassic and Jurassic, and largely disappeared from the fossil record thereafter. From the beginning, the terrestrial taxa had the body form still seen in the tuataras. *Glevosaurus* is their sister taxon and shared a similar habitus; however, it had triangular teeth with a shearing bite. The squamates are the sister group of the sphenodontidans (Fig. 1.13) and are more abundant and speciose than the latter group from their first appearance in the Late Jurassic to today. In an all-inclusive sense the squamates or lizards were and are predominantly small-bodied (>0.5 m) reptiles and carnivores. They apparently split early into the two major lineages, Iguania and Scleroglossa, that dominate the world's herpetofaunas. The fossil history of the Squamata and the other extant reptilian and amphibian groups is detailed in Chapter 3; similarly, the phylogenetic relationships of the major groups are examined in the Overview sections of each chapter of Part VI.

SYSTEMATICS—THEORY AND PRACTICE

Systematics is the practice and theory of biological classification. Classifying objects is part of human nature and has its origins deep in prehistory. The earliest human societies began to name and recognize plants and animals for practical reasons, such as what is good or bad to eat, or what will or will not eat humans. This partitioning of objects places them into conceptual groups and is practiced daily by all of us. In modern systematics, we attempt to discover the full diversity of life, to understand the processes producing this diversity, and to classify the diversity in a manner that expresses phylogenetic relationships (i.e., evolutionary history).

Systematics remains a vital and necessary tool for biologists. Whether unraveling the interworkings of a cell, tracing the transmission route of a disease, or conserving a fragment of natural habitat, we must know the organisms with which we are working. No one would knowingly attempt to install a Ford engine in a Mercedes or a Windows program on a Macintosh computer. Similarly, correct identification of an organism allows correct decisions in research and conservation. Further, correct identification provides immediate access to previously published information on that species, and knowledge of its classification—and hence its evolutionary relationships—opens a wider store of information because related species likely function similarly.

Basic Concepts

Evolution, the concept of descent with modification, is the glue that unites the diverse aspects of modern biology. Therefore, our classification should reflect the evolutionary history of organisms as closely as possible. Since we can never know the actual evolutionary history of a group, our classifications are inferences and estimates of phylogeny and will change as our knowledge of a group's relationships improves. Our classifications are schemes for naming and categorizing like organisms into the same groups. Each name identifies an organism or group of organisms and provides an index to information associated with that name. Biological classification is traditionally hierarchical (a system of nested sets), with each ascending level potentially containing more subgroups and characterized by the shared similarities of the included subgroups. Although the hierarchical system was introduced because of its efficiency for categorization and retrieval and prior to the recognition of organic evolution, hierarchies can be used to reflect evolutionary history.

Species are the basic units of our classifications and the only real units, existing not as artificial categories but as real entities. Each species is a set of unique, genetically cohesive populations of organisms, reproductively linked to past, present, and future populations as a single evolutionary lineage. Our hierarchical classification places closely related species together in the same genus, combines related genera into the same family, and so forth up through the various levels of the classification. At each level, we proceed backward in time to points of evolutionary divergence—specifically to a speciation event that gave rise to new lineages (Fig. 1.14).

For a hierarchical classification to reflect evolutionary history, rules (guidelines) are necessary. The principal rule is that the grouping of organisms is monophyletic (i.e., a unique history of descent), and thus represents a single evolutionary group containing the ancestor and all descendants, that is, a clade. This goal would seem easily achieved if the members of the group are adequately

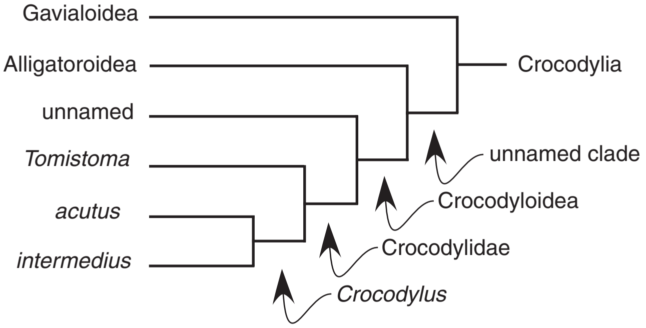


FIGURE 1.14 Schematic cladogram of the Crocodylia and its associated hierarchical classification. Indentations (reversed) within the classification mark the nodes of sister-group origins, and each node represents a past speciation (cladogenetic) event.

known and studied; however, aside from the difficulties of accurately estimating relationships of divergent species, there is difficulty of tradition. Many taxonomic groups were delimited before organic evolution was recognized. Because of tradition, there is a reluctance to discard the old group concepts. The former, common use of Reptilia is a case in point and made Reptilia a paraphyletic group, because it included the ancestor and many but not all descendant groups, specifically excluding birds (Fig. 1.15). Some biologists considered the Amphibia to include some of the anthracosaurs, thereby creating a polyphyletic Amphibia (Fig. 1.15), that is, a group composed of several clades but not the common ancestor of these clades. Presently the biological community is making a conceptual shift from a Linnean, non-evolution-based classification to an evolution-based one (de Queiroz and Gauthier, 1994).

Indeed, systematics is in the midst of a revolution. The revolution began in the mid-1960s with the adoption of Hennig's systematic concepts and practices, which has evolved into today's phylogenetic-based systematics or cladistics. Concurrently, biochemical and molecular techniques were adapted to generate characters for estimating phylogenetic relationships. This conceptual and practical revolution led to a rebirth in comparative biology because phylogenetic analyses produce testable dendrograms of phylogenetic relationships (i.e., cladograms). Biologists can examine the possible evolution of structure or function of an organism or an aspect thereof (e.g., courtship behavior, water-loss tolerance, reproductive output) by mapping the states of a particular character on a phylogeny (e.g., Fig. 1.9).

The following topics provide only a brief and incomplete introduction to modern systematics.

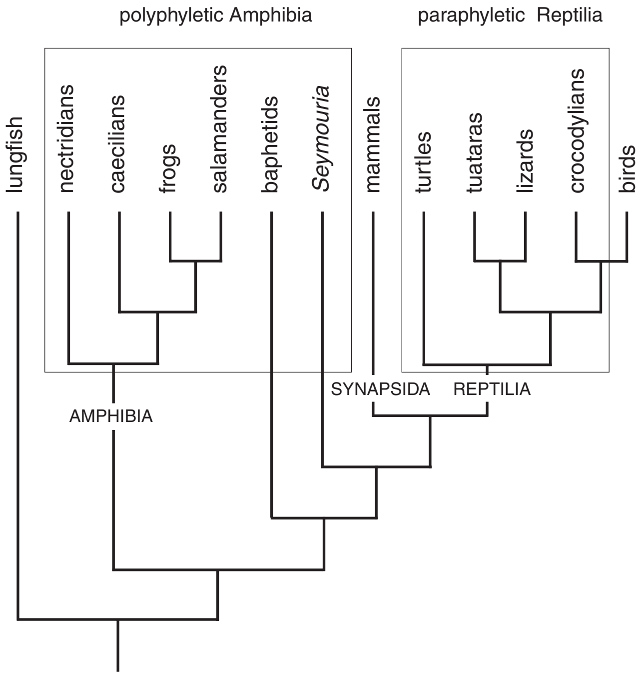


FIGURE 1.15 An abbreviated cladogram of tetrapods illustrating monophyly, paraphyly, and polyphyly. The heavier line and capitalized group names depict the monophyletic groups of Amphibia and Reptilia recognized in the text, and Figures 1.7 and 1.10–1.13 provide more detailed cladograms of each group. The boxes define earlier concepts of Amphibia (polyphyletic) and Reptilia (paraphyletic).

Systematic Analysis

Systematic research is a search for evolutionary patterns. Investigations span the spectrum from analyses of intraspecific variation to the deepest phylogenetic levels. At one end, the researcher examines species through the analysis and definition of variation within and among populations and/or closely related species. At the opposite end, research is directed at the resolution of genealogical relationships among species, genera, and higher taxonomic groups.

Species and their relationships are discerned by examining individuals. An individual's attributes provide a means to infer its affinities to another individual (or larger group). Such inferences of relationships provide a framework to examine evolutionary processes and the origin of diversity. Diversity occurs at many levels, from the variety of genotypes (individuals) within a deme to the number of species within a genus (or higher group) or within a habitat or geographical area (see Table 14.1). Only through the recognition of which group of individuals is a species and which ones are not can we address other biological questions.

Types of Characters

Any inheritable attribute of an organism can serve as a character. A character can be anatomical (e.g., a process or foramen on a bone, number of scales around midbody, snout-vent length), physiological (resting metabolic rate, thyroxine-sensitive metamorphosis), biochemical-molecular (composition of venom, DNA sequence), behavioral (courtship head bobbing sequence), or ecological (aquatic). The type of characters used depends upon the nature of the questions being asked. Only a sampling of characters can be presented here.

Systematic study involves the comparison of two or more samples of organisms through their characters. This comparison involves two procedural concepts: the OTU (operational taxonomic unit) and character states. OTUs are the units being compared and can be an individual, population, species, or higher taxonomic group. The actual conditions of a character are its states, for example, an eye iris being blue or green, or a body length of 25 or 50 mm. The assumption of homology is implicit in the comparison of character states; that is, all states of a character derive from the same ancestral state. The preceding characters and their states also illustrate that characters are either qualitative (descriptive) or quantitative (numeric). Qualitative characters have discrete states, that is, "either/or" states: vomer teeth present *or* absent, and *either* 6, 7, or 8 upper lip scales. Quantitative characters have continuous states: head length of an individual can be recorded as 2, 2.3, 2.34, or 2.339 cm.

To be useful for systematics, a character's states generally have lower variation within samples than among samples. A character with a single state (invariant condition) in all OTUs lacks discriminatory power among the samples. A highly variable character with numerous states in one or more samples adds confusion to an analysis and should be examined more closely to identify the cause of the high variability or be excluded from the study.

Knowledge of the sex and state of maturity of each specimen is critical for recognition of variation between females and males, and among ontogenetic stages. Both aspects must be considered whether the characters are anatomical, behavioral, or molecular in order to avoid confounding intraspecific variation with variation at the interspecific or higher level.

Morphology Anatomical characters include three discrete classes of characters: (1) mensural or morphometric characters are measurements or numeric derivatives (e.g., ratios, regression residuals) that convey information on size and shape of a structure or anatomical complex; (2) meristic characters are those anatomical features that can be counted, such as number of dorsal scale rows or toes on the forefoot; and (3) qualitative characters describe appearance, for example, a structure's presence or absence, color, location, or shape.

1. The most common morphometric character in herpetology is snout-vent length (SVL). This measurement gives the overall body size of all amphibians, squamates, and crocodylians, and its measurement differs only slightly from group to group depending on the orientation of the vent (transverse or longitudinal). Because of their shells, carapace length (CL) and plastral length (PL) are the standard body size measurements in turtles. Numerous other measurements are possible and have been employed to characterize differences in size and shape. Mensural characters are not confined to aspects of external morphology but are equally useful in the quantification of features of internal anatomy, for example, skeletal, visceral, or muscular characters.

As in all characters, the utility of measurements depends on the care and accuracy with which they are taken. Consistency is of utmost importance, so each measurement must be defined precisely and each act of measuring performed identically from specimen to specimen. The quality of the specimen and nature of the measurement also affect the accuracy of the measurement. Length (SVL) of the same specimen differs whether it is alive (struggling or relaxed) or preserved (shrunk by preservative, positioned properly or not); thus a researcher may wish to avoid mixing data from such specimens. Similarly, a skeletal measurement usually will be more accurate than a visceral one because soft tissue compresses when measured and the endpoints often are not as sharply defined. Differences can also occur when different researchers measure the same characters on the same set of animals. Thus within a sample, variation of each character includes the "natural" differences between individuals and the researcher's measurement "error." The latter is not serious and probably is encompassed within the natural variation if the researcher has practiced a modicum of care during data taking. The use of adequate samples (usually <20 individuals) and central tendency statistics subsume this "error" into the character's variation and further offer the opportunity to assess the differences among samples and to test the significance of the differences, as well as providing single, summary values for each character.

2. Meristic characters are discontinuous (= discrete). Each character has two or more states and the states do not grade into one another. There are 2, 3, or 4 teeth on the premaxillary bone, not 2.5 or 3.75 teeth. Meristic characters encompass any anatomical feature (external or internal) that can be counted. Researcher measurement error is also possible with meristic characters. These

characters also are examined and summarized by basic statistical analysis.

3. Qualitative characters encompass a broad range of external and internal features, but unlike mensural or meristic characters, they are categorized in descriptive classes. Often a single word or phrase is adequate to distinguish among various discontinuous states, for example, pupil vertical or horizontal, coronoid process present or absent, carotid foramen in occipital or in quadrate, and bicolor or tricolor bands at midbody. Qualitative characters can have multiple states (>2), not just binary states. Even though these characters are not mensural or meristic, they can be made numeric simply by the arbitrary assignment of numbers to the different states or by size comparison (e.g., 1× width versus 3× height).

The preceding characters emphasize aspects of gross anatomy, but microscopic characters may also be obtained. One of the more notable and widely used microscopic (cytological) characters is karyotype or chromosome structure (Green and Sessions, 1991; see Sessions, 1996, for molecular aspects). The most basic level is the description of chromosome number and size: diploid ($2N$) or haploid (N) number of chromosomes, and number of macro- and microchromosomes. A slightly more detailed level identifies the location of the centromere (metacentric, the centromere is in the center of the chromosome; acrocentric, the centromere is near the end; and telocentric, the centromere is at the end) and the number of chromosomes of each type or the total number (NF, nombre fundamental) of chromosome arms (segments on each side of the centromere). Special staining techniques allow the researcher to recognize specific regions (bands) on chromosomes and to more accurately match homologous pairs of chromosomes within an individual and between individuals.

Molecular Structure The preceding characters are largely visible to the unaided eye or with the assistance of a microscope. Chemical and molecular structures also offer suites of characters for systematic analysis (Moritz and Hillis, 1996). The nature of these characters can involve the actual structure of the compounds (e.g., chemical composition of the toxic skin secretions in the poison frogs or nucleotide sequences of DNA fragments) or comparative estimates of relative similarity of compounds (e.g., immunological assays).

Many systematists have widely and enthusiastically adopted techniques from molecular biology. Their use in systematics rests on the premise that a researcher can assess and compare the structure of genes among individuals, species, and higher taxa through the examination of the molecular structure of proteins and other compounds that are only a few steps removed from the gene. Molecular data have proved valuable, but like other characters, they have their own special problems in interpretation. They offer a different perspective, sometimes yield new insights, and in many instances permit us to answer questions that cannot be addressed with other kinds of characters. Importantly, whatever the nature of a character, the fundamental assumption is that the character being compared between two or more OTUs is homologous, and this requirement applies to molecular characters as well as gross anatomical ones.

The techniques of molecular systematics are varied and complex. Different techniques are selected to investigate different levels of relationships. Electrophoresis is especially good (and relatively inexpensive) for examining genetic relationships of individuals within and among populations and of populations within and among species (Guttman, 1985). Other techniques (e.g., DNA sequencing) may be used at this level of comparison, but often they are used more effectively in the examination of higher-level relationships, which represent older divergences and speciation. The next three sections offer a glimpse of molecular techniques in systematics.

Electrophoresis Proteins are the major structural components and chemical regulators of cells. Their structure is a direct reflection of the DNA sequence of genes that code their formation—a gene's DNA sequence is transcribed to make messenger RNA (mRNA), and mRNA is translated into a chain of amino acids, the protein. One group of proteins, the enzymes, catalyze the cell's chemical reactions. This high specificity makes them critical and key components in cellular metabolism and potentially useful systematic characters. This potential is further enhanced by the occurrence of structurally different forms (allozymes) of the same enzyme. The different allozymes arise from gene mutations that have altered the structure of the DNA, and this alteration is translated directly into an altered structure of the enzyme.

Electrophoresis can identify different allozymes (also other chemical compounds) via their different mobility in an electrical field (Murphy et al., 1996). Each enzyme is a chain of amino acids and has a specific size, shape, and net charge (positive, negative, or neutral). Mobility is a function of the allozyme's charge, shape, and size; minor mutations may alter one or more of these facets of allozymic structure and affect the allozyme's speed of migration.

In biological studies, the electrophoretic apparatus consists of an electric-power pack, positive and negative electrodes to a buffer tray, and a sheet of gel matrix stretching between the positive- and negative-charged buffer trays. Tissue samples (fluid homogenates, often of muscle or liver tissue) are placed in a row at one end of the gel, and when the power is turned on, the allozymes begin to migrate toward the positive or negative electrodes. After several hours, the gel is removed and stained (using specific biological dyes for each type of enzyme) to reveal the position of the allozymes for each sample (Fig. 1.16). Most current studies assay for 15–30 enzymes.

Each enzyme is a character, and its allozymes are its states. The stained gel (zymogram) comprises the raw data and shows whether each sample shares the same allozymes. Electrophoretic data are variously coded and can be simple counts of allozyme matches and mismatches, frequencies, or the presence or absence of heterozygotes. The manner of coding and analysis depends on the problem addressed, whether examining intrapopulational or intergeneric relationships.

Immunology The antigen-antibody or immunological reaction provides a mechanism for estimating the genetic affinities of species. The concept is simple. Homologous proteins of closely related species are structurally similar, and as relationships become distant (increasing divergence from a common ancestor), protein structure becomes increasingly different. When a foreign protein (the antigen) is introduced into a host animal, the host's normal reaction is to produce antibodies specifically constructed to intercept and deactivate the antigen. By using these antibodies to test the level of the immunological reaction with the antigens of many different species, the researcher obtains an estimate of the similarity of each test antigen to the antigen of the donor OTU. A strong reaction indicates a high similarity in protein structure, and a weak reaction a low similarity. The antibody "recognizes" (attaches to) specific amino acid sequences of the donor's antigen, and fewer and fewer sequences are recognized as the structural differences of the test antigens increase. The basic protocol requires the introduction of an antigen into a host animal (rabbit, goat, etc.), time for the host's immunological system to produce antibodies, removal of blood serum from host and purification of antiserum, and performing *in vitro* comparisons of the antisera reactions of the antigens from a series of test OTUs.

Of the several immunological tests, immunodiffusion, immunoelectrophoresis, and microcomplement fixation (MCF) are used in systematic studies, and blood albumins are the usual proteins compared. All three tests translate the level of antigen-antibody reaction into a numerical estimate of protein similarities and hence the relative similarity of the OTUs (Maxson and Maxson, 1986, 1990).

Nucleic Acids Molecular biology is providing systematics with a growing arsenal of techniques for assessing relationships. None appears more powerful than the ability to examine and compare the structure of DNA and RNA (Moritz and Hillis, 1996). The attractiveness of nucleic acids for inferring phylogenetic relationships is that their nucleotide sequences are the basic informational units encoding and regulating all of life's processes. Examination of nucleic acid sequences began in the 1980s as advances in methodology and equipment made the techniques more accessible and affordable to systematists. It has now become an indispensable part of systematics. A major feature of nucleic acid analyses is their broad comparative power and spectrum, ranging from the ability to examine and identify individual and familial affinities (e.g., DNA fingerprinting) to tracing matriarchal lineages (mitochondrial DNA, or mtDNA)

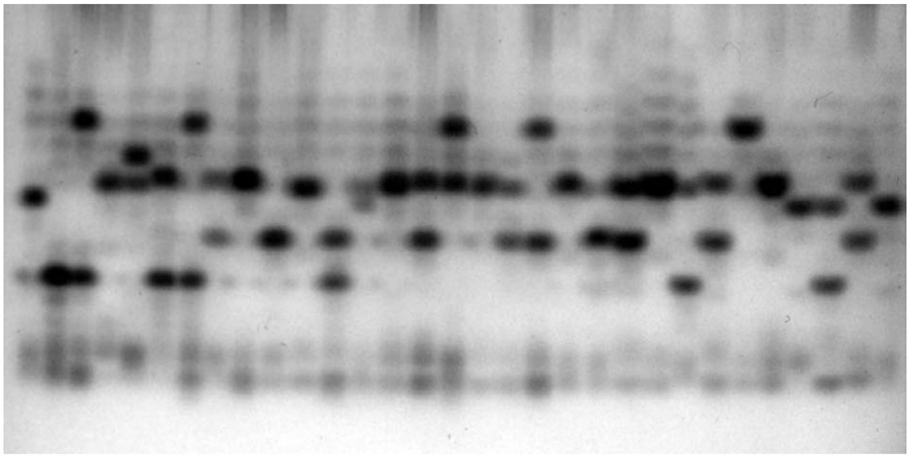


FIGURE 1.16 An electrophoretic gel (zymogram) of an esterase stain for the salamanders *Plethodon cinereus* and *P. shenandoah.* Courtesy of A. Wynn.

and estimating phylogenetic relationships within and among species to phyla (nuclear DNA). While extremely valuable for systematic studies, nucleic acid characters are not a panacea and have their own set of difficulties in analysis and interpretation.

Several techniques are available for comparing nucleotide sequences among different taxa. DNA-DNA hybridization was the first technique used on a large scale in vertebrate systematics although not in herpetology. It takes advantage of the disassociation of the two strands of DNA at high temperatures and the reassociation of complementary strands as the temperature drops. DNA from two OTUs is combined, disassociated, and then allowed to reassociate. Complementary strands from the same as well as different OTUs will reassociate. The number of mismatched base pairs (nucleotides) in the hybrid DNA molecules increases with evolutionary time of divergence, and this is also reflected in a depression of the melting or disassociation temperature. The difference in melting temperature between pure and hybrid DNA provides a measure for assessing the level of relationship.

More recently, the technology for determining the sequence of nucleotides (base pairs; see Table 1.5) has become increasingly accessible and is generally preferred, because sequence data provide discrete character information rather than estimates of relative similarity between nucleic acids (e.g., as in DNA hybridization) or their products (immunological tests). Several sequencing protocols are available, and in all, it is necessary to select or target a specific segment of a particular nucleic acid owing to the enormous number of available sequences within the cell and its organelles. First, the nucleic acid to be examined is selected (e.g., mitochondrial or nuclear DNA, ribosomal RNA) and then specific sequences within this molecule are targeted. The target sequence is then amplified using a polymerase chain reaction to produce multiple copies of the sequence for each OTU being compared (Palumbi, 1996). The sequence copies are isolated and purified for sequencing. Sequence determination relies on site-specific cleavage of the target sequence into fragments of known nucleotide sequences and the separation and identification of these fragments by electrophoresis. The homologous sequences are then aligned and provide the data for analyzing the phylogenetic relationships among the OTUs (Hillis et al., 1996).

TABLE 1.5 Sample of mtDNA Sequence Data for Select Iguania

Anolis	CAATT TCTCC CAATT ACTTT AGCTT TATGC CTATG ACACA CAACA
Basiliscus	CAATT TTTAC CAATC ACCCT AGCCC TCTGC CTATG ACACG TAGCC
Oplurus	CAATT TCTTC CAATC ACATT AGCCC TATGC CTATG GTATA CCTCA
Sauromalus	CAATT TCTCG CCCTC ACACT AGCCC TATGC CTATG TCTCA CTTTC
Chamaeleo	CAATT TCTAC CCCAT ACCCT AGCCA TATGC CTACT CTACA CTGCC
Uromastyx	CAATT CCTAC CCCTG ACCTT AGCCA TATGC CTATT ATACA CAAAC

Source: Macey et al. (1997), Figure 1.

Note: The sequences represent the 401st to 445th positions on the ND2 gene. They are presented here in sets of five to permit ease of comparison. Abbreviations are A, adenine; C, cytosine; G, guanine; and T, thymine.

Methods of Analysis

The opportunities for analysis are as varied as the characters. Choice of analytical methods depends on the nature of the question(s) asked and should be made at the beginning of a systematic study, not after the data are collected. With the breadth of systematic studies ranging from investigations of intrapopulational variation to the relationships of phyla, the need for a carefully designed research plan seems obvious.

Systematic research often begins when a biologist discovers a potentially new species, notes an anomalous distribution pattern of a species or a character complex, or wishes to examine the evolution of a structure, behavior, or other biological aspect, and thus requires a phylogenetic framework. Having formulated a research objective, a preliminary study will explore the adequacy of the characters and data collection and analysis protocols for solving the research question. A wide array of analytical techniques is available to evaluate the adequacy of the characters and protocols and then to examine the relationships among characters and among the samples and OTUs.

A small set of the available analytical techniques follows. These techniques segregate into numeric and phylogenetic ones. Numeric analyses offer a wide choice of methods to describe and compare the variation of OTUs and/or their similarity to one another. Phylogenetic analyses address common ancestry relationships of OTUs, specifically attempting to uncover the evolutionary divergence of taxa.

Numeric Analyses Any study of variation requires the examination of multiple characters scored over numerous individuals. The resulting data cannot be presented en masse but must be summarized and condensed. Numeric analyses provide this service (James and McCullough, 1985). The initial analysis examines the variation of single characters within each sample using univariate statistics. The next phase compares individual characters within subsamples (e.g., females to males), the relationship of characters to one another within samples, and character states of one sample to those of another sample using bivariate statistics. The final phase usually is the comparison of multiple characters within and among samples using multivariate analysis. Each phase yields a different level of data reduction and asks different questions of the data: for example, (1) what is the variability of each character; (2) what is the difference in the means and variance between sexes or among samples; and (3) what is the covariance of characters within and among samples (Table 1.6)?

Even the briefest species description requires univariate statistics. A new species is seldom described from a single specimen, so univariate analysis shows the variation of each character within the sample and provides an estimate of the actual variation within the species. Means, minima and maxima, and standard deviations are the usual statistics presented. An in-depth study of a group of species typically uses univariate and bivariate statistics to examine the variation within each species and one or more multivariate techniques to examine the variation of characters among the species and the similarities of species to one another.

Multivariate analysis has become increasingly important in the analysis of systematic data, particularly mensural and meristic data sets (Table 1.6). Multivariate analysis allows the researcher to examine all characters and all OTUs simultaneously and to identify patterns of variation and association within the characters, and/or similarities of OTUs within and among samples. For example, principal component analysis is often used in an exploratory manner to recognize sets of characters with maximum discriminatory potential or to identify preliminary OTU groups. These observations can then be used in a discriminant function analysis to test the reliability of the OTU groupings. Because these statistical techniques are readily available on microcomputers, there has been a tendency to use them without an awareness of their limitations and mathematical assumptions. Users should be aware that combining meristic and mensural characters, using differently scaled mensural characters, or comparing data sets of unequal variance can yield meaningless results.

Cluster analysis is another multivariate technique but not strictly statistical in the sense of being inferential or predictive. The numerous clustering algorithms use distance or similarity matrices and create a branching diagram or dendrogram. These matrices derive from a pairwise comparison of each OTU for every character to every other OTU in the sample (Fig. 1.17). The raw data in an OTU × character matrix are converted to an OTU × OTU matrix in which each matrix cell contains a distance or similarity value. The clustering algorithm uses these values to link similar OTUs and OTU groups to one another, proceeding from the most similar to the least similar.

TABLE 1.6 Examples and Definitions of Numeric Analytical Tools

Univariate

Frequency distributions. Presentation techniques to show frequency of occurrence of different data classes or character states. Frequency tables, histograms, pie charts, and other techniques permit easy visual inspection of the data to determine normality of distribution, range of variation, single or multiple composition, etc.

Central tendency statistics. Data reduction to reveal the midpoint of sample for each character and variation around the midpoint. Variables include mean (average value), mode (most frequent value), and median (value in middle of ranked values); variance, standard deviation, and standard errors (numeric estimates of sample's relative deviation from mean); and kurtosis and skewness (numeric estimates of the shape of a sample's distribution).

Bivariate

Ratios and proportions. Simple comparisons (A:B, $\% = [B/A] \times 100$) of the state of one character to that of another character in the same specimen.

Regression and correlation. Numeric descriptions (equation and value, respectively) of the linear relationship and association of one character set to another.

Tests of similarities between samples. A variety of statistical models (χ^2, Student's *t*, ANOVA [analysis of variance]) test the similarity of the data between samples.

Nonparametric statistics. Statistical models containing no implicit assumption of a particular form of data distribution. All other statistics in this table are parametric, and most assume a normal distribution.

Multivariate

Principal components analysis (PCA). Manipulation of original characters to produce new uncorrelated composite variables or characters ordered by decreasing variance.

Canonical correlation. Comparison of the correlation between the linear functions of two exclusive sets of characters from the same sample.

Discriminant function analysis (DFA). Data manipulation to identify a set of characters and assign weights (functions) to each character within the set in order to separate previously established groups within the sample.

Cluster analysis. A variety of algorithms for the groupings of OTUs on the basis of pairwise measures of distance or similarity.

Source: In part modified from James and McCullough (1985, 1990).

Phylogenetic Analyses The preceding numeric techniques do not provide estimates of phylogenetic relationships; rather, they summarize the level of similarity.

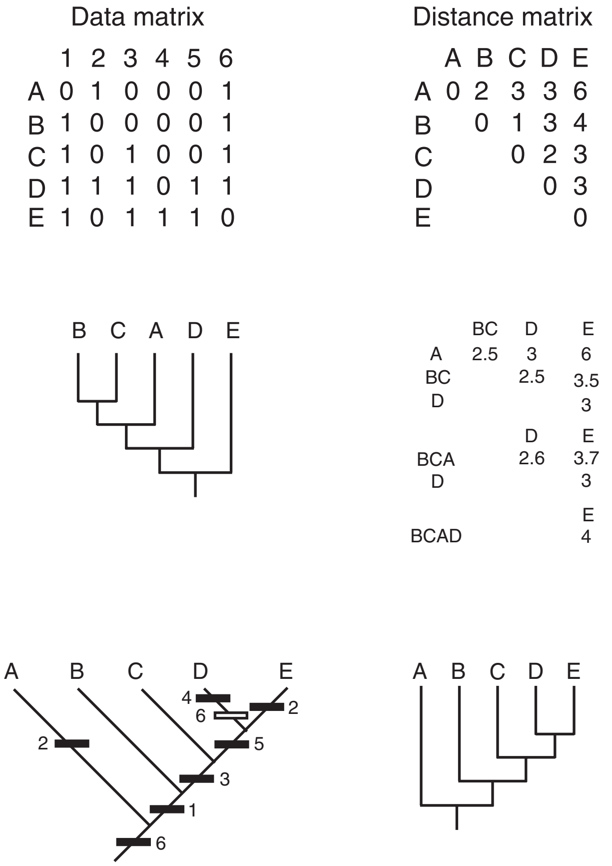


FIGURE 1.17 Construction of branching diagrams by two methods: phenetics and cladistics. The OTU × Character matrix (upper left) contains five OTUs (A–E) and six characters (1–6). Each character has two states, 0 or 1 (e.g., absent or present, small or large, etc.). Pairwise comparison of OTUs creates an OTU × OTU matrix (upper right). The distance values are the sums of the absolute difference between states for all six characters. Zeros fill the diagonal because each OTU is compared to itself; only half of the matrix is filled with the results of a single analysis because the two halves are mirror images of one another. An unweighted pair-group method (UPGM) clustering protocol produces a phenetic dendrogram (phenogram, middle left); in UPGM, the most similar OTUs are linked sequentially with a recalculation (middle right) of the OTU × OTU matrix after each linkage. The cladogram (lower left) derives directly from the OTU × Character matrix. The solid bars denote a derived character state that is shared (synapomorphic), the open bars denote an evolutionarily reversed state, and the numbers are the characters. For comparison with the UPGM phenogram, a cladogram (lower right) is presented in a different style without the depiction of character state information.

Overall similarity has been argued as an estimate of phylogenetic relationship. This concept is the basic tenet of the phenetic school of systematics (Sokal, 1986) which came into prominence in the late 1950s and was then rapidly replaced by phylogenetic systematics. Phenetics as a classification method has largely disappeared (although many of its analytical algorithms remain) because its basic premise of "similarity equals genealogical relationship" is demonstrably false in many instances, and the resulting classifications do not reflect accurately the evolutionary history of the organisms being studied. Another basic premise of the phenetic school was that large character sets produce more robust and stable classifications; unfortunately, the addition of more characters usually changes the position of OTUs on the dendrogram and yields a dissimilar classification. This instability of OTU clustering arises from the use of unweighted characters and the swamping of useful characters by ancestral (= primitive) and nonhomologous (= homoplasic) ones.

Phylogenetic analysis has been variously practiced since the publication of Darwin's *Origin of Species*. However, in the mid-1960s, with the publication of the English language edition of Willi Hennig's *Phylogenetic Systematics*, systematists began more rigorous and explicit character analyses and the reconstruction of phylogenies (taxa genealogies). This approach gives repeatability to systematic practices and is broadly known as cladistics. The basic tenets of phylogenetic systematics are: (1) only shared similarities that are derived are useful in deducing phylogenetic relationships; (2) speciation produces two sister species; and (3) speciation is recognizable only if the divergence of two populations is accompanied by the origin of a derived character state (Wiley, 1981; Wiley et al., 1991).

Character analysis plays a major role in phylogenetic reconstruction, because it is necessary to determine the ancestral or derived status for each character state. A special terminology is associated with the determination of character state polarity: plesiomorphic, the same state as in the ancestral species; apomorphic, a derived or modified state relative to the ancestral condition; autapomorphic, a derived state occurring in a single descendant or lineage; and synapomorphic, a derived state shared in two or more species. Sister groups are taxa uniquely sharing the same ancestor; synapomorphic characters identify sister groups.

Determination of character state polarity can use one or more protocols. Outgroup comparison is generally considered the most reliable method (Watrous and Wheeler, 1981). Operationally, the researcher identifies a candidate sister group(s) (outgroup) of the group being studied (ingroup) and then examines the distribution of character states for each character in these two groups. If a state occurs only in the ingroup (but not necessarily in all members of the group), it is hypothesized to be apomorphic, and if present in both in- and outgroups, it is considered plesiomorphic. Ontogenetic analysis, commonality, and geological precedence are supplementary methodologies and are rarely used now owing to their low reliability.

Once the characters have been polarized, the researcher can construct a cladogram by examining the distribution of apomorphic states. Numerous computer algorithms are available for the evaluation of character state distributions and cladogram construction (Swofford et al., 1996). For complex or large data sets, computer analysis is required. However, the following protocol demonstrates some fundamentals of cladogram construction. Figure 1.17 uses the OTU × Character matrix for the sequential linkage of sister groups and all "1" states are considered apomorphic. Linkage proceeds as follows: D and E are sister taxa, synapomorphic for character 5; C and D-E are sister groups, synapomorphic for character 3; B and C-D-E are sister groups, synapomorphic for character 1; A and B-C-D are sister groups, synapomorphic for character 6. Taxon E shows the plesiomorphic state for character 6, which might suggest that E is not a member of the ABCD clade; however, it does share three other apomorphic characters, and the most parsimonious assumption is that character 6 underwent an evolutionary reversal in E. Similarly, the most parsimonious assumption for the synapomorphy of character 2 in taxa A and D is convergent evolution. These shared character states of independent origin are nonhomologous or homoplasic. Construction, or rather inferring phylogeny, from most data sets, and particularly molecular ones, is much more complex. Phylogenetic inference experienced major advances in theory and application during the 1990s. The complexities of these issues are well explained in Swofford et al. (1996).

Nomenclature

Another important aspect of systematics is the assignment and use of taxonomic names—nomenclature. All biologists must correctly identify the animal or plant studied and then must use the correct taxonomic names in reporting the results of their study. Failure to provide the correct scientific name and higher taxonomic assignments will prevent other biologists, including ecologists, behaviorists, and even cell biologists, from recognizing that the results are important to them or cause others to compare the incorrectly labeled results with their own results derived from different organisms.

Brief History

Humans have classified and named plants and animals since language first appeared. Our formal system of animal classification dates from the Linnaeus's 10th edition of *Systema Naturae* in 1758. This catalog gave a concise diagnosis of all known species of plants and animals and arranged them in a hierarchical classification of genus, order, and class. Importantly, this edition of Linnaeus's catalog was the first publication to use consistently a two-part name (a binomial of genus and species), and hence the reason for selecting it as the beginning of zoological classification. Scientific names of plants and animals remain binomials and are given in Latin (the language of scholars in the 18th century).

While Linnaeus proposed a set of rules for naming plants, he offered none for animals except by example. Rules or not, later biologists began to describe and classify as they wished. With many naturalists and countries following their own rules of nomenclature, multiple names for the same species and higher taxa were adopted by different groups. Classifications were becoming idiosyncratic and unintelligible to outsiders, even those studying the same group of animals. To avoid the impending chaos, the botanical and zoological communities separately developed codes for the practice of nomenclature. The most recent code for zoologists is the *International Code of Zoological Nomenclature, Fourth Edition* (the Code), published in 1999.

Just as systematic analysis is in the midst of a revolution, so is nomenclature. Some aspects of the fourth edition are controversial because of a perceived relaxation of the rules. However, the revolution of nomenclature is not the revised Code; rather it derives from the failure of nomenclature and taxonomy to break from the Linnean typological paradigm and to develop a truly evolutionary approach (de Queiroz, 1997). Changes have been proposed (de Queiroz and Gauthier, 1992)—some have been adopted in this textbook—and others are gaining increased acceptance through publications by specialists in the field of systematics.

Rules and Practice

The Code is a legal document for the practice of classification, specifically for the selection and assignment of names to animals from species through family groups. Unlike our civil law, there are no enforcement officers. Enforcement occurs through the biological community's acceptance of a scholar's nomenclatural decisions. If the rules and recommendations are followed, the scholar's decisions are accepted; if the rules are not followed, the decisions are invalid and not accepted by the community. Where an interpretation of the Code is unclear or a scholar's decision uncertain relative to the Code, the matter is presented to the International Commission for Zoological Nomenclature (a panel of systematic zoologists), which, like the U.S. Supreme Court, provides an interpretation of the Code and selects or rejects the decision, thereby establishing a precedent for similar cases in the future.

The Code has six major tenets:

1. All animals extant or extinct are classified identically, using the same rules, classificatory hierarchies, and names where applicable. This practice avoids dual and conflicting terminology for living species that may have a fossil record. Further, extant and fossil taxa share evolutionary histories and are properly classified together.

2. Although the Code applies only to the naming of taxa at the family group rank and below, all classificatory ranks have Latinized formal names. All except the specific and subspecific epithets are capitalized when used formally; these latter two are never capitalized. For example, the major rank or category names (phylum, class, order, family, genus, species) for the green iguana of Central America are Chordata, Vertebrata, Tetrapoda, Iguanidae, *Iguana iguana*. The names may derive from any language, although the word must be transliterated into the Roman alphabet and converted to a Latin form.

3. To ensure that a name will be associated correctly with a taxon, a type is designated—type genus for a family, type species for a genus, and a type specimen for a species. Such a designation permits other systematists to confirm that what they are calling taxon X matches what the original author recognized as taxon X. Comparison of specimens to the type is critical in determining the specific identity of a population. Although the designation of a single specimen to represent a species is typological, a single specimen as the name-bearer unequivocally links a particular name to a single population of animals.

Of these three levels of types, only the type of the species is an actual specimen; nonetheless, this specimen serves conceptually and physically to delimit the genus and family. A family is linked to a single genus by the designation of a type genus, which in turn is linked to a single species by a type species, and hence to the type specimen of a particular species. The characterization at each level thus includes traits possessed or potentially possessed by the type specimen. An example of such a nomenclatural chain follows: *Xantusia* Baird, 1859 is the type genus of the family Xantusiidae Baird, 1859; *Xantusia vigilis* Baird, 1859 is the type species of *Xantusia*; and three specimens, USNM 3063 (in the U.S. National Museum of Natural History), are syntypes of *Xantusia vigilis.*

Several kinds of types are recognized by the Code. The holotype is the single specimen designated as the name-bearer in the original description of the new species or subspecies, or the single specimen on which a taxon was based when no type was designated. In many 19th century descriptions, several specimens were designated as a type series; these specimens are syntypes. (More recent Codes do not approve the designation of syntypes.) Often syntypic series contain individuals of more than one species, and sometimes to avoid confusion, a single specimen, a lectotype, is selected from the syntypic series. If the holotype or syntypes are lost or destroyed, a new specimen, a neotype, can be designated as the name-bearer for the species. Other types (paratypes, topotypes, etc.) are used in taxonomic publication; however, they have no official status under the Code.

4. Only one name may be used for each species. Yet commonly, a species has been recognized and described independently by different authors at different times. These multiple names for the same animal are known as synonyms and arise because different life history stages, geographically distant populations, or males and females were described separately, or because an author is unaware of another author's publication. Whatever the reason, the use of multiple names for the same animal would cause confusion, and hence only one name is correct.

Systematists have selected the simplest way to determine which of many names is correct, namely by using the oldest name that was published in concordance with rules of the Code. The concept of the first published name being the correct name is known as the Principle of Priority. The oldest name is the primary (senior) synonym and all names published subsequently are secondary (junior) synonyms (Table 1.7). Although simple in concept, the implementation of the Principle may not promote stability, especially when the oldest name of a common species has been unknown for many decades and then is rediscovered. Should *viridisquamosa* Lacépéde, 1788 replace the widely used *kempii* Garman, 1880 for the widely known Kemp's ridley seaturtle *Lepidochelys kempii*? No. The goal of the Code is to promote stability of taxonomic names, so the Code has a 50–year rule that allows commonly used and widely known secondary synonyms to be conserved and the primary synonym suppressed. The difficulty with deviating from priority is deciding when a name is commonly used and widely known—the extremes are easy to recognize but the middle ground is broad. In these circumstances, the case must be decided by the international commission.

In deciding whether one name should replace another name, a researcher determines whether a name is "available" prior to deciding which of the names is "valid." The concept of availability depends upon a taxonomic description of a new name obeying all the tenets of the Code in force at the time of the description. Some basic tenets are as follows: published subsequent to 1758 (10th edition of *Systema Naturae*), a binomial name for

TABLE 1.7 Abbreviated Synonymies of the European Viperine Snake (Common Name) and the Cosmopolitan Green Seaturtle

Natrix maura (Linnaeus)

1758. *Coluber maurus*, Linnaeus, Syst. Nat., ed. 10, 1:219. Type locality, Algeria. [Original description; primary synonym]

1802. *Coluber viperinus*, Sonnini and Latreille, Hist. nat. Rept. 4:47, fig. 4. Type locality, France. [Description of French population, considered to be distinct from Algerian population]

1824. *Natrix cherseoides*, Wagler in Spix, Serp. brasil. Spec. nov., 29, fig. 1. Type locality, Brazil. [Geographically mislabeled specimen mistaken as a new species]

1840. *Coluber terstriatus*, Duméril in Bonaparte, Mem. Accad. Sci. Torino, Sci. fis. mat. (2) 1:437. Type locality, Yugoslavia. Nomen nudum. [Naked name; name proposed without a description so *terstriatus* is not available]

1840. *Natrix viperina* var. *bilineata*, Bonaparte, Op. cit. (2) 1:437. Type locality, Yugoslavia. Non *Coluber bilineata*, Bibron and Bory, 1833; non *Tropidonotus viperinus* var. *bilineata*, Jan, 1863; non *Tropidonus natrix* var. *bilineata*, Jan, 1864. [Recognition of a distinct population of *viperina*; potential homonyms listed to avoid confusion of Bonaparte's description with other description using *bilineata* as a species epithet]

1929. *Natix maura*, Lindholm, Zool. Anz. 81:81. [First appearance of current usage]

Chelonia mydas (Linnaeus)

1758. *Testudo mydas*, Linnaeus, Syst. Nat., ed. 10, 1:197. Type locality, Ascension Island. [Original description; primary synonym]

1782. *Testudo macropus*, Wallbaum, Chelonogr., 112. Type locality, not stated. Nomen nudum.

1788. *Testudo marina vulgaris*, Lacédè, Hist. nat. Quadrup. ovip. 1: Synops. method., 54. Substitute name for *Testudo mydas* Linnaeus.

1798. *T. mydas minor*, Suckow, Anfangsg. theor. Naturg. Thiere. 3, Amphibien, 30. Type locality, not stated. Nomen oblitum, nomen dubium. [Forgotten name, not used for many years and then rediscovered; name of uncertain attribution, tentatively assigned to *mydas*]

1812. *Chelonia mydas*, Schweigger, Königsber. Arch. Naturgesch. Math. 1:291. [Present usage but many variants appeared after this]

1868. *Chelonia agassizii*, Bocourt, Ann. Sci. nat., Paris 10:122. Type locality, Guatemala. [Description of Pacific Guatemalan population as distinct species]

1962. *Chelonia mydas carrinegra*, Caldwell, Los Angeles Co. Mus. Contrib. Sci. (61), 4. Type locality, Baja California. [Description of Baja population as a subspecies]

Source: Modified from Mertens and Wermuth (1960) and the *Catalogue of American Amphibians and Reptiles*.

Note: The general format of each synonym is original date of publication; name as originally proposed; author; abbreviation of publication; volume number and first page of description; and type locality. Explanations of the synonyms are presented in brackets.

a species-group taxon, name in Roman alphabet, appearing in a permissible publication, and description differentiates the new taxon from existing ones. If the presentation of a new name meets these criteria and others, the name is available. Failure to meet even one of the criteria, such as publication in a mimeographed (not printed) newsletter, prevents the name from becoming available. Even if available, a name may not be valid. Only a single name is valid, no matter how many other names are available. Usually, the valid name is the primary synonym. The valid name is the only one that should be used in scientific publications.

5. Just as for a species, only one name is valid for each genus or family. Further, a taxonomic name may be used only once for an animal taxon. A homonym (the same name for different animals) creates confusion and is also eliminated by the Principle of Priority. The oldest name is the senior homonym and the valid one. The same names (identical spelling) published subsequently are junior homonyms and invalid names. Two types of homonyms are possible. Primary homonyms are the same names published for the same taxon, for example, *Natrix viperina bilineata* Bonaparte, 1840 and *Tropidonotus viperina bilineata* Jan 1863. Secondary homonyms are the same names for different taxa, for example, the insect family Caeciliidae Kolbe, 1880 and the amphibian family Caeciliidae Gray, 1825.

6. When a revised Code is approved and published, its rules immediately replace those of the previous edition. This action could be disruptive if the new Code differed greatly from the preceding one, but most rules remain largely unchanged. Such stasis is not surprising, for the major goal of the code is to establish and maintain a stable nomenclature. Rules tested by long use and found functional are not discarded. Those with ambiguities are modified to clarify the meaning. When a rule requires major alteration and the replacement rule results in an entirely different action, a qualifying statement is added so actions correctly executed under previous rules remain valid. For example, the first edition of the Code required that a family-group name be replaced if the generic name on which it was based was a secondary synonym; the second and third editions do not require such a replacement. Thus, the latter two editions permit the retention of the replacement name proposed prior to 1960 if the replacement has won general acceptance by the systematic community. Such exceptions promote nomenclature stability.

Evolution-Based Taxonomy

The preceding rules illustrate the typological approach of Linnean taxonomy, most especially the emphasis on named categories and fixed levels within the hierarchy. The adoption of cladistics as the major practice and conceptual base of current systematics has increased the advocacy for a taxonomy and nomenclature that are based on the principle of descent. Hierarchies can represent this basic evolutionary concept that organisms are related through common descent but not within the rigid categorization or ranking of the Linnean hierarchy system. Advocates for an evolution-based taxonomy argue that the taxonomic system should directly reflect phylogeny and retain only those elements that do not interfere with the accurate and efficient depiction of this phylogeny (de Queiroz, 1997). A consequence of this demand is a change in how a taxon is named. In the Linnean system, a taxon is defined in terms of its assumed category or hierarchical position; in contrast, the evolution-based system defines a taxon in terms of its content, that is, the clade containing the most recent ancestor of X and all its descendants. A result of the latter practice is a classification in which a species has a hierarchical position equivalent to a clade with dozens of species in several lower "level" clades (see Table 1.4). Another consequence is the abandonment of category labels such as family, order, or class. Biologists have long recognized that family names do not represent the same level of phylogenetic history even within larger clades such as frogs or lizards. Other conceptual and practical matters are involved in the adoption of a phylogenetic taxonomy (de Querioz and Gauthier, 1992, 1994) and are beyond the scope of this brief introduction. The taxonomic revolution has begun, but its end is not near. The new taxonomy still faces the resistance of tradition and the challenges of the concept of evolution.

ADDITIONAL READING

Benton, M. J. (1997a). "Vertebrate Paleontology," 2nd ed. Chapman & Hall, London.

Carroll, R. L. (1988). "Vertebrate Paleontology and Evolution." W. H. Freeman & Co., New York.

De Queiroz, K. (1997). The Linnean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* **15:** 125–144.

Hillis, D. M., Moritz, C., and Mable, B. K., Eds. (1996). "Molecular Systematics, Second Edition." Sinauer Assoc., Inc., Sunderland, MA.

Schultze, H.-P., and Trueb, L., Eds. (1991). "Origins of the Higher Groups of Tetrapods. Controversy and Consensus." Comstock Publ. Assoc., Ithaca, NY.

REFERENCES

General: Gibbons, 1990; Hertz et al., 1993; Jenssen and Nunez, 1998; Radtkey et al., 1995; Roughgarden, 1995; Ryan and Rand, 1995; Tinsley and Kobel, 1996; Wake and Hanken, 1966; Wilbur, 1997; Wright and Vitt, 1993.

Relationships among Vertebrates: Fish to Tetrapod: Coates and Clack, 1995; Edwards, 1989; Fox, 1985; Fritzsch, 1990; Gensel and Andrews, 1987; Graham, 1997; Hughes, 1976; Lauder and Gillis, 1997; Little, 1990; Romer, 1960; Schmalhausen, 1968; Schultze, 1991; Scott, 1980; Thomson, 1980, 1993; Whitear, 1977.

Fish Ancestors and Early Tetrapods: Clack, 1998; Eernisse and Kluge, 1993; Gauthier et al., 1988c, 1989; Hanken, 1986; Hedges et al., 1993a; Hedges and Maxson, 1996; Panchen, 1991; Panchen and Smithson, 1988; Schmalhausen, 1968; Schultze, 1991, 1994; Vorobyeva and Schultze, 1991.

Evolution of Early Anamniotes: Ancient Amphibians: Ahlberg, 1995; Ahlberg and Milner, 1994; Benton, 1997a; Carroll, 1988, 1995; Panchen and Smithson, 1988; Trueb and Cloutier, 1991a,b.

Modern Amphibians: Bolt, 1991; Carroll, 1988, 1997; Trueb and Cloutier, 1991b.

Evolution of Early Amniotes: Early Tetrapods and Terrestriality: Benton, 1991, 1997a; Carroll, 1988; Frolich, 1997; Goin, 1960; Hotton et al., 1997; Lauder and Gillis, 1997; Laurin and Reisz, 1997; Martin and Nagy, 1997; Packard and Kilgore, 1968; Packard and Packard, 1980; Packard and Seymour, 1997; Sumida, 1997.

Early Amniotes: Carroll, 1988; deBraga and Rieppel, 1997; Gaffney, 1980; Gauthier et al., 1988b, 1989; Hedges and Poling, 1999; Laurin and Reisz, 1995; Lee, 1993, 1995, 1997; Reisz and Laurin, 1991; Rieppel and deBraga, 1996; Zardoya and Meyer, 1998.

Radiation of Diapsids: Benton, 1997a; Benton and Clark, 1988; M. Caldwell, 1996; Callaway, 1997; Clark, 1994; Evans et al., 1988; Farlow and Brett-Surman, 1997; Feduccia, 1999; Feduccia and Wild, 1993; Gauthier, 1986, 1988c; Martin, 1991; Ostrom, 1991; Rieppel, 1993, 1994; Storrs, 1993; Tarsitano and Hecht, 1980; Witmer, 1991.

Systematics: Basic Concepts: de Queiroz and Gauthier, 1994; Oosterbrock, 1987; Simpson, 1961.

Systematic Analysis: Goodman et al., 1987; Swofford et al., 1996.

Types of Characters: Morphology: Green and Sessions, 1991; Sessions, 1996.

Molecular Structure: Guttman, 1985; Hillis and Moritz, 1990.

Electrophoresis: Buth, 1984; Murphy et al., 1990; Richardson et al., 1986.

Immunology: Maxson and Maxson, 1986, 1990.

Nucleic Acids: Hillis et al, 1996; Moritz and Hillis, 1996; Palumbi, 1996.

Methods of Analysis: Numeric Analyses: James and McCullough, 1985, 1990; Kachigan, 1982; Thorpe, 1976, 1987.

Phylogenetic Analyses: Hennig, 1966; Kluge and Farris, 1969; Schmitt, 1989; Sokal, 1986; Watrous and Wheeler, 1981; Wiley, 1981; Wiley et al., 1991; Swofford et al., 1996.

Nomenclature: Brief History: de Queiroz, 1997; de Queiroz and Gauthier, 1992;

Rules and Practice: Mayr and Ashlock, 1991.

Evolution-based Taxonomy: de Queiroz 1997; de Queiroz and Gauthier, 1992, 1994.

Chapter

2

Anatomy of Amphibians and Reptiles

DEVELOPMENT AND GROWTH

Ova, Sperm, and Fertilization

All vertebrate life begins with a single cell, the zygote. For most amphibians and reptiles, this single cell results from the fusion of an ovum and a spermatozoon, the female and the male sex cells. This act of fusion is the process of fertilization and occurs predominantly outside the female's body and reproductive system (external fertilization) in frogs and inside the female's reproductive system (internal fertilization) in all reptiles and caecilians, and most salamanders. The sex cells or gametes are unlike any other cells in the body because they possess one-half the number of chromosomes (a haploid condition) of the typical body cell. Their sole role is fusion and creation of a new individual. They of course differ in structure as well; these details and those of the subsequent aspects of gametogenesis and fertilization (Wassarman, 1987) are presented in Chapter 4.

The cells that will produce the gametes differentiate early in development and migrate from their origin along the neural tube to the gonadal area of the embryo. They will not form the gonads; the surrounding cell mass differentiates into the gonadal tissues and structures that support and nourish these precursors of the sex cells. The precursor cells can produce additional cells by the usual mode of cell division (mitosis); however, the production of gametes requires a special mode (meiosis) that halves the number of chromosomes, thereby allowing the fusion of the spermatozoon and ovum without doubling the number of chromosomes in each succeeding generation. The series of steps in this meiotic or reductive cell division is known as gametogenesis (oogenesis and spermatogenesis, or ova and spermatozoa production, respectively) and typically does not begin until the individual matures (or rather, the gametogenic event marks an individual's maturity).

TABLE 2.1 Summary of Development in Extant Amphibians and Reptiles

	Amphibia	Reptilia
Ovum size (diameter)	1–10 mm	6–100+ mm
Yolk content	Moderate to great	Great
Fertilization	External or internal	Internal
Cleavage	Holoblastic[1]	Meroblastic
Embryo	Ovum-zygote elongating to pharyngula	Cleavage-cell disk folding to pharyngula
Fate of ovum-zygote	Zygote becomes entire embryo	Cell disk forms embryo and extraembryonic structures
Mode of development	Indirect or direct	Direct

Source: In part, after Ellison (1987).

[1] In amphibians with large, yolked eggs and direct development, meroblastic cleavage has been reported only for the salamanders of the genus *Ensatina* (Hanken and Wake, 1996).

Early Development

Embryogenesis

The zygote is the single cell resulting from the fusion of the nuclei of the spermatozoon and ovum. The zygote soon begins to undergo successive divisions that result in formation of a blastula. This cell division is called cleavage and is a progressive division of the larger zygote cell into smaller and smaller cells. Cleavage continues until the cells of the blastula reach the size of normal tissue cells. There is no overall change in size or mass of the original zygote; however, the amount of yolk in the zygote greatly affects the manner of cleavage, the resulting blastula, and the blastula's subsequent development. Because of their differing yolk content, the transformation of amphibian and reptilian zygotes into embryos is not identical and, therefore, the term "development" has two different but overlapping meanings. Development usually refers to all embryological processes and the growth (enlargement) of the embryo. Development can also refer to just the embryological processes, including embryogenesis (the formation of the embryo and its embryology through metamorphosis, hatching, or birth), organogenesis (the formation of organs), and histogenesis (the formation of tissues).

Ova are categorized by their yolk content. Isolecithal ova have a small amount of yolk evenly distributed throughout the cell. Mammals have isolecithal ova, but amphibians and reptiles do not. These two clades have mesolecithal (moderately yolked) and macrolecithal (heavily yolked) ova, respectively (Table 2.1), although the ova of most direct-developing amphibians tend toward macrolecithal ova (Elinson, 1987). The latter situation highlights the developmental modes of the two yolk classes. Moderate amounts of yolk permit only partial development of an embryo within the egg and its protective capsules before it must hatch and become free-living, at which time it is called a larva. Large amounts of yolk permit complete development of an embryo within an egg or within or on one of its parents; when a "macrolecithal" embryo hatches, its development is largely complete and it is a miniature replicate of its parents.

But hatching is distant from the zygote, and the developmental routes are varied. Cleavage of the mesolecithal ovum is complete or holoblastic; that is, the first cleavage furrow divides the zygote into two equal halves, the second furrow into four equal-sized cells, and so on. Yolk concentration is greater in the bottom half of the zygote, and cell division is slower there. Nonetheless, the result is a blastula—a ball of cells with a small cavity in the upper half. In contrast, cleavage of a macrolecithal ovum is incomplete or meroblastic because the mass of yolk allows only a superficial penetration of the cleavage furrow (Table 2.1). Further, these furrows are confined to a small area on the top of the zygote, and the resulting blastula is a flat disk of cells covering about one-third of the surface of the original ovum. The entire mesolecithal blastula becomes the embryo, whereas only the disk-blastula of the macrolecithal ovum becomes the embryo and associated extraembryonic membranes.

The next phase, gastrulation, includes cell movement and cell division, and results in the formation of the three embryonic tissue layers. These layers (ectoderm, mesoderm, and endoderm) are the precursor tissues to all subsequent tissues. They still consist of undifferentiated cells at the conclusion of gastrulation, but by the cells' segregation into layers, their fate is decided. Ectoderm becomes epidermal and neural tissues; mesoderm forms skeletal, muscular, circulatory, and associated tissues; and endoderm forms the digestive system tissues. In amphibian gastrulation, an indentation appears on the upper surface of the blastula. The indentation marks the major area of cell movement as the cells migrate inwardly to form the embryonic gut tube with the mesoderm lying between this tube and the external (ectoderm) layer. At the end of gastrulation, the embryo is still largely a sphere. In reptilian gastrulation, cell movement creates an elongate, but unopened, indentation (the primitive streak) along the future anteroposterior axis of the embryonic disk. A cavity does not form and the endoderm appears by a delamination of the underside of the embryonic disk. This delamination typically precedes the formation of the primitive streak.

Before gastrulation concludes, a new set of cell movements and proliferation begins. This embryonic process is neurulation and, as the name suggests, establishes the neural tube, the precursor of the brain and spinal cord. Neurulation also is accompanied by an elongation of the embryo. The embryo is beginning to take on form. Simultaneously, endodermal and mesodermal layers are proliferating, moving, and continuing their differentiation, that is, assuming cellular and tissue specializations from which they will be unable to deviate. These processes in amphibians and reptiles result in a ''pharyngula'' stage in which the basic organ systems are established. However, amphibian and reptilian pharyngulae have strikingly different appearances and futures. The amphibian pharyngula contains all the yolk within its body as part of the digestive system. It will soon hatch from its gelatinous egg capsule and become a free-living larva; of course, direct-developing amphibian embryos follow a different development pathway, although their anatomy is largely the same as their less yolk-laden cousins.

The reptilian pharyngula is perched on top of a huge yolk mass, and this yolk mass is extraembryonic, that is, it is not part of the pharyngula. It only becomes part of the embryo through conversion of the yolk for nutrition. The endodermal tissue continues to grow outward and will eventually encompass the yolk mass, thereby forming the yolk sac (Figs. 2.1 and 4.3). While the reptilian pharyngula develops, the cells of superficial layers (ectoderm and mesoderm) of the extraembryonic disk also proliferate and move. They grow upward and over the pharyngula and enclose it in an amniotic sheath (Fig. 2.1). The overgrowth begins at the anterior end of the embryo and proceeds in a somewhat wavelike fashion to enclose the embryo. Because this up- and-over growth is a fold of tissue, the resulting sheath consists of four layers around a cavity: ectoderm, mesoderm, cavity, mesoderm, and ectoderm. The outer two layers form the chorion, the cavity is the amniotic cavity, and the inner two layers become the amnion. Eventually, the chorion grows to encase the entire zygotic mass including the yolk sac (Fig. 4.4), whereas the amnion encloses only the embryo (Fig. 2.1). The allantois is the third ''extraembryonic'' membrane, but unlike the amnion and chorion, it is an outpocketing of the hindgut. The allantois consists of endoderm and mesoderm tissue and grows outward into the amniotic cavity, in many instances filling the entire cavity, with its outward wall merging with the amnion. This amniotic complex forms a soft ''shell'' within the leathery or hard shell of the typical reptilian egg.

Morphogenesis

Developing Form and Function

Morphogenesis is the unfolding of form and structure. Unfolding refers to the differentiation of undifferentiated (unprogrammed) cells and the organization of these differentiated cells into tissues (histogenesis), organ systems (organogenesis), and a functional organism (embryogenesis). Growth simply refers to the enlargement of an organism and/or its component parts. While cells differentiate and take on specific functions, they also multiply. This multiplication can yield an increase in size (growth) of an organ or organism; however, cell multiplication also can produce migratory cells, such as neural crest cells, which migrate elsewhere in the embryo before forming a specialized tissue or organ, or cells with special functions such as blood cells, some of which transport oxygen and others that fight infections. These two phenomena and related ones are not considered as growth.

Morphogenesis has its beginning in the pharyngula and subsequent development focuses on organogenesis and histogenesis. Within many amphibians, these two processes proceed rapidly to produce structures that enable the embryo to live outside the egg (Fox, 1983). Most larvae possess full sensory capabilities for finding food and escaping predators, as well as other structures necessary to perform the full range of life processes essential for survival. The typical amphibian larva hatches using specialized epidermal cells that secrete a gelatinous-dissolving substance to exit the egg capsules. Direct-developing amphibians and reptiles stay within the egg capsules or shells until their embryogenesis is complete, hatching as miniature adult replicates. The details of organogenesis are available in embryological

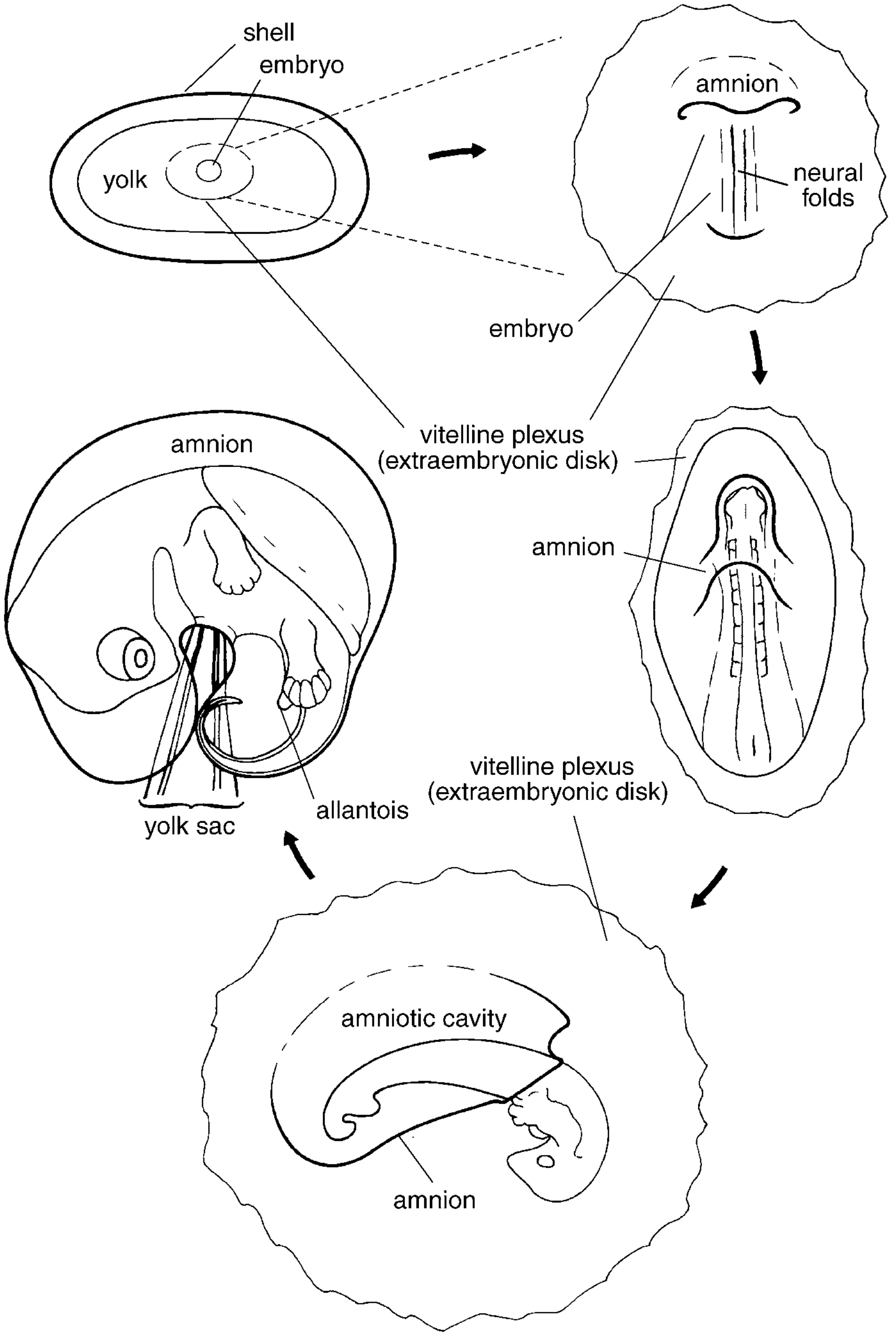


FIGURE 2.1 Selected developmental states of a turtle embryo showing the formation of the extraembryonic membranes. Clockwise from upper left: shelled egg showing early embryogenesis; embryonic disk during neural tube formation and initiation of amniotic folds; embryo during early morphogenesis as somites form, showing rearward growth of the amniotic fold as it envelops the embryo; embryo in early organogenesis with initial outgrowth of the allantois; and near-term embryo encased in amnion with the yolk-sac attachment protruding ventrally. Adapted from Agassiz (1857).

textbooks, but one aspect, the timing of ontogenetic events, is an essential ingredient of amphibian development and evolution, and indeed is critical to the evolution of new lifestyles and body forms in all organisms. Changes in developmental timing at any stage of an organism's ontogeny has the potential to create a structurally and physiologically different organism (Hanken, 1989).

Heterochrony

Shape arises from differential growth within a structure. If a ball of cells multiplies uniformly throughout, the result is an ever-enlarging sphere; however, if the cells in one area grow slower than the surrounding cells, the sphere will form a dimple of slow-growing cells. Such differential growth is a regular process of development, and each pattern of differential growth is usually genetically programmed so that every individual of a species has the same, or at least similar, body form, although environmental factors can alter the pattern. Timing and rate of growth are the essential ingredients for the production of specific shapes and structures, and shape and structure affect the function of tissues, organs, and organisms.

Changes in timing and/or rate (i.e., heterochrony) have been a common feature in the evolution of amphibians and reptiles, and especially salamanders. The recognition of heterochrony as a concept arose from the observation that differences in the morphology of some species could be explained by changes in their ontogeny. Ontogenetic processes can begin earlier (predisplacement) or later (postdisplacement), or end earlier (hypomorphosis) or later (hypermorphosis), than in an ancestor (Table 2.2). These alterations are measured relative to the normal onset (beginning) or offset (termination) times; they refer specifically to the development of a trait or feature of an organism, such as foot structure or head shape. Alterations of the ontogeny also occur when the speed of the developmental rate is shifted either faster (acceleration) or slower (deceleration); either of these shifts can result in a different morphology. The final condition of the trait relative to its condition in the ancestor determines the pattern of heterochrony. A trait might not develop fully (truncation), it might develop beyond the ancestral condition (extension), or it might remain the same as the ancestral trait even though the developmental path differs. A single or related set of traits can change in descendants without affecting the developmental timing and rates of other traits; paedogenesis (Table 2.2) is a common heterochronic event in amphibians. These processes and the resulting patterns occur at two different scales, intraspecifically and interspecifically. Changes in a trait within populations (intraspecific) or a species result in different morphs within the same population, such as carnivorous morphs of spadefoot tadpoles. Differences in a trait's development among species (interspecific) reflect phylogenesis. These two levels of heterochrony and the complex interplay of heterochronic processes have led to confusion and an inconsistent use of terms. Reilly and his colleagues (1997) offer a solution (Table 2.2).

Paedomorphosis and paedogenesis refer to a developmental process in which a trait fails to develop the state possessed by the ancestral species or individuals, respectively. The axolotl (*Ambystoma mexicanum*) is a paedomorphic species. Morphological development of certain traits in the axolotl is truncated relative to that in its ancestral species *Ambystoma tigrinum*. Intraspecifically, some morphs of *Ambystoma talpoideum* with larval traits can reproduce; hence they display paedogenesis. Development of external larval traits is delayed (deceleration) relative to the development or maturation of the gonads in some individuals within the population (Fig. 2.2).

Peramorphosis and peragenesis refer to a developmental process in which a trait develops beyond the state or condition of that trait in the ancestral species or individuals, respectively. Male *Eumeces laticeps* develop very large heads relative to the head size in their sister species *Eumeces fasciatus*, which presumably represents the ancestral condition. The larger head is an example of peramorphosis in the preceding situation; however, individuals within populations of *E. laticeps* have variable head size. This intraspecific difference likely arises from sexual selection and represents peragenesis, assuming that a smaller head size is the population's ancestral condition.

TABLE 2.2 Patterns and Processes of Heterochrony

Pattern	Simple Pertubations (process)	Pattern	
		Interspecific (process)	Intraspecific (process)
Truncation of trait offset shape	Decelerated (deceleration) Hypomorphic (hypomorphosis) Post-displaced (post-displacement)	Paedomorphic (paedomorphosis)	Paedotypic (paedogenesis)
Extension of trait offset shape	Accelerated (acceleration) Hypermorphic (hypermorphosis) Pre-displaced (pre-displacement)	Peramorphic (peramorphosis)	Peratypic (peragenesis)
No change in trait offset shape	Must involve more than one pure perturbation	Isomorphic (isomorphosis)	Isotypic (isogenesis)

Source: Reilly et al., 1997.

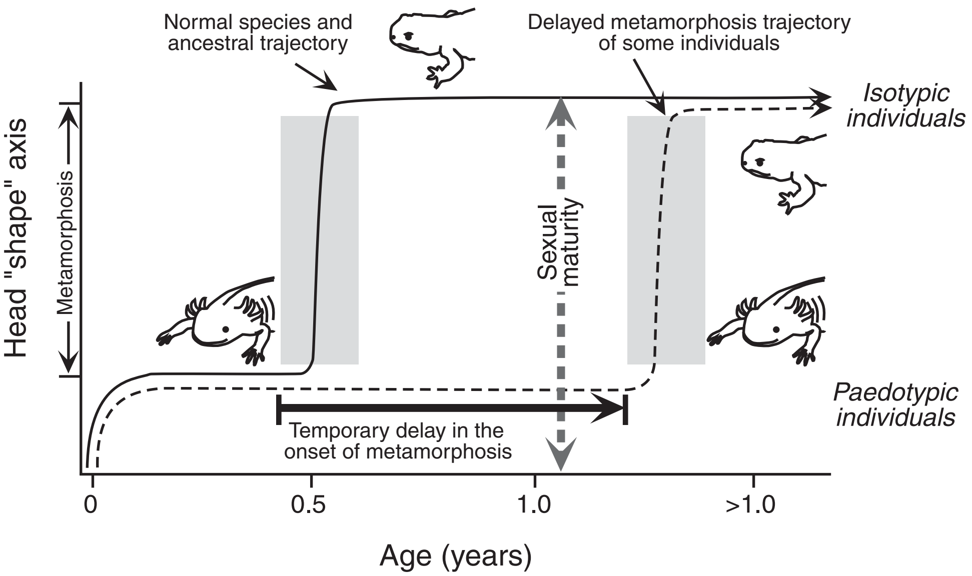


FIGURE 2.2 Paedogenesis and isogenesis in *Ambystoma talpoideum*. The life history of *A. talpoideum* demonstrates the complexities of trait development patterns. The ancestral condition for this species is metamorphosis into a terrestrial salamander in less than one year. Under certain environmental conditions, paedogenesis occurs when metamorphosis is delayed, resulting in sexual maturation of the individual with retention of larval traits (i.e., the larval morphology) and producing paedotypic individuals. Isogenesis occurs when similar early larvae follow different developmental trajectories but ultimately produce similar adults. The adults are termed isotypic individuals. Figure courtesy of S. M. Reilly.

Isomorphosis and isogenesis refer to a developmental process in which a trait is identical to the trait in the ancestral species or individuals, respectively, but the developmental pathway is different. For isomorphy or isogenesis to occur, development must undergo two or more heterochronic processes in order to ‘‘counteract’’ differences in developmental timing and speed. The various species of the salamander *Desmognathus* display direct and indirect development with variable durations of embryogenesis, yet adult morphology (head shape, skull, and hypobranchial architecture) is nearly identical, exemplifying isomorphosis. Isogenesis occurs in *A. talpoideum* when adult terrestrial morphology is identical in those individuals that have undergone a typical developmental pattern and in those individuals that were paedogenetic (Fig. 2.2).

Embryonic Lifestyles

Protective Barriers

Tetrapod zygotes have barriers to protect them from predation by micro- and macroorganisms, from physiological challenges, and from abiotic physical threats. For those amphibians and reptiles with internal development, whether intra- or extrauterine, the parent's body provides the shield. However, for externally deposited zygotes, a protective barrier must be deposited around the ova before they are released to the outside. Amphibians encase their gametes in several mucoprotein and mucopolysaccharide layers which can be penetrated by the sperm in the cloaca or immediately upon shedding. These layers form the gelatinous capsules and egg masses of amphibians (Fig. 4.4). Reptiles, which have internal fertilization, can encase their zygotes in a fibrous capsule that is made even more durable by the addition of calcium salts, thereby producing the calcareous shells (Packard and DeMarco, 1991). Additional details of protective barriers are in Chapter 4.

Larvae—Free-Living Embryos

The diversity of amphibian larval morphology equals the diversity of the adult stages. Most larvae feed during their free-living developmental period; however, some do not eat and depend upon the yolk stores of the original ovum (Townsend and Stewart, 1985). Caecilian and salamander larvae resemble their adult stages in general appearance and anatomical organization (Fig. 2.3). Their transition (metamorphosis) from embryonic larva to nonembryonic juvenile is gradual with only minor reorganization. In contrast, the anuran larva (tadpole) undergoes a major reorganization during its metamorphosis from embryo to juvenile because the tadpole is anatomically different from the juvenile and adult.

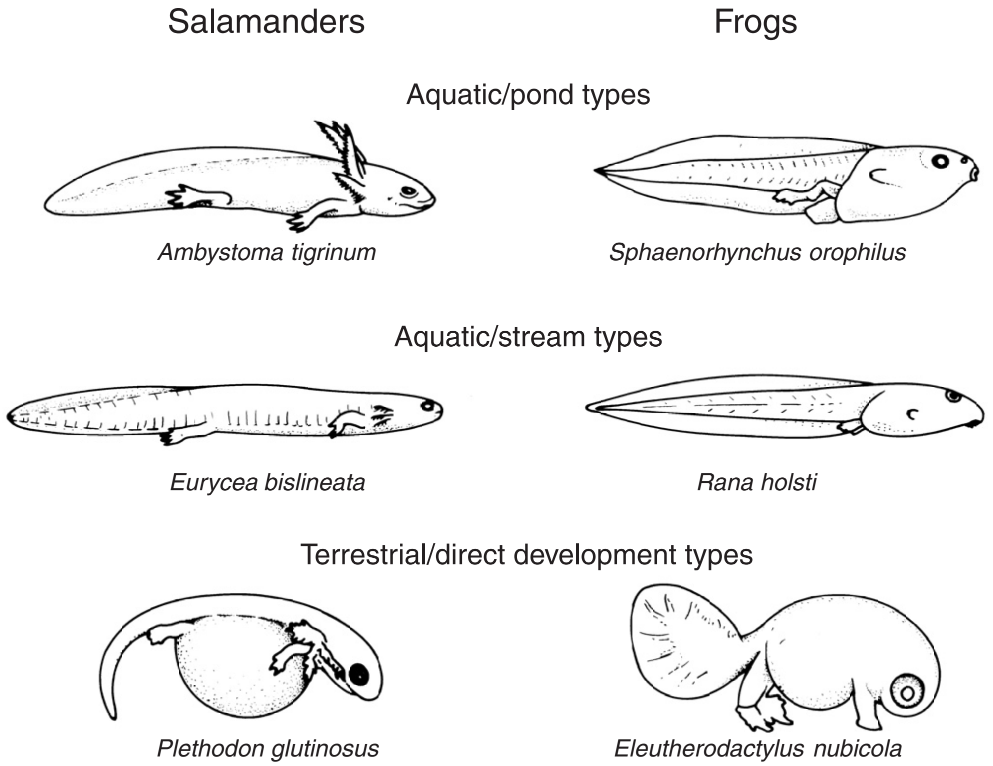


FIGURE 2.3 Body forms of some amphibian larvae arranged by habitat type.

With few exceptions, larvae of the three amphibian groups are aquatic. All share anatomical characteristics associated with an aquatic existence. They have thin, fragile skin consisting of two or three epidermal layers. The skin is also heavily vascularized owing to its role as a major respiratory surface, a role shared with the gills. All amphibian larvae develop pharyngeal slits and external gills—usually three pairs that project from the outside of the pharyngeal arches. The external gills persist and function throughout the larval period in salamanders, basal anurans, and caecilians. In tadpoles of neobatrachian frogs, external gills are resorbed and replaced by internal gills, which are lamellar structures on the walls of the pharyngeal slits. All larvae have lidless eyes and large, nonvalvular nares. They have muscular trunks and tails for undulatory swimming, and the tails have dorsal and ventral fins. The skeleton is entirely or mainly cartilaginous. All have well-developed lateral line systems.

Caecilian and salamander larvae are miniature adult replicates, differing mainly by their smaller size, pharyngeal slits and gills, tail fins, a rudimentary tongue, and specialized larval dentition. In contrast, the body plan of the anuran tadpole bears little similarity to the adult's. In general, tadpoles are well designed for consuming food and growing; the most salient feature of the body is a large coiled intestine. Mouth and eyes are present at one end and a muscular tail at the other end. Functional limbs do not appear until late in larval life and then only the hindlimbs are visible externally. The front limbs develop at the same time as the hindlimbs, but they are enclosed within the operculum and emerge only at metamorphosis.

The general tadpole body form has been modified into hundreds of different shapes and sizes (Altig and Johnston, 1986), each adapted to a specific aquatic or semiterrestrial habitat and feeding behavior. This diversity has been variously partitioned. Orton's (1953) classic division recognized four basic body plans; her morphotypes defined the evolutionary grade of the tadpole and to some extent its phylogenetic relationships. Another approach is to examine the relationship between the tadpole's morphology and its ecological niche. One such analysis defined 18 ecomorphological guilds, which, with their subcategories, recognized 33 body types; these morphotypes define a tadpole's adaptive zone but not its phylogenetic relationships (Altig and Johnston, 1989). Both classifications emphasize external, oral, and pharyngeal morphology.

Most tadpoles have a large, fleshy disc encircling their mouth. Depending on the manner of feeding and the type of food, the oral disc ranges in position from ventral horizontal (suctorial, to anchor in swift water and scrape food off rocks) to dorsal horizontal (grazing on surface film in calm water) and in shape from round to dumbbell.

The margin of the disc is variously covered with papillae, and these have a variety of shapes. Their actual function remains uncertain, although chemosensory, tactile, and current detection are some possibilities. Tadpoles lack teeth on their jaws; instead many tadpoles have keratinous jaw sheaths (beaks) and parallel rows of keratinous labial teeth on the oral disc above and below the mouth. The jaw sheaths serve to cut large food items into smaller pieces; the rows of labial teeth act as scrapers or raspers to remove food from rock and plant surfaces. The oral-pharyngeal cavity is large. Its structures trap and guide food into the esophagus, as well as pump water through the cavity and across the gills. The gills are initially visible externally, but at hatching or shortly thereafter, an operculum grows posteriorly from the back of the head to fuse to the trunk, enclosing the gills and the developing forelimbs. To permit water flow, one or two spiracles remain open on the posterior margin of the operculum. Since the operculum covers the gill region, the head and body form a single globular mass. Adhesive glands are transient structures present near the mouth in early embryonic stages at the time of hatching. The glands secrete a sticky substance that tadpoles use to adhere to their disintegrating egg mass or to some structure in the environment. Because of the fragility of the newly hatched larvae, adherence provides stability for the larva until the oral disc and tail musculature develop fully and locomotion becomes possible.

FIGURE 2.4 Embryos of *Eumeces fasciatus* inside of eggs. Shown are developmental stages 39 (upper) and 40 (lower). Photographs by James R. Stewart.

Life in an Eggshell

The eggshell protects the reptile embryo, but in so doing, it imposes special costs on embryo growth and physiology. An amphibian larva can grow to near adult size before metamorphosing, although most do not. A reptile in an egg shell is limited in size to what can fit inside the shell, and egg size is limited by the size and structure of the female and her life history parameters (see "Life Histories" in Chapter 5). By folding and curling (Fig. 2.4), the reptile embryo can attain surprising lengths, but it is still smaller than would be possible outside a shell. Most reptile hatchlings are, however, heavier than the mass of the original ovum. Metabolism of the yolk uses water absorbed through the shell, and the embryo grows beyond the original gamete mass.

Just as temperature, water availability, and gas exchange affect physiological processes of juveniles and adults, they also have the greatest impact on developing eggs (Packard et al., 1977; Packard and Packard, 1988). Eggs are not laid randomly in the environment; females select sites that offer the greatest potential for egg and hatchling survival. Oviposition site selection has been honed by natural selection over generations of females. Nevertheless, the abiotic and biotic environment is extremely variable, and eggs and their enclosed embryos must tolerate and respond to these varying conditions. A few examples can illustrate the breadth of nesting environments and egg—embryo physiological responses.

Temperature tolerances of embryos lie typically within the tolerance range of the juveniles and adults of their species, but because the rate of development is temperature-dependent and eggs lack the mobility to avoid extremes, exposure to extremes is likely to be fatal. At low temperatures, development is slowed and hatching is delayed, resulting in emergence at suboptimal times or embryos that never complete development. At high temperatures, the embryo's metabolism increases exponentially so that yolk stores are depleted before development is completed, and of course, either extreme can be directly lethal by damaging cells and/or disrupting biochemical activity. The selection of protected oviposition sites potentially avoids the extremes of temperature and provides a stable temperature environment. But, temperatures do fluctuate within and among nests, as demonstrated by the occurrence of skewed sex ratios among clutches of hatchlings owing to their temperature-dependent sex determination (see Chapter 5).

Moisture is no less critical for the proper development and survival of reptile embryos than it is for amphibians; however, amphibians typically require immersion in water, whereas immersion of most reptile eggs results in the suffocation of embryos. The embryos do not drown; rather, the surrounding water creates a gaseous-exchange barrier at the shell water interface, and the small amounts of gases that cross are inadequate to support cellular metabolism. The Australian sideneck turtle *Chelodina rugosa* avoids this dilemma, even though females lay their eggs in submerged nests (Kennett et al., 1993a). Once the eggs are laid, development stops. Developmental arrest typically occurs in the gastrulation phase and embryogenesis begins only when the water disappears and the soil dries, permitting the eggs and/or the embryos to respire. The relative availability of water affects the rate of development and absolute size of the hatchlings, at least in turtles. *Chrysemys picta* eggs in high-moisture nests hatch sooner and produce larger hatchlings than those from nests with lower moisture (Packard et al., 1991). This phenomenon and related ones likely occur in other reptile species because developmental abnormalities have been observed in snake hatchlings that experience dehydration as embryos.

Adequate gas exchange is an unlikely problem for species that lay or attach their eggs openly in cavities or crevices (e.g., many geckos), but for the majority of reptiles that bury their eggs, adequate gas exchange can be critical. Changes in soil permeability affect the diffusion of air, drier soils having the highest diffusion rates and wet soils the lowest. Similarly, the friability of soils and associated aspects of particle size and adhesiveness influence the movement of gas through the soil. In selecting a nesting site, a female must balance her ability to dig an egg chamber with the presence of adequate moisture to prevent desiccation and yet not retard gaseous diffusion, as well as a multitude of other factors.

Changing Worlds—Metamorphosis, Hatching, and Birth

Metamorphosis

Metamorphosis in amphibians is the transformation of the larva to a miniature adult replicate, and usually from an aquatic to a terrestrial or semiterrestrial life. It signals the completion of embryogenesis. Some developmental processes, such as maturation of gonads, continue through the juvenile stage, but the major structural and physiological features are in place at the conclusion of metamorphosis. Metamorphosis is nearly imperceptible in caecilians and salamanders but dramatic in frogs (Table 2.3). Anuran larvae require major structural and physiological reorganization because of the striking

TABLE 2.3 Anatomical Changes Accompanying Metamorphosis in Frogs and Salamanders

Frogs	Salamanders
Buccal Region	
Major remodeling	Slight remodeling
Oral disk with papillae and keratinous denticles; beak disappears	
Jaws elongate, enlarging mouth, and teeth develop	Teeth change from bicuspid to monocuspid
Buccal musculature reorganized	
Tongue muscles develop	Tongue muscles develop
Pharyngeal region	
Remodeling with shortening of the pharynx	
Gills and pharyngeal slits disappear	Gills and pharyngeal slits disappear
Rearrangement of aortic arches	Rearrangement of aortic arches
Modification of hyoid and segments of the branchial skeleton for tongue support	Modification of hyoid and segments of the branchial skeleton for tongue support
Viscera	
Lung development completed	Lung development completed
Stomach develops	Digestive tube modified slightly
Reduction of intestine and change of digestive epithelium	
Reduction of pancreas	
Pronephros kidney disappears	Pronephros kidney disappears
Skin	
Number of epidermal cell layers increases	Number of epidermal cell layers increases
Pigmentation and pattern change	Pigmentation and pattern change
Skeleton	
Ossification moderate to strong	Ossification slight to moderate
Major remodeling of cranial skeleton	Little change in cranial skeleton
Loss of tail; development of urostyle	
Sense organs	
Protrusion of eyes with development of eyelids	Protrusion of eyes with development of eyelids
Remodeling of eye and growth of eye muscles	
Development of stapes in middle ear	

Source: Hourdry and Beaumont (1985).

Note: These structural changes represent only a portion of anatomical changes occurring during metamorphsis.

differences between the larval and the juvenile/adult stages. Change does not occur all at once but gradually, each step leading to next level of transformation. Unlike insect pupae, metamorphosing tadpoles remain active, capable of avoiding predators and environmental stresses.

During much of larval life, growth is emphasized over morphogenesis. Morphogenesis is greatest in the early stages and then slows for caecilian and salamander larvae. Frog larvae similarly undergo major development changes in their early stages, but they also display distinct structural changes throughout larval life (Fig. 2.5). Larval life span is variable—from less than 20 days in some spadefoot toad populations to several years in other frogs and salamanders. The duration is species specific and genetically fixed, but not rigidly so. Metamorphosis marks the beginning of the end of larval life; once begun, metamorphosis usually proceeds rapidly. Rapidity is necessary to reduce the transforming amphibian's exposure to predation or other potential stresses when it is neither fully aquatic nor fully terrestrial (Werner, 1986).

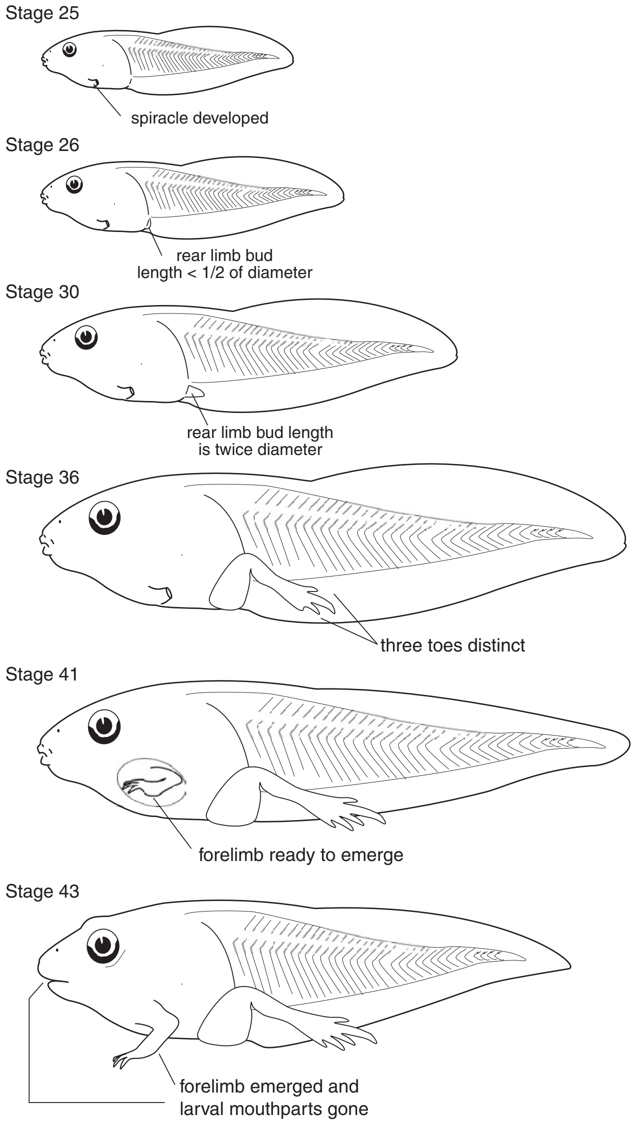


FIGURE 2.5 Selected larval stages of a typical anuran. Stage terminology from Gosner (1960).

Metamorphosis is initiated internally by the hormone thyroxine, but environmental factors can initiate early thyroxine release if a larva has completed certain morphogenic events. For example, crowding, reduced food or oxygen, drying up of water, or increased predation can result in thyroxine release (Denver, 1997). Although thyroxine and its derivatives promote metamorphosis, they do not operate alone. The thyroid is present early in larval life, but its secretory activity is apparently inhibited by corticoid hormones, such as corticosterone (Hayes, 1997b). Furthermore, prolactin is abundant in early larval stages and makes the body tissues insensitive to thyroxin. When these inhibitions are removed, thyroxin prepares the organs and tissues for their transformation and regulates their transformation.

Hatching and Birth

In amphibians, the timing of hatching depends upon the life history. For those species with larvae, hatching occurs early in embryogenesis, typically at Gosner stage 17, and for those species with direct-developing embryos, hatching occurs at the completion of development. Direct-developing embryos do not pass through a major metamorphic event. Exit from the egg in either situation requires penetration of the gelatinous egg capsules. The actual hatching mechanism is known only for a few species, but because these all share ‘‘hatching’’ glands on the snout and head of the larvae, the mechanism is probably common to most other amphibians. These glands secrete proteolytic enzymes that weaken and dissolve the capsules, allowing the larvae or juvenile to escape. Froglets in the genus *Eleutherodactylus* are assisted by an egg tooth, a bicuspid structure located on the upper lip. Stage 15 embryos use the structure to slice through the tough outer egg capsules. The structure sloughs off within two days after hatching (Townsend and Stewart, 1985). Birth, whether from an intrauterine or extrauterine situation and whether as a larval or juvenile neonate, appears to be triggered by a combination of maternal hormonal activity and embryonic/fetal secretions.

Birth in reptiles appears to be triggered largely by maternal hormonal activity, although a maternal-fetal feedback mechanism plays an essential role in the female's hormonal cycles. Hatching in reptiles requires the penetration of the amnionic membranes and the eggshell (Fig. 2.6). Reptiles use a projection on the tip of the snout to break through these two enclosures. In turtles, crocodylians, and *Sphenodon*, the projection is a keratinous protuberance, the egg-caruncle, which slices through the encasing layers. Crocodilians and turtle embryos extract calcium from the eggshell during their embryogenesis (Packard, 1994), and this weakening of the eggshell makes it easier to rupture. Squamates presumably lost the caruncle and replaced it with an egg tooth that projects outward from the premaxillary. Hatching is often an extended affair, requiring several hours to a day for complete emergence. A few turtles have delayed emergence, hatching in autumn but not emerging from the nest until spring (Ewert, 1985). This situation alerts us to the possibility that hatching and nest emergence are potentially separate events in other reptile species as well. Our present knowledge indicates that hatching and emergence are assisted by a parent only in crocodylians.

Growth

Growth is the addition of new tissue in excess of that required for the replacement of worn-out or damaged tissue. As a cellular process, growth rate in ectotherms depends on temperature, slowing and ceasing as temperature declines; excessive temperature also slows or halts growth because maintenance and metabolic costs exceed energy procurement. Growth is influenced by the availability and quality of food. In this respect, ectotherms have an advantage over endotherms by ceasing to grow during food shortages and renewing growth when food becomes available.

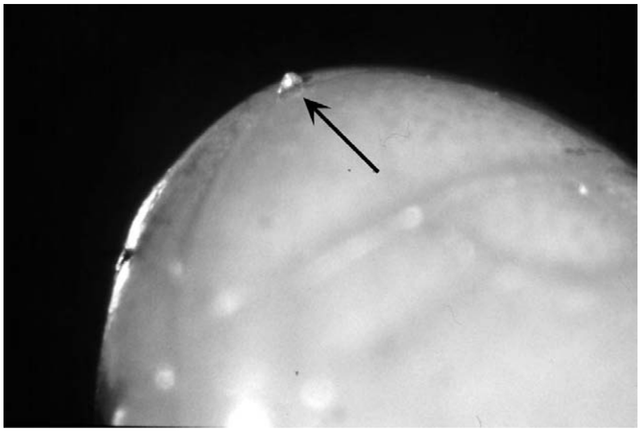


FIGURE 2.6 Photograph of the egg of a *Eumeces fasciatus* just beginning to hatch. The arrow points to the emerging egg tooth as it begins to slice through the leathery shell. Photograph by James R. Stewart.

Growth occurs primarily in the embryonic and juvenile stages of amphibians and reptiles. Embryonic growth usually is proportionately greater than juvenile growth, because embryos possess abundant, high-quality energy resources in the form of the yolk that require little energy expenditure for acquiring and processing. Juveniles and also free-living amphibian larvae face variable food supplies, often with low energy content, and must expend energy to obtain and process food while simultaneously avoiding predation and environmental hazards. From hatching or birth, most reptiles and amphibians will increase 3- to 20-fold in length, but some species may increase over 100-fold in mass. Growth may or may not continue indefinitely throughout life; data are inadequate in most cases to state whether a species has determinate or indeterminate growth.

Mechanics of Growth

All tissues grow during juvenile life, although the rate varies among tissues. Growth may be measured by changes in overall size, most often in length. Mass is more variable owing to numerous factors, such as hydration, gut contents, and reproductive state, that change an animal's weight without changing its overall length. Skeletal growth is the ultimate determinant of size because the skeleton is the animal's supportive framework. Skeletal elements of amphibians and reptiles usually lack epiphyses and grow by apposition, a process in which one layer forms on top of another. Because of these attributes, continual growth is possible and leads to the assumption of indeterminate growth in these animals. Other reasons for assuming that indeterminate growth occurs are the large sizes of individuals in some species and the continuation of growth long after sexual maturity. In contrast, growth stops soon after maturity in endotherms.

Both indeterminate (attenuated) and determinate (asymptotic) growth exist in amphibians and reptiles, but the evidence for one or the other is lacking for most species (Fig. 2.7). Indeterminate growth may be less frequent than commonly assumed. Adult size for most species lies within a narrow range, suggesting that growth ceases. Older adults of some reptilian species have fused epiphyses. The two growth patterns in natural populations are difficult to distinguish because a narrow adult size range may indicate only that high mortality truncates the growth or size potential of the species or population.

Whatever the end point, juvenile growth is rapid and slows as sexual maturity is approached. Most juvenile growth fits one of two curvilinear patterns: parabolic growth, which may begin rapidly and remain rapid for

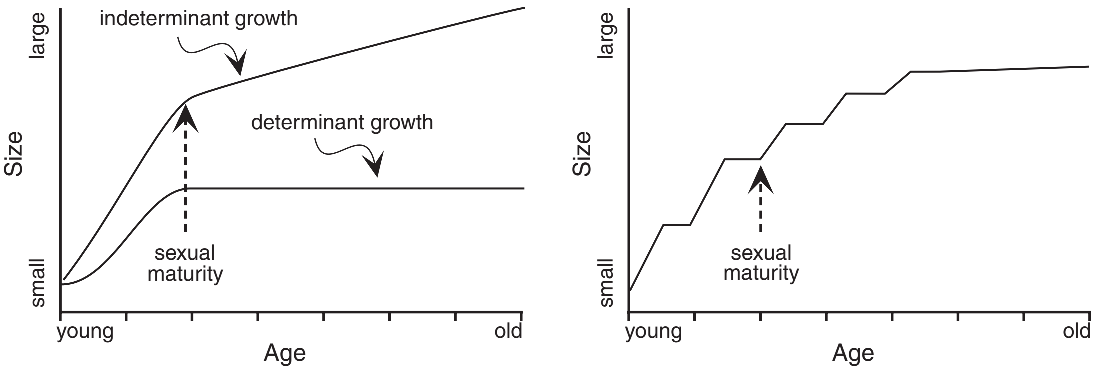


FIGURE 2.7 General growth pattern trends for amphibians and reptiles. (Left) Comparison of indeterminant and determinant growth. When growth is relatively indeterminant, constant growth rate as a juvenile is followed by slower but continuous growth once sexual maturity is reached. When growth is determinant or asymptotic, a sigmoid pattern during juvenile stages is followed by slower growth after sexual maturity and finally curtailment of growth. (Right) Hypothetical growth for an ectotherm in a seasonal environment follows a pattern of rapid growth during equable seasons and greatly reduced or no growth during adverse seasons.

most of juvenile life, or sigmoid growth, which is initially slow, becomes rapid, and then slows again. Both patterns show a plateau associated with maturity, owing to the reallocation of energy resources to reproduction (Andrews, 1982a). Individual growth curves are not smooth (Fig. 2.7), particularly in ectotherms. Growth proceeds fast or slow depending on the abundance of food, and it may halt for months at a time in species from seasonal environments, including tropical wet and dry seasons. Growth may proceed ratchetlike for the first few years of sexual maturity because energy is alternately allocated to reproduction and then to growth.

The ultimate size of an individual depends on genetic potential, size at hatching, abundance and quality of food during juvenile growth, and its sex. Heredity determines the potential range of growth rate and size or age at sexual maturity. Beginning with hatchlings of the same size, species, and sex, faster growth or longer juvenile life yields larger adults. These factors and others yield the variations in adult size within and between species.

Age

The length of time an individual lives is not as critical as the time required to reach the major life-history events of hatching or birth, sexual maturity, and reproductive senility. Reproductive periodicity, the time interval between production of offspring, although not an event, is another critical age-related aspect of an individual's life history. In amphibians with a larval stage, two intervals are critical: embryogenesis within the egg, and larval period to metamorphosis. All of these events are regularly subjected to selection within a population, and the modal condition within a population can shift.

Age at sexual maturity ranges from 4 to 6 months (*Arthroleptis poecilonotus*, an artholeptid frog; Barbault and Rodriques, 1979) to 7 years (*Cryptobranchus*, the hellbender salamander; Peterson et al., 1983) for amphibians and from 2 to 4 months (*Anolis poecilopus*, a polychrotine lizard; Andrews, 1976) to 40+ years (*Chelonia mydas*, a green seaturtle) for reptiles. These marked extremes reflect differences in adult size only in part, because not all small species mature so quickly or large ones so slowly (Table 2.4). Age of maturity is a compromise among many variables on which selection may operate to maximize an individual's contribution to the next generation. Maturing and reproducing quickly is one strategy for achieving this goal; however, small body size reduces the number and/or size of offspring and smaller adults tend to experience higher predation. Maturing later at a larger body size permits the production of more and/or larger offspring but increases the probability of death prior to reproducing, and may yield a smaller total lifetime output of offspring. The resulting diversity in size and age at sexual maturity, number and size of offspring, and frequency of reproduction illustrate the numerous options molded by natural selection for attaining reproductive success.

Longevity often indicates a long reproductive life span of an individual or species. The reproductive life span of some species is a single reproductive season, and total longevity may be as little as one year in natural populations (e.g., *Uta stansburiana*). For other species the reproductive life span can be a decade or longer and individuals may live more than half a century (e.g., *Geochelone gigantea*; Grubb, 1971). Annual or biennial species have little time for growth, so these species typically are small; the opposite is not true for the long-lived species. Although many long-lived species are large,

TABLE 2.4 Natural Longevity of Select Amphibians and Reptiles

Taxon	Adult size (mm)	Age at maturity (months)	Maximum age (months)
Cryptobranchus alleganiensis	330	84	300
Desmognathus quadramaculatus	73	84	124
Eurycea wilderae	34	48	96
Bufo americanus	72	36	60
Rana catesbeiana	116	36	96
Chrysemys picta	119	72	360
Geochelone gigantea	400	132	840±
Trachemys scripta	195	50	288
Sphenodon punctatus	180	132	420+
Cnemidophorus tigris	80	21	94
Gallotia stehlini	120	48	132+
Uta stansburiana	42	9	58
Diadophis punctatus	235	32	180+
Pituophis melanoleucus	790	34	180+

Sources: Salamanders include *Ca* (Peterson et al., 1983), *Dq* (Bruce, 1988b), Organ (1961), and *Ew* (Bruce, 1988a). Frogs include *Ba* (Kalb and Zug, 1990) and *Rc* (Howard, 1978b). Turtles include *Cp* (Wilbur, 1975a), *Gg* (Bourn and Coe, 1978; Grubb, 1971), and *Ts* (Frazer et al., 1990). Tuatara includes *Sp* (Castanet et al., 1988). Lizards include *Ct* (Turner et al., 1969), *Gs* (Castanet and Baez, 1991), and *Us* (Tinkle, 1967; Medica and Turner, 1984). Snakes include *Dp* (Fitch, 1975) and *Pmd* (Parker and Brown, 1980).

Note: Adult size is for females at sexual maturity (snout–vent length except carapace length for turtles); age of maturity is for females; and maxium age is of either sex.

some, such as the yucca ghost lizard, *Xantusia vigilis*, are tiny. Often small-bodied long-lived reptiles or amphibians have a secretive lifestyle.

INTEGUMENT—THE EXTERNAL ENVELOPE

The skin is the cellular envelope that forms the boundary between the animal and its external environment, and as such, serves multiple roles. Foremost are its roles in support and protection. The skin holds the other tissues and organs in place, and yet it is sufficiently elastic and flexible to permit expansion, movement, and growth. As a protective barrier, it prevents the invasion of microbes and inhibits access by potential parasites, resists mechanical invasion and abrasion, and buffers the internal environment from the extremes of the external environment. The skin also serves in physiological regulation (e.g., heat and osmotic regulation), sensory detection (chemo- and mechanoreception), respiration, and coloration.

Amphibian skin consists of an external layer, the epidermis, which is separated from the internal layer, the dermis, by a thin basement membrane (Fig. 2.8). The epidermis is typically two to three cell layers thick in larvae and five to seven layers thick in juvenile and adult amphibians. The innermost layer of cells (stratum germinativum) divides continuously to replace the worn outer layer of epidermal cells. The outer cell layer is alive in larvae, but in most juveniles and adults, cells slowly flatten, keratinize, and die as they are pushed outward. This layer of dead, keratinous cells (stratum corneum) shields the inner layers of living cells from injury. The dermis is a thicker layer, containing many cell types and structures, including pigment cells, mucous and granular glands, blood vessels, and nerves, embedded in a connective tissue matrix (Figure 2.8). The innermost layer of dermis is a densely knit connective tissue (stratum compactum), and the outer layer (stratum spongiosum) is a looser matrix of connective tissue, blood vessels, nerve endings, glands, and other cellular structures. In caecilians and salamanders, the stratum compactum is tightly linked with the connective tissue sheaths of the muscles and bones. In contrast, much of the body skin is loosely attached in frogs.

The skin of reptiles has the same cellular organization as in amphibians. Notably, the epidermis is thicker with numerous differentiated layers above the stratum germinativum. The differentiation produces an increasingly thick, keratinous cell membrane and the eventual death of each cell. This basic pattern is variously modified among reptilian groups and occasionally among different parts of the body of the same individual. Reptiles uniquely produce β-keratin as well as α-keratin, which they share with other vertebrates. β-keratin is a hard and brittle compound, whereas α-keratin is elastic and pliable.

On all or most of the body, the skin is modified into scales. The scales are termed plates, scutes, shields, laminae, lamellae, scansors, or tubercles, depending upon the taxonomic group, the size and shape of the scales, and the location of the scales on the body. Some names are interchangeable, whereas others refer to specific structures. For example, scutes are the same as shields, but scansors are scales or lamellae beneath the digits that allow geckos to cling to nonhorizontal surfaces. All reptilian scales are keratinized epidermal structures, but those of the lepidosaurs are not strict homologues of crocodylian and turtle scales. Scales commonly overlap in squamates but seldom do in crocodylians and turtles.

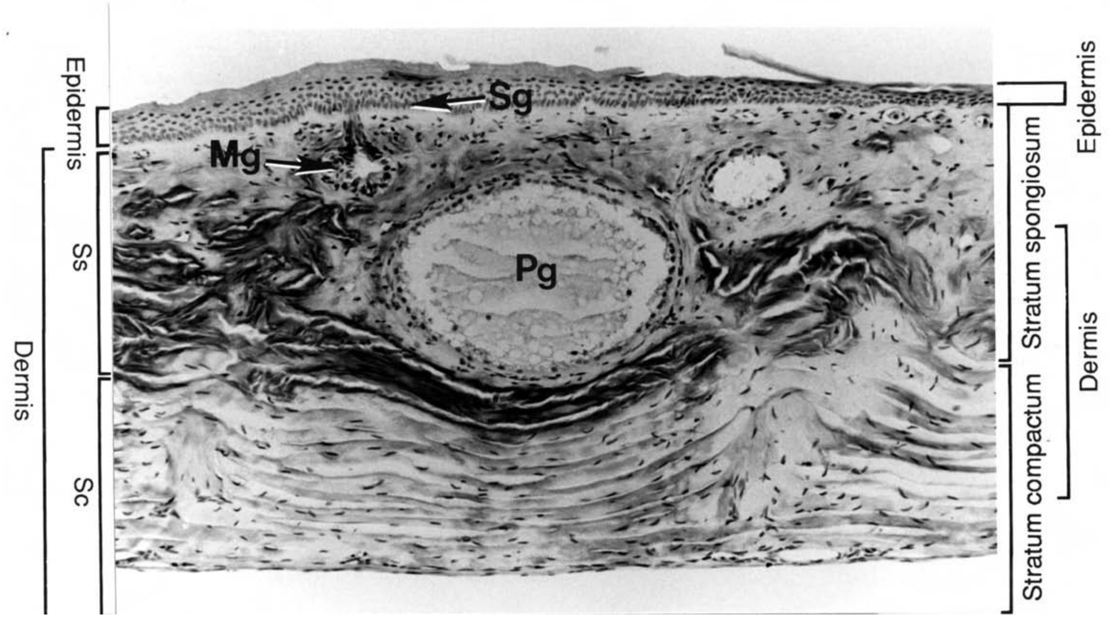


FIGURE 2.8 Cross section through the ventral skin of a marine toad *Bufo marinus.* Abbreviations are Mg, mucus gland; Pg, poison or granular gland; Sc, stratum compactum; Sg, stratum germinativum; and Ss, stratum spongiosum.

Two patterns of epidermal growth occur. In crocodylians and turtles, the cells of the stratum germinativum divide continuously throughout an individual's life, stopping only during hibernation or torpor. This pattern is shared with most other vertebrates, from fishes to mammals. A second pattern, in which growth is discontinuous but cyclic, occurs in lepidosaurs (Fig. 2.9). Upon shedding of the outer epidermal sheath (Oberhautchen), the germinative cells enter a resting phase with no mitotic division. The renewal phase begins with the synchronous division of the germinative cells and the differentiation of the upward moving epithelium into two distinct layers separated by a narrow layer of cell secretions.

The surface of each reptilian scale is composed entirely of β-keratin, and the interscalar space or suture is composed of α-keratin. This distribution of keratin produces a durable and protective scale surface with junctures

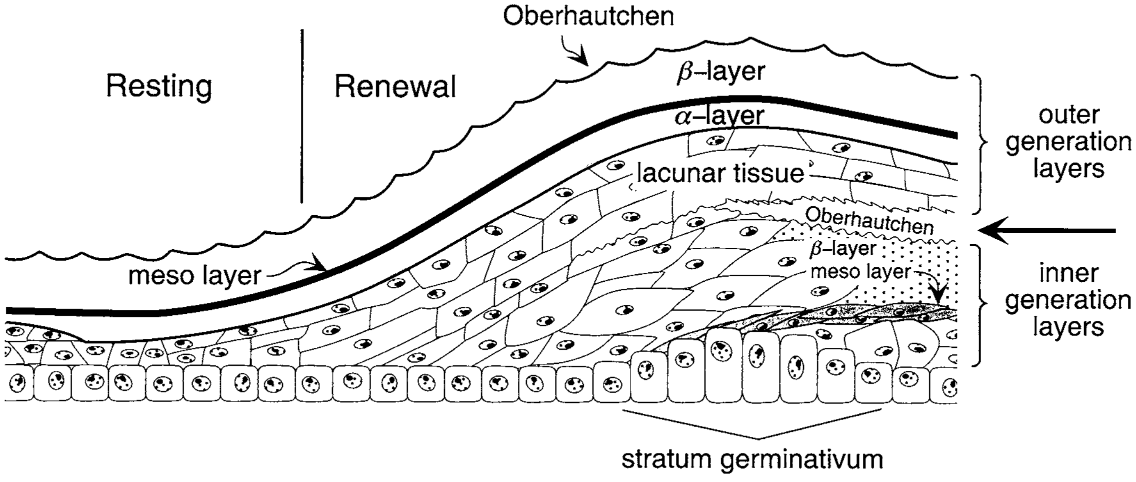


FIGURE 2.9 Diagram of the sequential cellular changes during a single shedding cycle in squamate epidermis. Adapted from Landmann (1986).

between the scales that allow flexibility and expansion of the skin. Although the preceding pattern is typical, the scales on the limbs of some turtles have surfaces composed of α-keratin, and in softshell and leatherback turtles the surface of the shell is composed of α-keratin. In most of the hard-shelled turtles, the scutes and sutures contain only β-keratin. The two-layered epidermis of the lepidosaurs has an α-keratin inner layer and a β-keratin Oberhautchen.

An anomaly of special interest is the occurrence of nearly scaleless individual snakes in several species of colubrids and viperids (Bechtel and Bechtel, 1991). Only the labial and ventral scales are usually present. The remainder of the skin is a smooth sheet of soft, keratinous epidermis. Genetically, scalelessness appears to be a simple Mendelian homozygous recessive trait.

Integumentary Structures

Amphibian Glands and Skin Structures

Amphibians possess several types of epidermal glands. Mucous and granular (poison) glands occur in all postmetamorphic (i.e., juvenile and adult) amphibians and are numerous and widespread on the head, body, and limbs (Fig. 2.8). Both types are multicellular, flask-shaped glands with the bulbous, secretory portion lying within the stratum spongiosum of the dermis; their narrow necks extend through the epidermis and open on its surface. Although occurring over the entire body, the glands are not evenly distributed; their role determines their density and location. Mucous glands are the most abundant; about 10 of them are present for every granular gland. The mucous glands are especially dense dorsally, and they continuously secrete a clear, slimy mucus that maintains a thin, moist film over the skin. The granular glands tend to be concentrated on the head and shoulders, where their poisonous or noxious secretions will be immediately encountered by predators. The granular glands may be aggregated into macroglands, such as the parotoid glands of some frogs and salamanders. Usually these macroglands contain more complex individual glands.

Larvae have a greater variety of epidermal glands. Most are single-celled (unicellular) glands, although many may be concentrated in a single region. For example, the hatching glands are clustered on the dorsal forepart of the head. Unicellular mucous glands are widespread and secrete a protective mucous coat over the surface of the living epidermis. This mucous coat also serves as a lubricant to enhance the flow of water over the larva when swimming. Merkel and flask cells are scattered throughout the larval epidermis, but they are not abundant in any region. Their functions are uncertain. Merkel cells might be mechanoreceptors, and flask cells may be involved in salt and water balance.

The skin of amphibians ranges from smooth to rough. Some of the integumentary projections are strictly epidermal, but most involve both the epidermis and the dermis. Integumentary annuli of caecilians and costal grooves of salamanders match the segmentation of the axial musculature and vertebral column. Each primary annulus and each costal groove lies directly over the myosepta (connective tissue sheet) between the muscle masses; thus, the number of annuli equals the number of trunk vertebrae. In caecilians, this annular pattern can be complicated by the development of secondary and tertiary grooves; the secondary ones appear directly above the myosepta. The warts, papillae, flaps, tubercles, and ridges in frogs and salamanders may be aggregations of glands or simply thickenings in the underlying dermis and epidermis.

Although amphibians lack epidermal scales, they do possess keratinous structures. The clawlike toe tips of pipid frogs, the spades of pelobatid frogs, and the rough, spiny skin of some frogs and salamanders are keratinous. These structures persist year around; other keratinous structures are seasonal and usually associated with reproduction. Many male salamanders and frogs have keratinous nuptial pads on their thumbs at the beginning of the mating season; some even develop keratinous spines or tubercles on their arms or chests. Usually at the end of the mating season, these specialized mating structures are shed, developing repeatedly in subsequent breeding seasons.

Dermal scales exist only in caecilians, although not in all species. These scales are flat, bony plates that are buried deeply in pockets within the annular grooves. Whether these scales are homologues of fish scales remains uncertain. A few species of unrelated frogs, for example, some species of *Ceratophrys* and *Megophrys*, have osteoderms (bony plates) embedded in or immediately adjacent to the dermis (Ruibal and Shoemaker, 1984). Also in some species of frogs, the dorsal skin of the head is compacted and the connective tissue of the dermis is co-ossified with the skull bones, a condition known as exostosis.

Reptilian Scales, Glands, and Skin Structures

The scales of crocodylians, turtles, and some lizards (e.g., anguids, cordylids, scincids) are underlain by bony plates, called osteoderms or osteoscutes, in the dermis. The bony organization of the osteoderms matches the organization of the dermis. The outer layer is spongy, porous bone; the inner layer is compact, dense bone. Usually osteoderms are confined to the back and sides of the animal and attach loosely to one another in symmetrical rows and columns to permit flexibility while maintaining a protective bony armor. In crocodylians and a few lizards (*Heloderma*), the osteoderms fuse with the dorsal skull elements, forming a rigid skull cap. The carapace and plastron, upper and lower shells of turtles, respectively, arose from the fusion of osteoderms with vertebrae and ribs dorsally, and osteoderms and the sternum ventrally.

Reptiles have a variety of skin glands. Although common over the body, the small and inconspicuous glands are typically multicellular. Their secretions are mainly lipid- and wax-based compounds that serve as waterproofing, surfactant, and pheromonal agents.

Aggregations of glandular tissues occur in many reptiles. Musk or Rathke's glands are present in all turtles except tortoises (Testudinidae) and the pseudemyd turtles. These glands are usually bilaterally paired and lie within the bridge between the top and bottom shells, opening to the outside through individual ducts in the axilla and inguen or on the bridge. Male tortoises have a mental gland just behind the tip of the lower jaw. Both male and female crocodylians have paired mandibular and cloacal glands. The occurrence of large glands is more erratic in lepidosaurs. Some geckos and iguanians have a series of secretory pores on the underside of the thighs and pubis. Each pore arises from the center of an enlarged scale and extrudes a waxy compound containing cell fragments. These femoral and precloacal (pubic) pores do not open until the lizards attain sexual maturity and often occur only in males. They may function as sexual scent glands, although this remains unconfirmed. Snakes and some autarchoglossan lizards have paired scent glands at the base of the tail; each gland opens at the outer edge of the cloacal opening. These saclike glands release copious amounts of semisolid, malodorous fluids. For some species, the fluid may serve in defense, whereas in other situations, they may function for sexual recognition. Other glandular aggregations occur but are limited to a few reptiles. For example, a few Australian geckos have specialized squirting glands in their tails, and some marine and desert species of turtles, crocodylians, and lepidosaurs have salt glands.

Specialized keratinous structures are common in reptiles. All limbed species with functional digits have claws, which are keratinous sheaths that encase the tips of the terminal phalanges. The sheaths have three layers, the outermost of which is formed of hard β-keratin. The claws form either as full keratinous cones, as in crocodylians and turtles, or as partial cones as in lepidosaurs. The upper and lower jaw sheaths of turtles are also keratinous structures and replace the teeth as the cutting and crushing surfaces. Hatchling turtles, crocodylians, and *Sphenodon* have an egg caruncle on the snout to assist in hatching.

A dozen or more types of small, epidermal sense organs occur in reptiles, particularly in lepidosaurs. Most are barely visible, appearing as tiny pits or projections. These epidermal structures are not shed during the sloughing cycle. Presumably, most of these structures respond to tactile stimuli; however, the recent discovery of a light-sensitive region on the tail of a seasnake (Zimmerman and Heatwole, 1990) suggests a broader range of receptors and sensitivities. These organs are often concentrated on the head but are also widespread on the body, limbs, and tail.

Ecdysis

Adult amphibians shed their skin in a cyclic pattern of several days to a few weeks. This shedding, called ecdysis, sloughing, or molting, involves only the stratum corneum and is commonly divided into several phases. At its simplest, the shedding cycle consists of epidermal germination and maturation phases, pre-ecdysis, and actual ecdysis. These phases are controlled hormonally, although timing and mechanisms differ between species and amphibian groups. The stratum germinativum produces new cells that move outward and upward in a conveyer-belt-like fashion as new cells are produced beneath them. Once these new cells lose contact with the basement membrane, they cease dividing and begin to mature, losing their subcellular organelles. Pre-ecdysis is signaled by appearance of mucous lakes between the maturing cells and the stratum corneum. The lakes expand and coalesce, and the cellular connections between the dead cells of the stratum corneum and the underlying, maturing cells break. Externally, the skin commonly splits middorsally first over the head and then continues down the back. Using its limbs, the frog or salamander emerges from the old skin, which is often consumed. During the pre-ecdytic and/or the ecdytic phase, the epidermal cells beneath the mucous lakes complete their keratinization and die.

The shedding process of larval amphibians is not well known. In the mudpuppy *Necturus maculosus* and probably in most other larvae, the skin is shed as single cells or in small pieces. The shed skin is not keratinized and may be alive when shed. The epidermal cells mature as they are pushed to the surface, but keratinization is not part of maturation.

In reptiles, different epidermal organizations and growth patterns produce different shedding or sloughing patterns. In the epidermis of crocodylians and the nonshell epidermis of turtles, cell growth is continuous and portions of the outer surface of the skin are shed continuously in flakes and small sheets. Depending on species, the scutes of hard-shelled turtles are either retained or shed seasonally. When retained, successive scutes form a flattened pyramid stack, because an entire new scute develops beneath the older scute at the beginning of each growing season. Scute growth is not confined to the margins, although each new scute is thickest there and much compressed beneath the older scutes.

The shedding pattern in lepidosaurs is more complex and intimately tied to the unique epidermal growth pattern (Maderson, 1965; Maderson et al., 1998). In the tuataras and most lizards, the skin is shed in large patches, whereas in snakes the skin is usually shed as a single piece. But in all lepidosaurs, the sequence of epidermal growth and shedding is identical (Fig. 2.9). During the resting stage, the epidermis has a basal germinative layer of cells, a narrow band of α precursor cells, a thin mesolayer of mucus and other cell secretions, and externally the beginnings of an outer-generation layer capped by the Oberhautchen. The resting stage ends as cell proliferation and differentiation begins in the outer-generation layer. Then the germinative cells begin to divide. As each newly formed layer of cells is pushed upward and outward by cell division below them, the cells differentiate and produce the inner-generation layer. This inner-generation layer forms the precursor of the scales (outer-generation layer) for the next epidermal cycle. As the Oberhautchen nears completion, the outer-generation layer separates from the inner layer and is shed, completing the shedding or sloughing cycle. This cycle is repeated at regular intervals when food is abundant. This growth-shedding (renewal) phase requires about 14 days. The resting phase may last from a few days to many months.

Coloration

The color of amphibians is affected by the presence of pigment cells (chromatophores) in the dermal layer of the skin (Bagnara, 1986). Three classes of chromatophores include melanophores with black, brown, or red pigment; white or reflective iridophores; and xanthophores with yellow, orange, or red pigment. In addition to containing different pigments, each of the three cell types is structurally different. The three classes of chromatophores are arranged as a unit and produce an animal's external coloration. For example, the blue color of iridophores combined with the yellow color of xanthophores produces a green-colored skin.

Melanophores have a central cell body with long, attenuated processes radiating outward. Melanophores occur individually in the epidermis or as part of the dermal chromatophore unit. The epidermal melanophores (melanocytes) are common in larvae and are often lost or reduced in number at metamorphosis. The dermal chromatophore unit contains a basal melanophore, an iridophore, and a terminal xanthophore; the processes of the melanophore extend upward and over the iridophore (see Fig. 6.3). The color produced by the unit depends largely upon the color of the pigment in the xanthophore and the reflectivity of the iridophore. Melanophores are largely responsible for lightening or darkening of the color produced in the other two chromatophores. Color changes can occur quickly, in less than a minute, by dispersal or reduction of the melanin within the melanophores' processes. Increased melanin darkens the observable color of the skin, while reduced melanin allows colors produced by the iridophores and xanthophores to predominate. Slow color changes may take weeks to months and occur when pigment concentration increases or decreases within the chromatophores or when pigment is deposited in adjacent cells. Short-term color changes are controlled by hormonal or nervous stimulation.

Reptiles generally have two types of color-producing cells. Melanocytes are scattered throughout the basal layers of the epidermis. During the renewal phase of epidermal growth, the melanocytes send out pseudopodia that transfer melanin into the differentiating keratocytes. The melanin-bearing keratocytes occur in the β-layer of crocodylians, iguanian lizards, and snakes, and in the α- and β-layers in many other lizards.

The second type of cell that produces color is the chromatophore, which is structurally similar to that in amphibians. The chromatophores are stacked in the outer portion of the dermis. A single layer of xanthophores (= lipophores and erythrophores) lies beneath the basal membrane of the epidermis. Beneath the xanthophores are two to four layers of iridophores (= guanophores and leukophores), and at the bottom are large melanophores. This organization may represent the general pattern for all reptiles that change color, because stacked chromatophores are absent in some species that do not change color. The presence, density, and distribution of chromatophores within each layer vary within an individual and among species to produce the different colors and color patterns.

SKELETON AND MUSCLES—SUPPORT, MOVEMENT, AND FORM

The phyletic transition from fish to amphibian was accompanied by major reorganizations within the musculoskeletal system. As the ancestral tetrapods shifted their activities from an aquatic to a terrestrial environment, the buoyant support of water disappeared, and the pull of gravity required a strengthening of the vertebral column to support the viscera. Simultaneously, these ancient tetrapods were shifting from undulatory locomotion to limbed locomotion. The new functions and demands on the musculoskeletal system required a more tightly linked vertebral column, elaboration of the limbs and girdles, and modification of the cranium for capture and ingestion of terrestrial food. As in amphibians, the reptilian musculoskeletal system is adapted primarily for terrestrial limbed locomotion, and some species are secondarily modified for aquatic or terrestrial limbless locomotion. With the exception of turtles, reptiles retain considerable lateral flexure of the body and only in archosaurs does dorsoventral flexure become an important component of locomotion.

Each amphibian group has had a long and independent evolutionary history. Many structural differences appeared during this long divergence, and these differences are nowhere more apparent than in the composition and organization of the musculoskeletal system. Similarly, the long independent evolution of each reptilian group is strongly evident in all aspects of their musculoskeletal system. This great diversity permits only a general survey.

Head and Hyoid

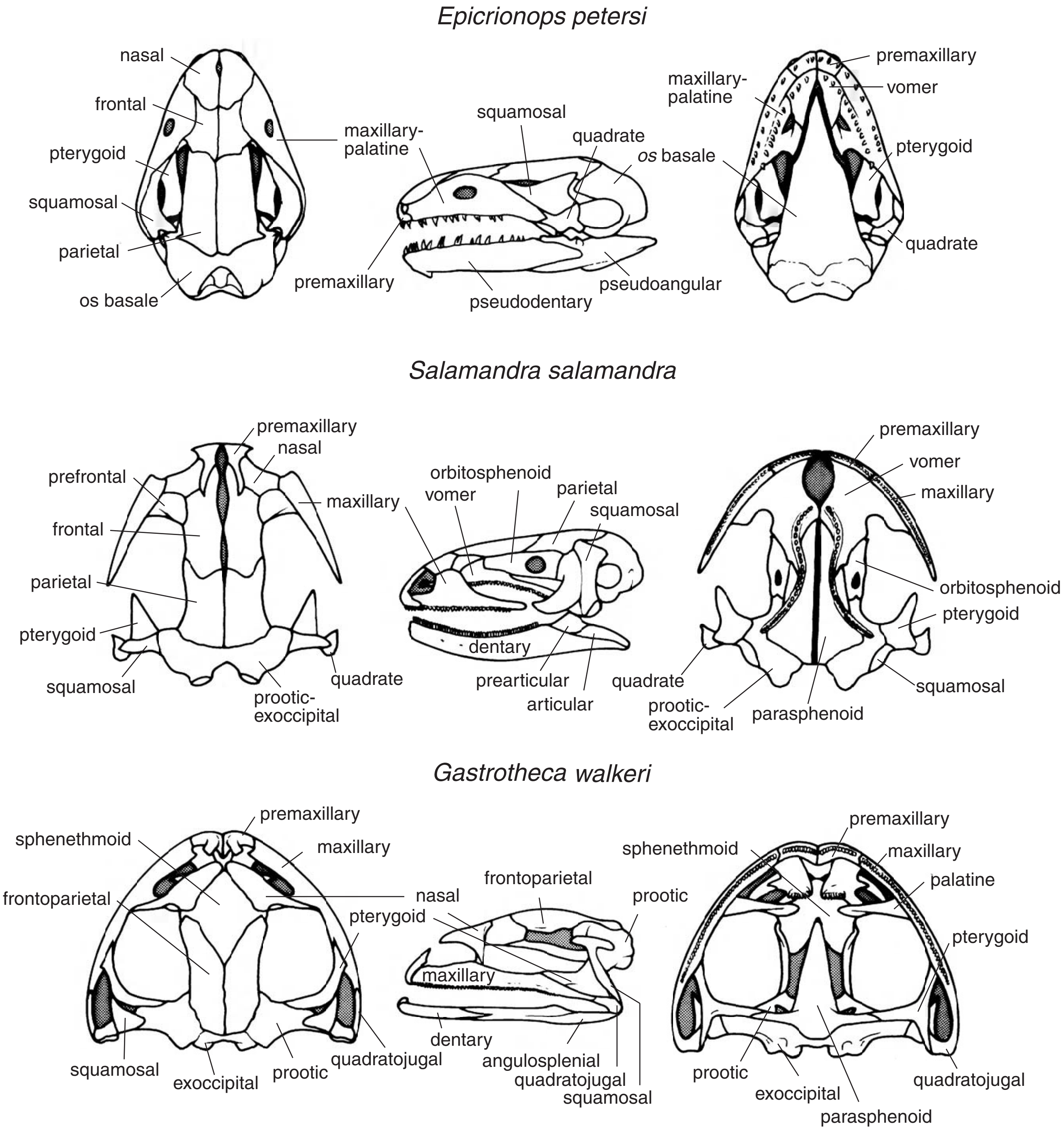
The cranial skeleton of vertebrates contains elements from three units: the chondrocranium, the splanchnocranium, and the dermocranium. The chondrocranium (neurocranium) comprises the skeleton surrounding the brain and the sense organs, that is, the olfactory, optic, and otic capsules. The splanchnocranium is the branchial or visceral arch skeleton and includes the upper and lower jaws, the hyobranchium, and the gill arches and their derivatives. Most elements from these two cranial skeletons appear first as cartilage. The cartilaginous precursors define the position of the later developing bony element. Bone formed by replacement of cartilage is called replacement or endochondral bone. The dermocranium contains the roofing elements that lie external to the chondro- and splanchnocranial elements. These roofing elements have no cartilaginous precursors; instead, ossification centers develop in the dermis and form dermal or membrane bones.

All three crania are represented by numerous skeletal elements in fish and in the fish ancestors of amphibians. The earliest amphibians showed a loss of elements from each of the crania and a firmer articulation of the remaining elements. The reduction has continued in the modern tetrapod clades, which have lost additional, but often different, elements in each group. Fewer elements have been lost in the caecilians, in which the skull is a major digging tool and must remain sturdy and firmly knit, often by the fusion of adjacent elements.

In extant amphibians, much of the chondrocranium remains cartilaginous throughout life (Fig. 2.10). Only the sphenethmoid (orbitosphenoid in salamanders), which forms the inner wall of the orbit, and the fused prootic and exoccipital, which form the rear of the skull, ossify. Within the skull proper, the bony elements of the splanchnocranium are the stapes (ear) and the quadrate (upper jaw). Meckel's cartilage forms the core of the mandible (lower jaw), and ossification in its anterior and posterior ends form the mentomeckelian bone and articular, respectively. The dermal bones form the major portion of the adult skull, linking the various cranial elements and forming a protective sheath over the cartilaginous elements, the brain, and the sense organs. The skull is roofed from its anterior to its posterior by the premaxillae, nasals, frontals, and parietals; each side of the skull contains the maxilla, septomaxilla, prefrontal, and squamosal. Dermal bones also sheath the skull ventrally, creating the primary palate (roof of mouth). The palate consists of vomers, palatines, pterygoids, quadratojugals, and a parasphenoid, which is the only unpaired dermal bone in the amphibian skull. The dermal bones of the mandible are the dentary, angular, and prearticular, which encases Meckel's cartilage. Teeth occur commonly on the premaxillae, maxillae, vomers, palatines, and dentaries.

The jaws of vertebrates arose evolutionarily from the first visceral or branchial arch. The second visceral, hyomandibular, arch supported the jaws and bore gills, and the third and subsequent visceral arches composed the major gill arches. Remnants of these arches remain in modern amphibians. The jaws consist mostly of dermal bones; only the mentomeckelian, articular, and quadrate are bony remnants of the first arch. The quadrate becomes part of the skull proper, and the dorsalmost element of the hyomandibular arch becomes the stapes for transmission of sound waves from the external eardrum, the tympanum, to the inner ear. The ventral portion of the second arch persists as part of the hyoid apparatus. The subsequent two to four visceral arches may persist, at least in part, as gill arches in larvae and in some gilled adults (e.g., Proteidae), and also as elements of the hyoid in juveniles and adults. Some elements from the more posterior visceral arch become structural supports in the glottis, larynx, and trachea.

The composition and architecture of the hyoid is highly variable within and between each group of living amphibians. However, in all, the hyoid lies in the floor of the mouth and forms the structural support for the tongue. In some species, the components of the hyoid can be traced accurately to their visceral arch origin; in others species, their origin from a specific arch element is uncertain. The hyoid elements in primitive salamanders retain an architecture similar to that of the visceral arches



Epicrionops petersi

Salamandra salamandra

Gastrotheca walkeri

FIGURE 2.10 Cranial skeletons of representatives of the three clades of extant amphibians. Dorsal, lateral, and ventral views (left to right) of the caecilian *Epicrionops petersi*, the salamander *Salamandra salamandra*, and the frog *Gastrotheca walkeri*. Reproduced, with permission, from Duellman and Trueb (1986).

of fishes, but with the loss of arch elements (Fig. 2.11). In more advanced salamanders, the number of hyoid elements is further reduced. The hyoid remains cartilaginous in caecilians without segmentation of hyoid arms into individual elements (Fig. 2.11). The anuran hyoid is a single cartilaginous plate with two to four processes and has little resemblance to its visceral arch precursor (Fig. 2.11).

The cranial musculature contains one functional group for jaw movement and another for respiring and

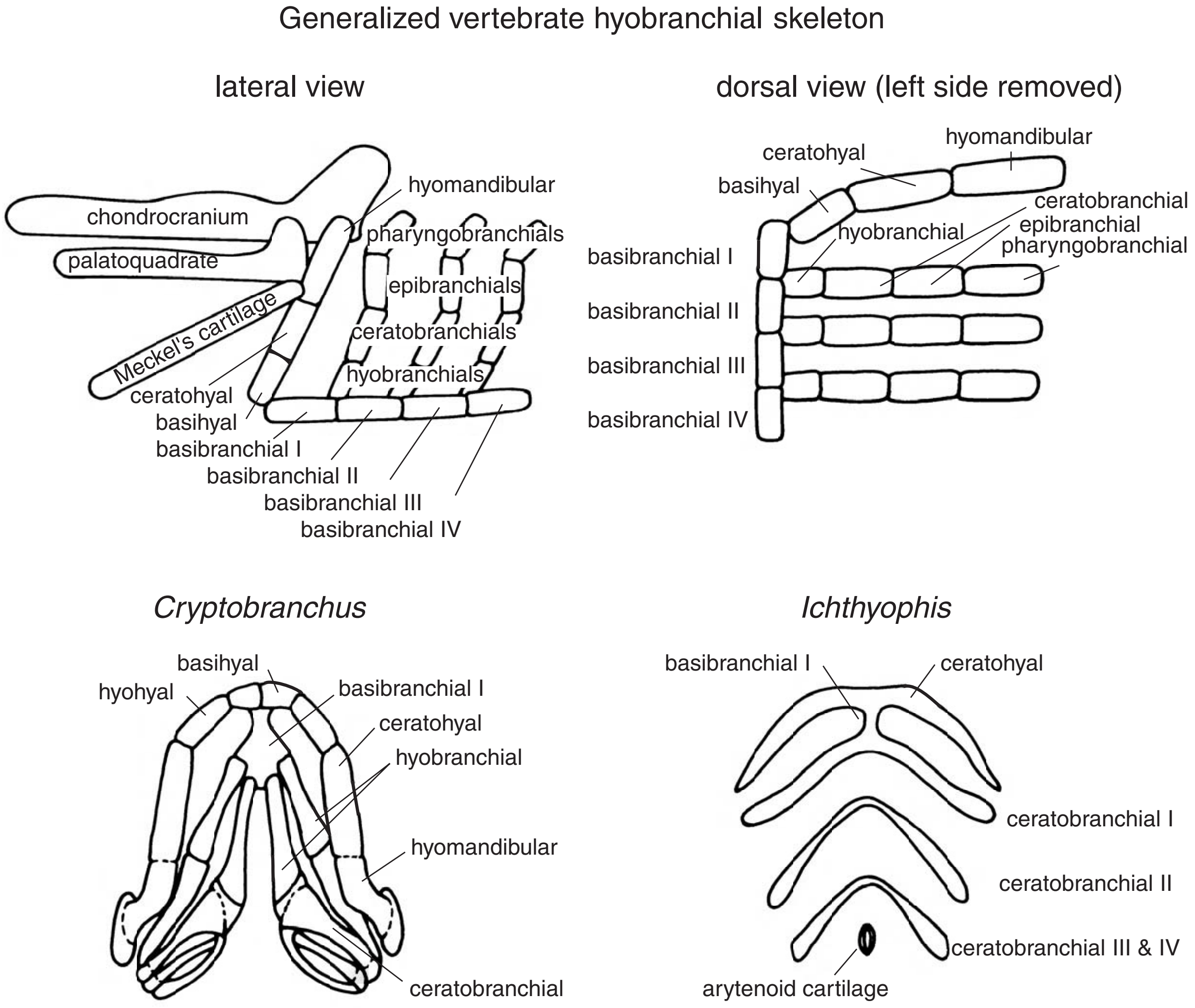
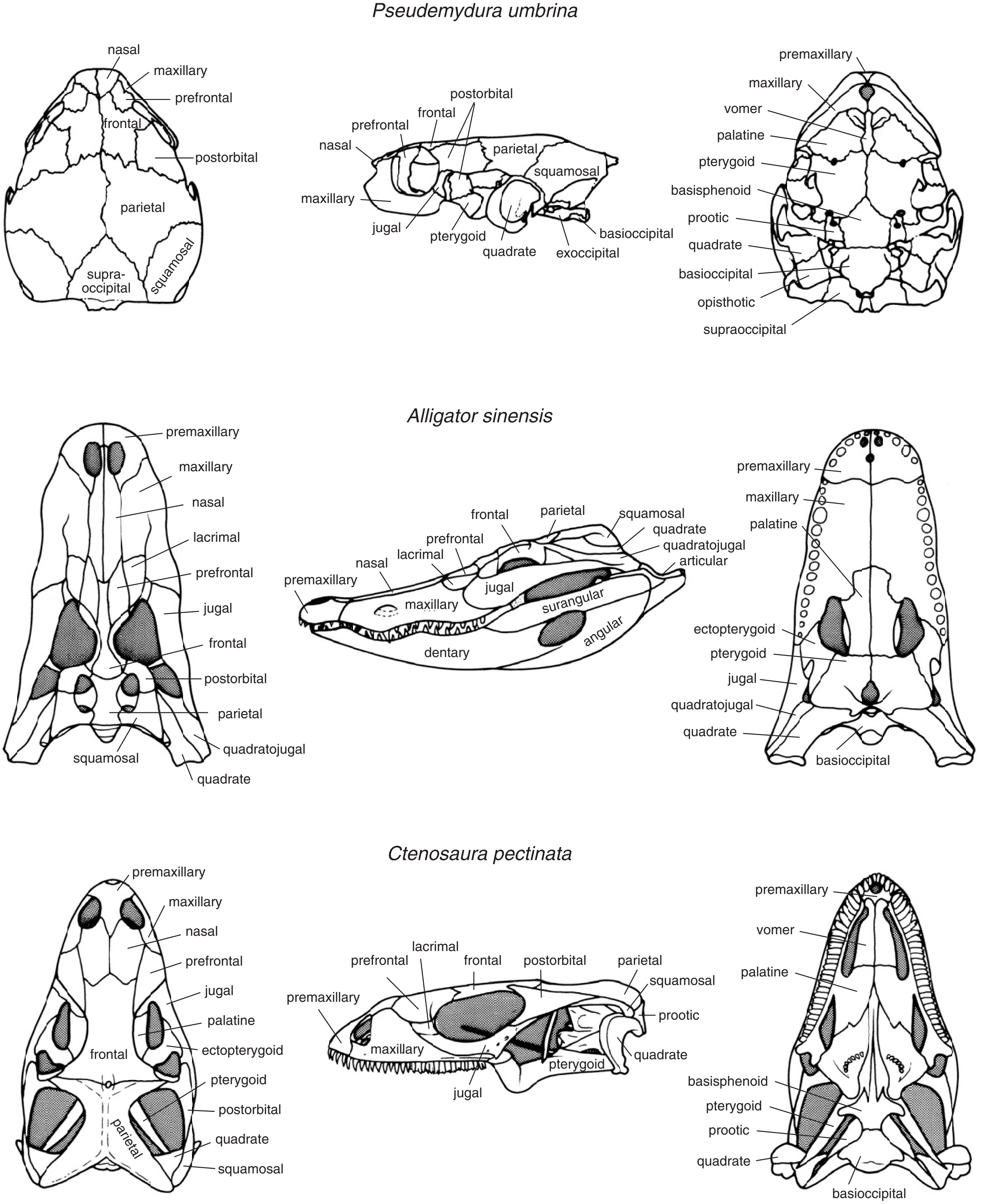


FIGURE 2.11 The hypobranchial skeleton of a typical vertebrate, the salamander *Cryptobranchus* (dorsal view), and the caecilian *Ichythyophis* (ventral view). Reproduced, with permission, from Duellman and Trueb (1986).

swallowing. The jaw muscles fill the temporal area of the skull, extending from the area of the parietal, prootic, and squamosal to the mandible. The muscles that attach to the dorsal surface of the mandible close the mouth, and those that attach to the lateral and ventral surface of the mandible open the mouth. The muscles that function in respiration and swallowing form the floor of the mouth, throat, and neck. These muscles move and support the gills and/or the hyoid and the tongue.

In reptiles, the anterior portion of the chondrocranium remains cartilaginous, even in adults, and consists mainly of continuous internasal and interorbital septa and a pair of nasal conchae that support olfactory tissue. Between the eyes and ears, the chondrocranium ossifies as the basisphenoid, and further posteriorly, the basioccipital, a pair of exoccipitals, and the supraocciptal bones develop below and behind the brain (Fig. 2.12). The occipital elements encircle the foramen magnum, the site at which the spinal cord exits the skull. Below the foramen magnum, the exoccipitals and the basioccipital join to form a single occipital condyle, which bears the articular surface between the first cervical vertebra, or the atlas, and the skull. Portions of each otic capsule remain cartilaginous, although much of the capsule becomes the epiotic, prootic, and opisthotic bones.

The stapes of the middle ear is a splanchnocranial element, as are the quadrate and the epipterygoid; the latter is small in lizards and turtles and is lost in snakes and archosaurs. The quadrate is a large bone on the posterolateral margin of each side of the skull. It bears the articular surface for the lower jaw. On the mandible, the articular bone provides the opposing articular surface and is the only splanchnocranial element of the lower jaw. The reptilian hyoid arch is reduced and consists of a


Pseudemydura umbrina

Alligator sinensis

Ctenosaura pectinata

FIGURE 2.12 Cranial skeletons of representatives of the three clades of living reptiles. Dorsal, lateral, and ventral views (left to right) of the turtle *Pseudemydura umbrina*, the crocodylian *Alligator sinensis*, and the lizard *Ctenosaura pectinata*. Adapted from Gaffney (1979), Iordansky (1973), and Oelrich (1956), respectively.

large midventral plate, usually with three processes that extend upward and posteriorly.

Dermal bones compose the major portion of the reptilian skull and mandible, forming over and around the endochondral bones. From its anterior to its posterior, the roof of the dermocranium contains the nasals, prefrontals, frontals, and parietals, all of which are paired. The upper jaws, the premaxillae and the maxillae, join the roofing bones directly. The cheek and temporal areas contain a postorbital, postfrontal, jugal, quadratojugal, and squamosal bone on each side. The primary palate or roof of the mouth consists of premaxillae and maxillae anteriorly, and a median vomer that is bordered laterally by the palatines and posteriorly by the pterygoids and occasionally a parasphenoid. When a secondary palate forms as in crocodylians, it derives largely from the premaxillae and maxillae. A few other dermal bones, for example, the septomaxilla and the lacrimal, are present in some extant reptiles. The jugals, the quadratojugals, prefrontals, postfrontals, and squamosals are absent individually or in various combinations in some taxa.

The mandible or lower jaw contains numerous paired dermal bones including dentaries, splenials, angulars, surangulars, coronoids, and prearticulars (Fig. 2.12). Only the dentary bears teeth, and in the upper jaw, only the maxilla, premaxilla, palatine, and pterygoid bear teeth. Teeth can be absent on one or more of these teeth-bearing bones. In turtles, teeth are entirely absent; their cutting and crushing functions are performed by the keratinous jaw sheaths.

Typical reptilian teeth are cone-shaped and arranged in a single, longitudinal row (Edmund, 1969). This basic shape has been variously modified. For example, the teeth are laterally compressed and have serrated edges in some herbivorous lizards, and are elongated and posteriorly curved in snakes. When the teeth attach to the bone by sitting in sockets as in crocodylians, they are referred to as thecodont. Teeth arise from a one-sided groove in the jaw, that is, pleurodont, in most lepidosaurs, and they attach directly to the bone surface, that is, acrodont, in two lizard clades. Tooth replacement is continuous throughout life except in most acrodont forms, where teeth are replaced only in juveniles.

The skulls of the two extant reptilian lineages, turtles and diapsids, are distinct (Fig. 2.12). In the turtle skull, the bony temporal arcade is composed of parietals, squamosals, postorbitals, and jugals, and the quadratojugal lacks openings. This condition is the ancestral reptilian state. In the diapsid skull, the temporal area has two openings called fenestrae, an upper one between the parietal, postorbital, and squamosal, and a lower one between the squamosal, jugal, and quadratojugal. Both of these skull types have been modified in extant reptiles. Most living turtles have emarginated temporal arcades, leaving a small arch of bone behind each eye. Only a few turtles, such as the seaturtles, retain a nearly complete arcade. The crocodylians retain the basic diapsid architecture, although the upper or superior temporal fenestra is small (Fig. 2.12). In lepidosaurs, only *Sphenodon* retains the two fenestrae. The squamates have only one upper fenestra or none at all, losing the lower temporal arch, composed of the squamosal, quadratojugal, and the jugal, in the first case, or losing the upper arch, composed of the squamosal and parietal, or the upper and middle arches, composed of the squamosal and postorbital, in the latter case.

The loss of arches and fenestrae in the diapsid skull is associated with increased flexibility (kinesis) of the skull (Frazzetta, 1986). Kinesis derives from the presence of hinges between various sections of the skull. A hinge can occur in the back of the skull (a metakinetic joint) between the dermal skull and the braincase at the parietal-supraocciptal junction; this hinge is the oldest kinetic joint and occurred early in reptilian evolution and today occurs in *Sphenodon*. Two other joints develop in the dermal roofing bones. A dorsal mesokinetic joint lies between the frontals and parietals in many lizards, and in many snakes, a prokinetic joint occurs at the contact between the nasals and the prefrontals or frontals. The most striking kinesis of the lepidosaurs, particularly in the snakes, is streptostyly or quadrate rotation; each quadrate is loosely attached to the dermocranium and has a free ventral end. These loose ligamentous attachments allow the quadrates to rotate and to swing forward and backward, and inward and outward. Streptostyly enhances the jaw's grasping ability and increases the gape.

The complexity in the arrangement and subdivision of muscles mirrors the diversity of the bony architecture of the head. There are no facial muscles in reptiles, but the diversity of jaw and tongue muscles permits a wide range of feeding and defense behaviors. The jaw's depressor and adductor muscles arise from within the temporal arcade and attach to the inside and outside of the mandible. In highly kinetic skulls, muscles are more finely subdivided and permit a wider range of movements of the individual bones, including those of the upper jaw. Throat muscles are typically flat sheets of muscles that extend onto the neck. Beneath these muscles, the hyoid muscles are thicker sheets and longer bundles that attach the hyoid plate and processes to the mandible and to the rear of the skull and the cervical vertebrae.

Vertebral Column

The amphibian vertebral column combines rigidity and strength to support the head, limb girdles, and viscera, and yet it allows enough flexibility to permit lateral and dorsoventral flexure of the column. These seemingly conflicting roles are facilitated by the presence of sliding and rotating articular facets on the ends of each vertebra and by overlapping sets of muscular slips linking adjacent vertebrae.

Each vertebra consists of a ventral cylinder, the centrum, and a dorsal neural arch that may have a dorsal projection, the neural spine (Fig. 2.13). The anterior end of the centrum articulates with the posterior end of the preceding centrum. These central articular surfaces are variously shaped. In opisthocoelous vertebrae, the anterior surface is convex and the posterior surface is concave. In procoelous vertebrae, the anterior surface is concave and the posterior surface is convex. In amphicoelous vertebrae, both surfaces are concave. Intervertebral disks, usually of fibrocartilage, lie between central surfaces of adjacent vertebrae. A pair of flat processes extends from the prezygapophyses and postzygapophyses that form the anterior and posterior edges of the neural arch, respectively (Fig. 2.13). These processes form another set of articulations between adjacent vertebrae. Articular surfaces for the ribs lie on the sides of each vertebra; a diapophysis lies dorsal to the base of the neural arch and a parapophysis lies on the side of the centrum. Ribs are much shorter in amphibians than in the other tetrapods, such as Reptilia and Mammalia, and do not extend more than half way down the sides.

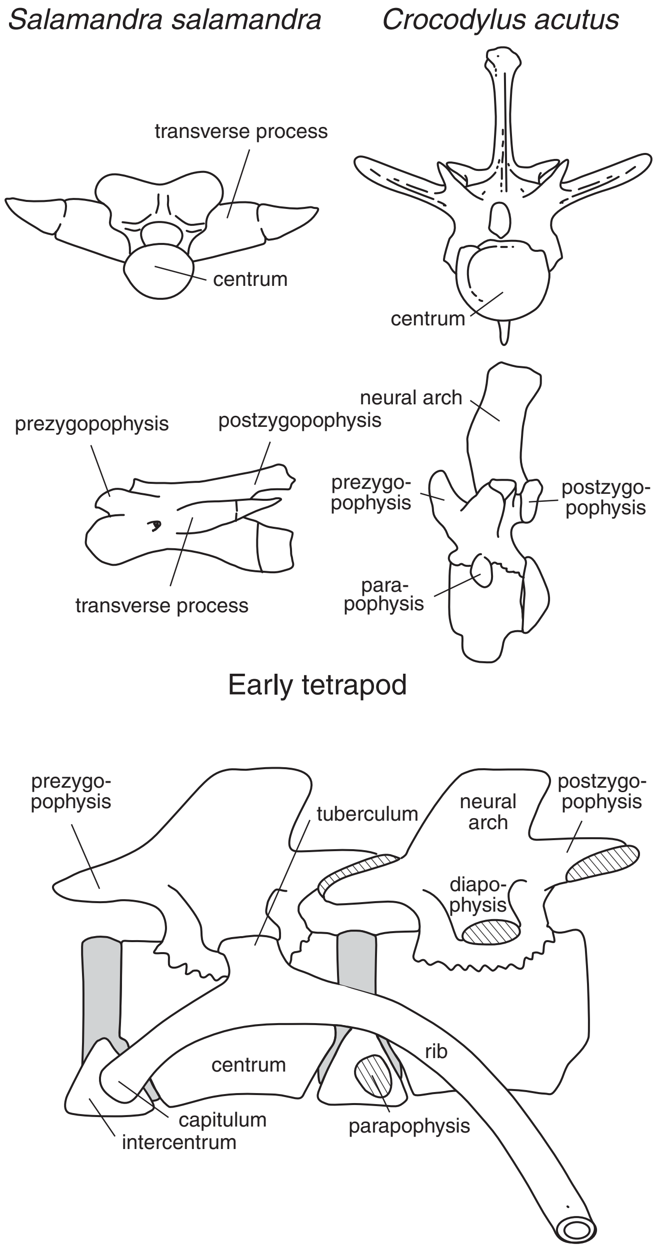


FIGURE 2.13 Anterior and lateral views of vertebral morphology of the tetrapods *Salamandra salamandra* and *Crocodylus acutus* and a schematic lateral view of an early tetrapod. Adapted in part from Francis (1934), Mook (1921), and Goodrich (1930).

The first postcranial vertebra, the atlas, is modified to create a mobile attachment between the skull and the vertebral column. The atlantal condyles on the anterior surface articulate with the paired occipital condyles of the skull. The succeeding vertebrae of the trunk match the general pattern described above. The number and shape of the vertebrae differ in the three amphibian groups. Salamanders have 10 to 60 presacral vertebrae, including a single atlas or cervical vertebra and a variable number of trunk vertebrae. The trunk vertebrae are all similar and possess well-developed zygapophyses, neural spines, and usually bicapitate, or two-headed, ribs. Rather than exiting intervertebrally between neural arches of adjacent vertebrae as in other vertebrates, the spinal nerves of salamanders often exit through foramina in the neural arches. Postsacral vertebrae are always present in variable numbers and are differentiated into two to four precaudal (cloacal) and numerous caudal vertebrae. Caecilians have 60 to 285 vertebrae: a single atlas, numerous trunk vertebrae, no sacral vertebrae, and a few irregular bony nodules representing precaudal vertebrae. The trunk vertebrae are robust with large centra and neural spines; most bear bicapitate ribs. Frogs have 5 to 8 presacral vertebrae. The atlas (presacral I) lacks transverse processes, which are usually present on all other presacral vertebrae. Ribs are absent in most frogs but are present on presacrals II-IV only in *Ascaphus*, *Leiopelma*, discoglossids, bombinatorids, and pipids. The sacral vertebra has large transverse processes called sacral diapophyses, although whether they are true diapophyses is uncertain. The sacral vertebra articulates posteriorly with an elongate urostyle, which represents a rod of fused postsacral vertebrae (Fig. 2.14).

The musculature of the vertebral column consists of epaxial, or dorsal trunk, muscles and hypaxial, or flank or

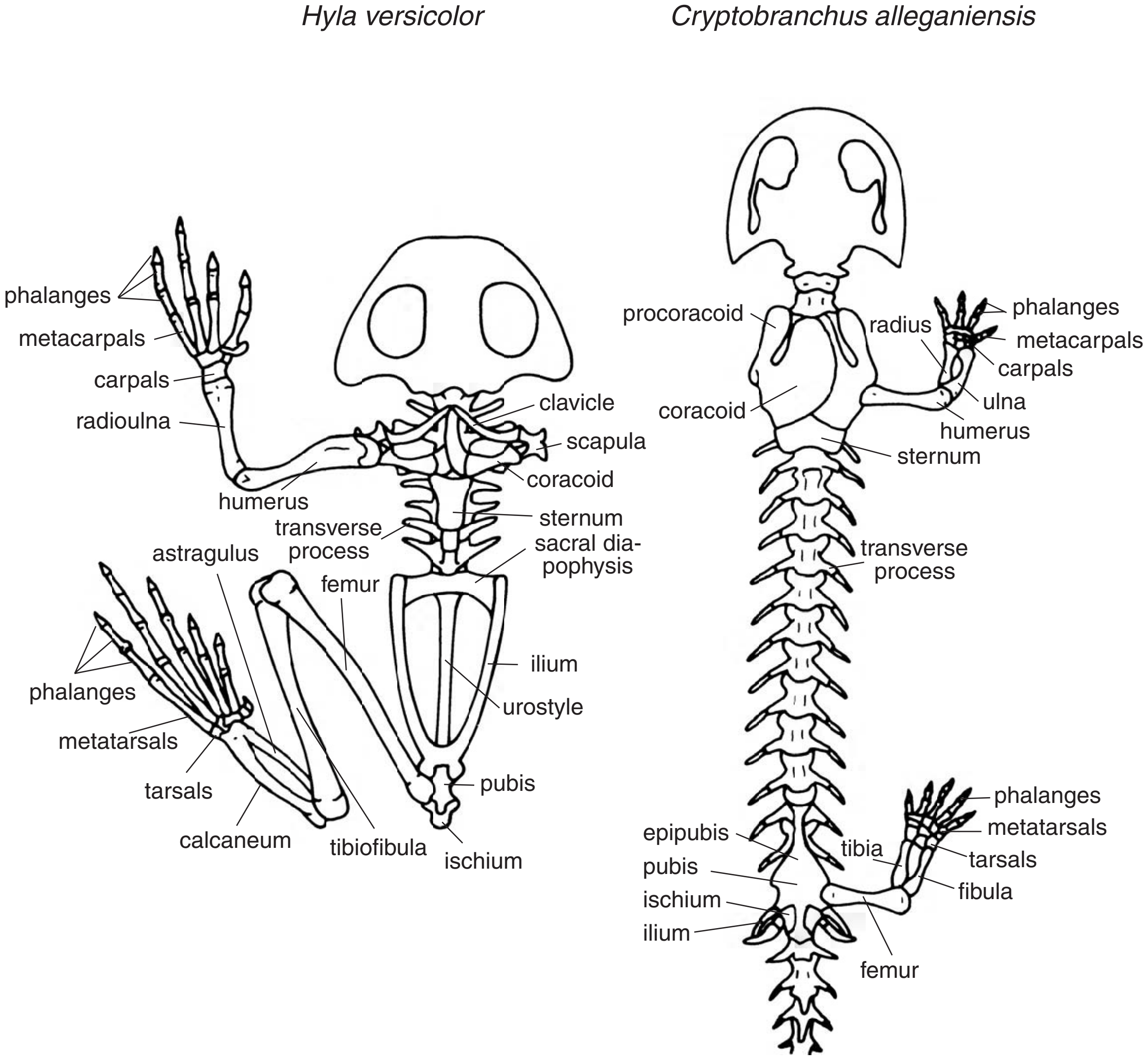


FIGURE 2.14 Postcranial skeletons (ventral view) of a gray tree frog (*Hyla versicolor*) and a hellbender (*Cryptobranchus alleganiensis*). Adapted from Cope (1889).

ventral trunk, muscles. The epaxial muscles consist largely of longitudinal slips that link various combinations of adjacent vertebrae. These muscles lie principally above rib attachments (apophyses) and attach to the neural arches and spines. These muscular components provide rigidity and strength to the vertebral column. The hypaxial muscles support the viscera and contain the oblique muscle series that occurs on the flanks and the rectus muscle series that occurs midventrally along the abdomen.

The trend for increased rigidity of the vertebral column that began in early tetrapods is further elaborated in reptiles. The vertebrae form a firmly linked series and additionally elaborated intervertebral articular surfaces interwoven with a complex fragmentation of the intervertebral muscles. In reptiles, vertebral rigidity is augmented by regional differentiation of the vertebrae. This regionalization permits different segments of the column to have different directions and degrees of movement, and is reflected in the architecture of both bones and muscles.

Reptilian vertebrae and vertebral columns are variable across taxa, but some features are shared by most reptiles (Fig. 2.13). The centra are the weight-bearing units of the vertebral column. Each centrum is typically a solid spool-shaped bone, but in *Sphenodon* and some geckos, the notochord persists and perforates each centrum. A neural arch sits astride the spinal cord on each centrum. The legs or pedicels of each arch fuse to the centrum or insert into notches on the centrum. Neural spines vary from short to long, and wide to narrow, depending upon the position within the column and the type of reptile. The intervertebral articular surfaces, or zygapophyses, consist of an anterior and a posterior pair on each vertebra and arise from the top of pedicels. The articular surfaces of the anterior zygapophyses flare outward and upward, and the posterior surfaces are inward and downward. The angle of these articular surfaces determines the amount of lateral flexibility. When the articular surfaces are angled toward the horizontal plane, flexibility between adjacent vertebrae increases, but if the surfaces are angled toward the vertical plane, rigidity increases. The pedicels also bear the articular surfaces for the ribs. For two-headed ribs, the upper surface is the transverse process or diapophysis, and the lower surface is the parapophysis. The ribs of extant reptiles are single-headed and articulate with the transverse process in all lineages except crocodylians. In many lepidosaurs, accessory articular surfaces occur at the base of the neural spine; a zygosphene projects from the front of the arch into a pocket, the zygantrum, on the rear of the preceding vertebra. The articular surfaces between the centra are variable, but the procoelous ball-and-socket condition is widespread, occurring in all extant crocodylians and most lepidosaurs. The most variable central articular patterns occur in the cervical vertebrae, where, for example, procoelous, opisthocoelous, and biconvex centra exist in the neck of an individual turtle.

Regional differentiation of the vertebrae is characteristic of crocodylians. There are 9 cervical, 15 trunk, 2 sacral, and numerous caudal vertebrae. The first 2 cervical vertebrae, the atlas and axis, are constructed of several unfused components. The atlas bears a single anterior surface for articulation with the occipital condyle of the skull. The axis and subsequent cervical vertebrae bear two-headed ribs that become progressively longer toward the trunk. The first 8 or 9 trunk vertebrae have ribs that extend ventrally to join the sternum and form the thoracic basket. The remaining thoracic vertebrae have progressively shorter ribs. The ribs of the sacral vertebrae anchor the vertebral column to the ilia of the pelvic girdle. The caudal or postsacral vertebrae become sequentially smaller and laterally compressed, and progressively lose their processes posteriorly.

The limbed lepidosaurs have the same regional differentiation pattern as crocodylians. Vertebral number is much more variable, although all have a pair of sacral vertebrae. Generally, 8 cervical vertebrae and ribs exist only on the posterior 4 or 5 vertebrae; however, *Varanus* has 9, and chameleons have 3 to 5, cervical vertebrae. Trunk vertebrae are even more variable in number; 16 to 18 vertebrae appear to be the primitive condition, but the vertebral number can be fewer than 11 in chameleons and considerably more in elongated lizards, particularly in limbless and reduced-limbed anguids and skinks. Caudal vertebrae are similarly variable in number. In limbless squamates, differentiation is limited; the atlas and axis are present, followed by 100 to 300 trunk or precloacal vertebrae, several cloacal vertebrae, and 10 to 120 caudal vertebrae.

In contrast, vertebral number is nearly invariable in turtles. All living turtles have 8 cervical vertebrae; when present, cervical ribs are rudimentary and confined to the posteriormost vertebrae. The variable neck lengths of different species of turtles arise from the elongation or shortening of vertebrae. There are 10 trunk or dorsal vertebrae. The first and last are attached but not fused to the carapace. The middle 8 are firmly fused or co-ossified with the neural bones of the carapace. The trunk ribs extend outward and fuse with the costal bones of the shell. The 2 sacral vertebrae link the pelvic girdle to the vertebral column by short, stout ribs. The caudal number is variable but less than 24 in most species.

The division of the vertebral column muscles into epaxial and hypaxial bundles persists in reptiles, although the distinctiveness of the two types is not obvious. Similarly, the segmental division largely disappears in reptiles. Most axial muscles span two or more vertebral segments and often have attachments to several vertebrae. The complexity of the intervertebral muscles is greatest in the limbless taxa. Unlike fish, their undulatory locomotion is not a uniform wave of contraction but requires individualized contraction patterns, depending upon which part of the body is pushing against the substrate. Turtles lack trunk musculature. Epaxial and hypaxial muscles, however, do extend inward from the neck and tail to attach to the carapace and dorsal vertebrae.

Girdles and Limbs

The limbs of amphibians and other tetrapods have evolved for terrestrial locomotion from the fins of fishes. The girdle and limb components, the appendicular muscles and skeleton, of tetrapod vertebrates derive from the girdle and fin components of their fish ancestors. Several opposite trends are evident in the evolution of limbs from fins. The anterior (pectoral) girdle loses its articulation with the skull and reduces the number of elements. In contrast, the posterior (pelvic) girdle becomes elaborated and enlarged; it articulates with the vertebral column. Within the limbs, the number of skeletal elements is reduced, and a series of highly flexible joints appears between the proximal and distal limb segments. These include the propodial segment of the humerus or femur, the epipodial segment of the radius and ulna or fibula and tibia, the mesopodial segment of the carpal or tarsal elements, the metapodial segment of the metacarpals or metatarsals, and the phalanges (Fig.

2.14). These morphological specializations largely reflect the change in function of the appendages from steering and stability in fish locomotion to support and propulsion in tetrapod locomotion.

The girdles provide internal support for the limbs and translate limb movement into locomotion. Primitively, the amphibian pectoral girdle contained dermal and endochondral elements. The endochondral coracoid and scapula form the two arms of a V-shaped strut that has a concave facet, the glenoid fossa, at their juncture; the glenoid fossa is the articular surface for the head of the humerus. The dermal elements, including the cleithral elements and a clavicle, strengthen the endochondral girdle. A dermal interclavicle—the only unpaired pectoral element—provides midventral strengthening to the articulation of the left and right clavicles and coracoids. This midventral articulation includes the sternum posteriorly. The pelvic girdle, forelimbs, and hindlimbs contain only endochondral elements. Three paired elements form the pelvic girdle. A ventral plate contains the pubes anteriorly and the ischia posteriorly; an ilium projects upward on each side from the edge of the puboischial plate and articulates with the diapophyses of the sacral vertebra. A concave facet, the acetabulum, lies at the juncture of the three pelvic elements and is the articular surface for the head of the femur.

The girdles are anchored to the trunk by axial muscles. Because the pectoral girdle lacks an attachment to the axial skeleton, a series of muscles forms a sling that extends from the back of the skull across the anterior trunk vertebrae to insert on the scapula and humerus. The pelvic girdle has a bony attachment to the vertebral column, and its muscular sling is less extensive. The muscles of the limbs divide into a dorsal extensor and a ventral flexor unit. Within each unit, most of the muscles cross only a single joint, such as from the girdle to the humerus or from the humerus to ulna.

Caecilians have lost all components of the appendicular skeleton and musculature. Limbs and girdles are present in most salamanders, although they may be reduced in size and have lost distal elements, as in the dwarf siren. All frogs possess well-developed limbs and girdles. Salamanders and frogs have only four, or sometimes fewer, digits on the forefeet. The missing digit in frogs and salamanders is the fifth or postaxial (outer) digit. The hindfeet of anurans and salamanders usually retain all digits, but if one is lost, it is also the fifth digit.

Reduction and loss are common features of the salamander skeleton. The pectoral girdle is largely cartilaginous and contains only the scapula, procoracoid, and coracoid. These three elements are regularly indistinguishably fused and ossified only in the area of the glenoid fossa. The left and right halves of the girdle overlap but do not articulate with one another. A small, diamond-shaped, cartilaginous sternum lies on the ventral midline posterior to the girdle halves and is grooved anteriorly for a sliding articulation with the edges of the coracoids. The humerus, the radius, and the ulna have ossified shafts, but their ends remain cartilaginous. The carpals are often entirely cartilaginous or have a small ossification node in the center of larger cartilaginous elements. Reduction by loss and fusion of adjacent carpals is common in salamanders. The phalanges ossify, but their number in each digit is reduced. The common phalangeal formula for most modern amphibians is 1–2–3–2 or 2–2–3–3, compared to the 2–3–4–5–4 formula of ancestral tetrapods.

The salamander pelvic girdle has a more robust appearance than the pectoral girdle. The ilia and ischia are ossified, although the pubes remain largely cartilaginous. The two halves of the girdle are firmly articulated, and a Y-shaped cartilaginous rod, the ypsiloid cartilage, extends forward and likely supports the viscera. The hindlimb elements show the same pattern of ossification as those of the forelimbs; the hindfoot is typically 1–2–3–3–2 and the loss of the fifth toe is common, for example, in *Hemidactylium*.

The appendicular skeleton of frogs is robust and well ossified. The saltatory locomotion of anurans, both in jumping and in landing, requires a strong skeleton. The pectoral girdle contains a scapula capped by a bony cleithrum and a cartilaginous suprascapula and, ventrally, a clavicle and a coracoid; an omosternum (or episternum) and a sternum extend anteriorly and posteriorly, respectively, from the midline of the girdle. Two types of girdles, arciferal and firmisternal, occur in anurans. In both types, the clavicles articulate firmly on the midline. In the firmisternal girdle, the coracoids are joined firmly through the fusion of their epicoracoid caps. In contrast, the epicoracoid caps overlap in arciferal girdles and can slide past one another. The two girdle types are quite distinct in many species, although in others, the girdle structure is intermediate. The humerus is entirely ossified and has an elevated, spherical head. The epipodial elements fuse into a single bony element, the radioulna. The carpal elements are bony and reduced in number by fusion. The phalangeal formula is rarely reduced from 2–2–3–3.

The anuran pelvic girdle is unlike that of any other tetrapod. The puboischiac plate is compressed into a bony, vertical semicircular block on the midline; the ischia lie posterodorsally and the pubes form the ventral edge. The ilia complete the anterior portion of the pelvic block, and each ilium also projects forward as an elongate blade that attaches to the sacral diapophysis. The hindlimb elements are elongate and proportionately much longer than the forelimb. The epipodial elements are also fused into a single bone, the tibiofibula, which is typically as long as or longer than the femur. Two mesopodial elements, the fibulare and the tibiale, are greatly elongate, giving frogs a long ankle. Most of the other mesopodial elements are lost or greatly reduced in size. With the exception of a few species, frogs have five toes and seldom deviate from a 2–2–3–4–3 phalangeal formula.

The limb and girdle skeletons of extant reptiles share many components with that of extant amphibians; nonetheless, the morphology and function of the muscular and skeletal components are different. Little of the reptilian endochondral skeleton remains unossified. The reptilian rib or thoracic cage is linked to the pectoral girdle through the sternum. A shift in limb posture occurred with the development of a less sprawled locomotion. Lizards and salamanders share gait patterns and considerable lateral body undulation when walking or running, but lizards have more elevated postures and a greater range of limb movements. No reptile has a musculoskeletal system so tightly linked to saltatory locomotion as that of frogs.

Early reptiles had a pectoral girdle composed of five dermal components—including paired clavicles and cleithra, and an interclavicle— and the paired, endochondral scapulocoracoids, each with two or three ossification centers—the scapula, the coracoid, or the anterior and posterior coracoids. A cleithrum lies on the anterolateral edge of each scapula. Cleithra disappeared early in reptilian evolution and do not exist in extant reptiles. The interclavicle is a new girdle element, lying ventromedial and superficial to the sternum (Fig. 2.15). The clavicles extend medially along the base of the scapulae to articulate with the anterior ends of the interclavicles. The endochondral components lie deep to the dermal ones. The scapula is a vertical element, and the coracoid is horizontal; at their junction, they support the glenoid fossa for the articulation of the humerus. The coracoids of the left and right sides meet medially and are usually narrowly separated by a cartilaginous band, which is continuous posteriorly with the broader, cartilaginous sternum. The sternum bears the attachments for the anterior thoracic ribs and often a pair of posterior processes that receive the attachments for additional ribs. Posterior to the thoracic ribs, a series of dermal ribs, the gastralia, may support the ventral abdominal wall. These abdominal ribs are superficial to, and are not joined to, the thoracic ribs or any sternal processes, although the connective tissue sheath of the gastralia may attach to the epipubis of the pelvic girdle.

Crocodylians, *Sphenodon*, and some lizards have gastralia, whereas they, along with the sternum, are absent in snakes and turtles. The ventral portion of the shells of turtles, the plastron, is largely a bony neomorph, defined as a novel and unique structure; only the clavicles and the interclavicle appear to have become part of the plastron. Snakes have lost all pectoral girdle elements, and many limbless lizards have greatly reduced endochondral elements; occasionally, the dermal elements are lost. Even limbed lizards show a reduction of dermal elements; the interclavicle is reduced to a thin cruciform rod of bone in most. Chameleons lack the clavicles and interclavicles. Clavicles are absent in crocodylians, but the interclavicle remains as a median rod.

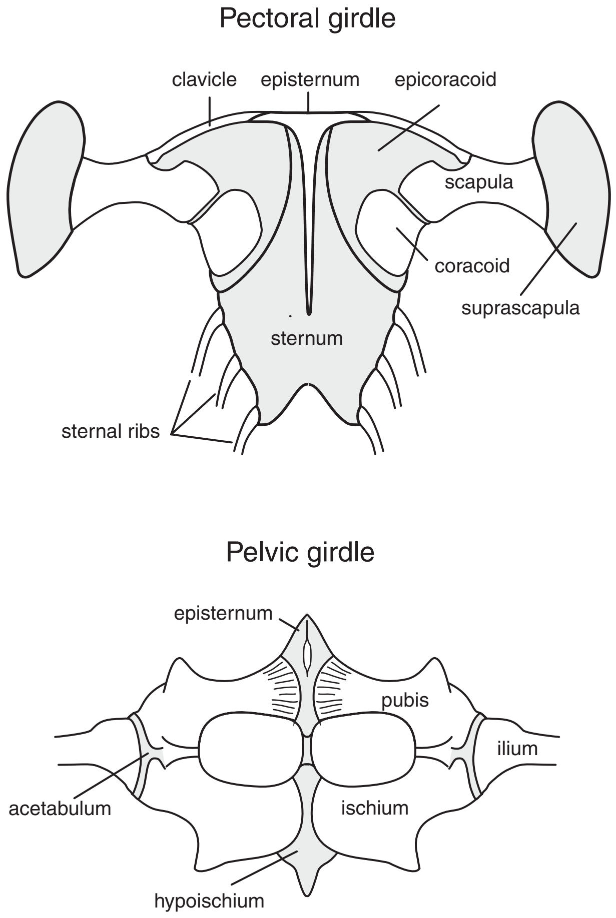


FIGURE 2.15 Ventral views of the pectoral and pelvic girdles of a juvenile tuatara (*Sphenodon punctatus*). Adapted from Schauinsland (1903).

The reptilian pelvic girdle contains three pairs of endochondral elements: the vertical ilia that attach to the sacral vertebrae dorsally, and the horizontal pubes (anterior) and ischia (posterior). The elements form a ventral plate that joins the left and right sides of the girdle (Fig. 2.15). An acetabulum occurs on each side at the juncture of the three bones. These elements persist in all living reptiles, with the exception of most snakes. In all, the puboischiac plate develops a pair of fenestrae that often fuse into a single large opening encircled by the pubes and ischia. The plate becomes V-shaped as the girdle deepens and narrows. In most reptiles, the ilia are rodlike. In a few primitive snake families, a rod-shaped pelvic bone remains on each side. Its precise homologues are unknown, but it does bear an acetabulum and usually processes that are labeled as ilial, ischial, and pubic processes. The femur is vestigial and externally covered by a keratinous spur.

The early reptiles had short, robust limb bones with numerous processes. In modern species, the propodial elements, the humerus and femur, are generally smooth, long, and columnar with a slight curve; their heads are little more than rounded ends of the bony element. Only in turtles are the heads elevated and tilted from the shaft as distinct articular surfaces. The epipodial pairs are of unequal size, with the ulna or tibia the longer, more robust weight-supporting element of the pair. With the rotation of the epipodium, the ulna developed a proximal olecranon process and a sigmoid notch for articulation with the humerus. The tibia lacks an elevated process but has a broad proximal surface for femoral articulation. The mesopodial elements consist of numerous small blocklike bones. The arrangement, fusion, and loss of these elements are highly variable, and the wrist or ankle flexure usually lies within the mesopodium. The metapodial elements are elongate and form the base of the digits. The basic phalangeal formula for the reptilian forefoot (manus) is 2–3–4–5–3, and that for the hindfoot (pes) is 2–3–4–5–4. Most extant reptiles have lost phalanges within digits or occasionally entire digits.

The pectoral girdle and forelimbs attach to the axial skeleton by muscles that extend from the vertebrae to the interior of the girdle or to the humerus. A similar pattern of muscular attachment exists for the pelvic girdle and hindlimbs, although this girdle attaches firmly and directly to the vertebral column through the sacral ribs-ilia buttress. Within the limbs, the single-jointed muscles serve mainly as rotators, and the multiple-jointed muscles serve as extensors and flexors, many of which extend from the distal end of the propodium to the manus or pes.

NERVES AND SENSE ORGANS—COORDINATION AND PERCEPTION

The nervous system of vertebrates has four morphologically distinct, but integrated, units: the central nervous system, the peripheral nervous system, the autonomic nervous system, and various sense organs. The first three of these units are composed principally of neurons or nerve cells, each of which consists of a cell body and one or more axons and dendrites of varying lengths. The appearance of nervous system structures depends upon the organization of various parts of the neurons within the structure. For example, nerves are bundles of axons, and the gray matter of the brain results from concentrations of cell bodies. The sense organs show a greater diversity of structure and organization, ranging from single-cell units for mechanoreception to multicellular eyes and ears. Neurons or parts of neurons are important components of sense organs, but most sense organs require and contain a variety of other cell and tissue types to become functional organs.

Nervous Systems

The central nervous system includes the brain and the spinal cord. Both derive embryologically and evolutionarily from a middorsal neural tube. The anterior end of this tube enlarges to form the brain, which serves as the major center for the coordination of neuromuscular activity and for the integration of, and response to, all sensory input. The brain is divided during development by a flexure into the forebrain and hindbrain. The fore- and hindbrain are each further partitioned, structurally and functionally, into distinct units (Fig. 2.16). From its anterior to its posterior, the forebrain consists of the telencephalon, the diencephalon, and the mesencephalon; the metencephalon and the myelencephalon (medulla oblongata) form the hindbrain. Twelve pairs (10 in extant amphibians) of cranial nerves arise from the brain, olfactory (I) from the telencephalon; optic (II) from the diencephalon; oculomotor (III), trochlear (IV), and abducens (VI) from the mesencephalon; and trigeminal (V), facial (VII), auditory (VIII), glossopharyngeal (IX), and vagus (X) from the medulla. The accessory (XI) and hypoglossal (XII) cranial nerves also originate from the medulla in other vertebrates, but apparently a shortening of the cranium places them outside the skull in amphibians; hence, they become spinal nerves.

The embryonic flexure disappears in amphibians as subsequent embryonic growth straightens the brain. The morphology of the brain is similar in the three living groups, although the brain is shortened in frogs and more elongate in salamanders and caecilians. The telencephalon contains elongate and swollen cerebral hemispheres dorsally encompassing the ventral olfactory lobes. The cerebral hemispheres compose half of the total amphibian brain (Fig. 2.16). The small, unpaired diencephalon lies behind the hemispheres and merges smoothly into the mesencephalon's bulbous optic lobes. Internally, the diencephalon is divided into the epithalamus, thalamus, and hypothalamus. A small pineal organ, the epiphysis, projects dorsally from the epithalamus; a parietal process, lying anterior to the epiphysis, is

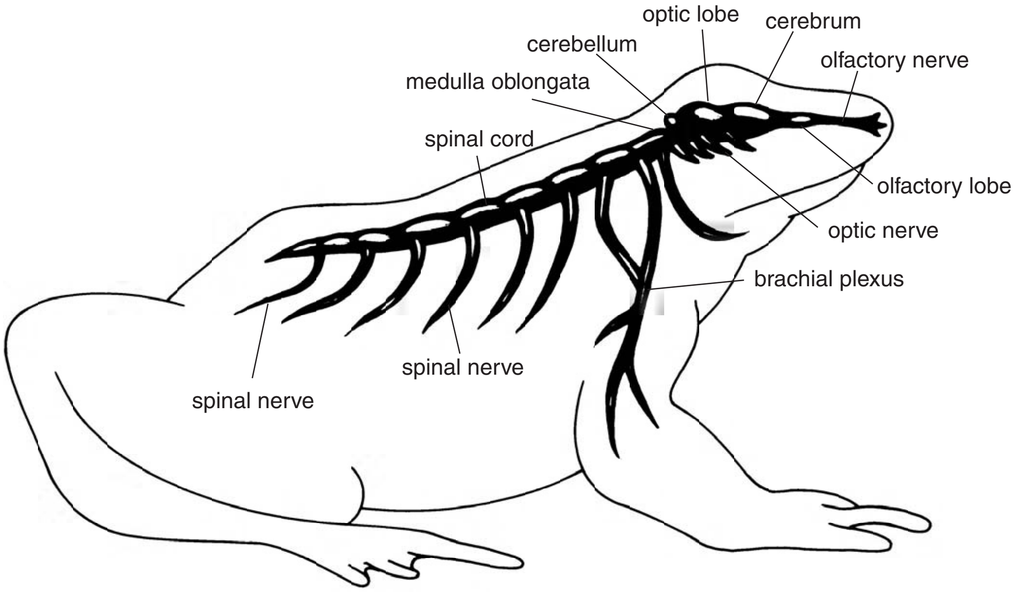


FIGURE 2.16 A diagrammatic lateral view of the brain and spinal cord of a frog.

absent in extant amphibians. The anterior part of the ventral hypothalamus holds the optic chiasma where the optic nerves cross as they enter the brain, and the posterior part holds the infundibular area, from which the hypophysis or pituitary gland projects. Behind the optic lobes, the hindbrain is a flattened triangular area tapering gradually into the spinal cord. Neither the cerebellum, the base of the triangle abutting the optic lobes, or the medulla are enlarged.

Just as reptiles display a multitude of body forms, they display a variety of brain sizes and morphologies. In all reptiles, the basic vertebrate plan of two regions, the forebrain and the hindbrain, is maintained, and flexure of the brain stem is limited. The braincase is commonly larger than the brain, so that its size and shape does not accurately reflect the dimensions and morphology of the brain. The forebrain of adult reptiles contains the cerebral hemispheres, the thalamic segment, and the optic tectum, and the hindbrain contains the cerebellum and medulla oblongata (Fig. 12.17). The cerebral hemispheres are pear-shaped with olfactory lobes that project anteriorly and end in olfactory bulbs. These lobes range from long, narrow stalks with tiny bulbs in many iguanian lizards to short, stout stalks and bulbs in tortoises. Their sizes reflect the reliance on olfaction for many functions in amphibians and reptiles. The thalamic area is a thick-walled tube compressed and hidden by the cerebral lobes and the optic tectum. The dorsal, epithalamic portion has two dorsal projections. The anteriormost projection is the parietal (parapineal) body; in many lizards and *Sphenodon*, it penetrates the skull and forms a parietal eye. The posterior projection, the epiphysis, is the pineal organ and is typically glandular in turtles, snakes, and most lizards, although in some lizards and *Sphenodon*, it is a composite with a rudimentary retinal structure like the parietal body and glandular tissue (Fig. 2.17). Crocodylians lack a parietal-pineal complex. The ventral portion of the thalamic area is the hypothalamus. In addition to its nervous function, the thalamus, the hypothalamus, and the adjacent pituitary gland function together as a major endocrine organ. The dorsal part of the posterior portion of the forebrain is the optical tectum and the ventral portion is the optic chiasma. The cerebellum and medulla are small in extant reptiles.

The spinal cord is a flattened cylinder of nerve cells that extend caudad through the vertebrae (Fig. 2.17). A bilateral pair of spinal nerves arises segmentally in association with each vertebrae for the entire length of the cord. Each spinal nerve has a dorsal sensory and ventral motor root which fuse near their origins and soon divide into dorsal, ventral, and communicating nerve branches. The neurons of the first two branches innervate the body wall, as well as the skin, muscle, and skeleton; the neurons of the communicating branches join the central nervous system and the autonomic system to innervate the viscera, including the digestive, urogenital, circulatory, endocrine, and respiratory organs.

The spinal cord extends to the end of the vertebral column in salamanders and caecilians, but in anurans, the cord ends at the level of the 6th or 7th vertebra, and a bundle of spinal nerves, the cauda equina, continues caudad through the neural canal. In all reptiles, the spinal cord extends from the medulla posteriorly to the end of

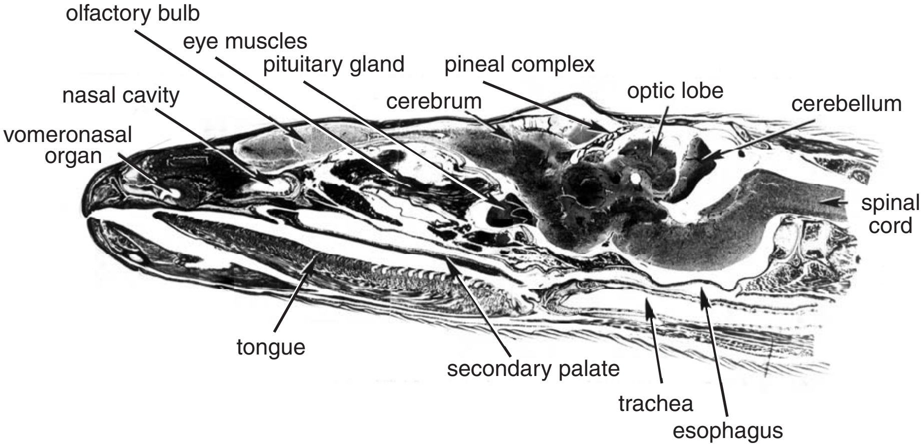


FIGURE 2.17 Parasagittal section of the head of the skink *Emoia cyanura*.

the vertebral column. The diameter of the cord is nearly uniform from brain to base of tail, except for a slight expansion in the region of the limbs. The organization of the spinal nerves is similar in all living amphibians and reptiles. The dorsal root contains somatic and visceral sensory neurons and some visceral motor neurons; the somatic motor and some visceral motor neurons compose the ventral root.

The nerves and their ganglia aggregations of neuron cell bodies, exclusive of the skull and vertebral column, compose the peripheral and autonomic nerve systems. The peripheral system contains the somatic sensory neurons and axons of motor neurons; the autonomic system contains the visceral sensory and some motor neurons. The latter are generally associated with the involuntary activity of the smooth muscles and glands of the viscera. Both the peripheral and autonomic systems are similar in the three amphibian groups, but neither system has been studied extensively, especially the autonomic system. The peripheral nerves transmit the animal's perception of the outside world to the central nervous system and then transmit messages to the appropriate organs for the animal's response.

Sense Organs

Sense organs provide the animal with information about itself and its surroundings. The sense organs that monitor the internal environment and those that monitor the external environment are integrated either directly with the central nervous system or indirectly with it through the autonomic and peripheral networks. The eyes, ears, and nose are obvious external receptors. Heat and pressure receptors of the skin are less obvious, as are internal receptors, such as the proprioceptors of joints and muscles.

Cutaneous Sense Organs

The skin contains a variety of receptors that register the environment's impingement on the animal's exterior. Pain and temperature receptors consist of free and encapsulated nerve endings, most lying in the dermis but a few extending into the epidermis (Spray, 1976). Mechanoreceptors, sensitive to pressure and touch, are similarly positioned in the skin. The pressure receptors may also sense temperature.

The lateral line system of larval and a few adult amphibians is the most evident of the cutaneous sense organs. Superficially it appears as the series of pores on the head and body of aquatic larvae and some aquatic adults, such as cryptobranchid, amphiumid, proteid, and sirenid salamanders; typhlonectid caecilians; and pipid frogs. The mechanoreceptor organs or neuromasts are arranged singly or in compact linear arrays called stitches to form the various lines or canals that traverse the head and trunk (Lannoo, 1987a,b). Each neuromast contains a small set of cilia projecting from its outer surface. The cilia bend in only one axis, thereby sensing water pressure or current changes only along that axis. They are sensitive to light currents and are used to locate food. Neuromasts are reduced only in species living in rapidly flowing water.

Recently, ampullary organs were discovered on the heads of some larval salamanders and caecilians. These electroreceptors are less numerous, lying in rows parallel to the neuromasts. Like neuromasts, ampullary organs provide the larva with a sense of its surroundings, identifying both stationary and moving objects lying within the electrical field surrounding the larva.

Cutaneous sense organs are especially common in reptiles and occur in a variety of forms (During and Miller, 1979). In addition to pain and temperature receptors, several types of intraepithelial mechanoreceptors register pressure, tension, or stretching within the skin. Mechanoreceptors with discoid endings or terminals occur over most of the body, and mechanoreceptors with branching terminals lie within the hinges between scales of lepidosaurs. Mechanoreceptors with coiled, lanceolate, or free terminals are confined to the dermis. On the surface of the skin, tactile sense organs are abundant; they range in shapes from buttonlike and smooth to those with barbed bristles (Landmann, 1975).

The pit organs of some boids, pythonids, and viperids are specialized structures in the dermis and epidermis that house infrared heat receptors. In *Boa*, these receptors, both intraepidermal and intradermal types, are scattered on unmodified supra- and infralabial scales. In *Python*, a series of pits occurs in the labial scales, and the heat receptors are concentrated on the floor of the pit. In crotaline snakes, a pit organ occurs on each side of the head between the naris and the eye. The openings face forward and their receptor fields overlap, giving them stereoscopic infrared vision. Further, the heat receptors lie within a membrane stretched across the pit.

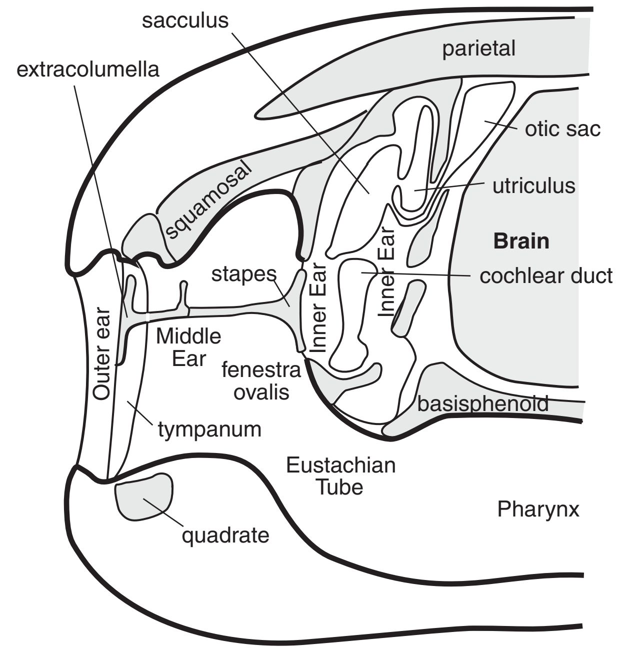


FIGURE 2.18 Lateral view of the anatomy of a lizard's ear. The otic capsule consists mainly of the opisthotic and prootic. Adapted from Baird (1970).

Ears

The ears of tetrapods, including frogs, lizards, and mammals, are structurally similar and serve two functions: hearing, the reception of sound waves, and balance, the detection of the position and movement of the animal's head (Wever, 1978, 1985). The receptors for both functions are neuromasts located in the inner ear. These neuromasts differ somewhat from those of the lateral line system, but they similarly record fluid movements along a single axis by the deflection of terminal cilia.

Ears are paired structures, one on each side of the head just above and behind the articulation of the lower jaw. Each ear consists of an inner, middle, and outer unit (Fig. 2.18). The inner ear is a fluid-filled membranous sac, containing the sensory receptors and suspended in a fluid-filled cavity of the bony or cartilaginous otic capsule. The middle ear contains the bone and muscular links that transfer vibrations from the ear drum, the tympanum, to the inner ear. An outer ear is usually no more than a slight depression of the tympanum or may be absent. Salamanders, caecilians, and some frogs lack tympana. In these amphibians, low-frequency sounds may be transmitted via the appendicular and cranial skeleton to the inner ear. For reptiles, an outer ear occurs only in crocodylians and some lizards; tympana are flush with the surface of the head in turtles and some lizards. A special muscle allows crocodylians and most geckos to close the ear cavity.

In reptiles, the middle ear contains a tympanum and two ear ossicles, the stapes, and the extracolumella, within an air cavity (Baird, 1970). The tympanum receives sounds and transmits the vibrations along the extracolumella-stapes chain to the oval window of the inner ear. The middle ear cavities are large in turtles, large with left and right cavities connected in crocodylians, small and nearly continuous with the pharynx in most lizards, narrow canals in snakes, and usually absent in amphisbaenians. The stapes is typically a slender columnar bone, and its cartilaginous tip, the extracolumella, has three or four processes that reach the tympanum. In snakes, the stapes abuts against the quadrate bone for transmission of vibrations.

Unlike reptiles, the amphibian middle ear has two auditory pathways: the tympanum-stapes path for airborne sounds and the forelimb-opercular path for seismic sounds. Both pathways reach the inner ear through the fenestra ovalis of the otic capsule. The tympanum-stapes path is shared with the tetrapods. In amphibians the stapes is a single bony rod that extends between the external eardrum and the fenestra ovalis of the inner ear. In most frogs, the stapes lies within an air-filled cavity, and in salamanders and caecilians, the stapes is embedded in muscles. The limb—opercular path is unique to frogs and salamanders (Hetherington, 1985; Hetherington et al., 1986). Sound waves are transmitted from the ground through the forelimb skeleton onto the tensed opercular muscle that joins the shoulder girdle to the operculum lying in the fenestra ovalis.

The membranous inner ear basically consists of two sacs joined by a broad passage. The dorsal sac or utriculus has three semicircular canals that project outward from it. One of these canals lies horizontally, the other two are vertical, and all three are perpendicular to one another. This orientation allows movement to be recorded in three different planes and provides information for the sense of balance. The neuromasts are clustered in patches, one patch in each semicircular canal and one or more patches in the utriculus and the ventral sac, the sacculus. In amphibians, the sacculus also contains several outpocketings, including the amphibian papilla, basilar papilla, lagena, and endolymphatic duct. The two papillae contain patches of neuromasts specialized for acoustic reception. Reptiles lack the amphibian papilla but have a cochlear duct from which the auditory sensory area projects ventrally from the sacculus and adjacent to the oval window.

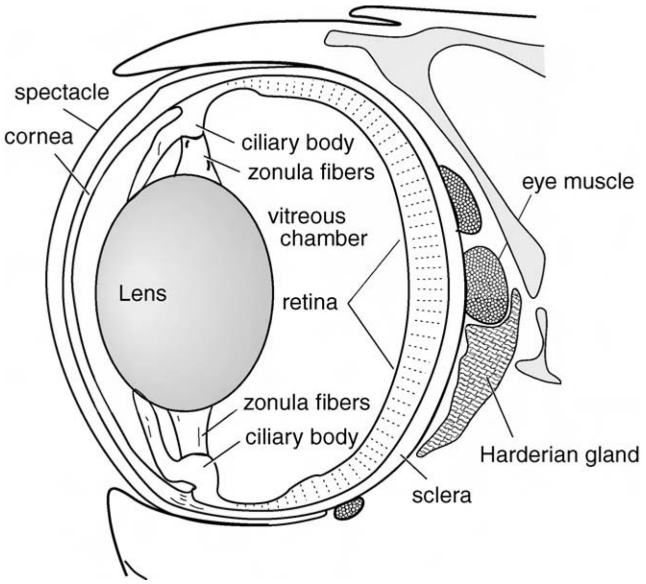


FIGURE 2.19 Cross section of the anatomy of a snake's eye. Adapted from Underwood (1970).

Eyes

Eyes vary from large and prominent to small and inconspicuous in extant amphibians. All have a pair of eyes located laterally or dorsolaterally on the head. Most terrestrial and arboreal salamanders and frogs have moderate to large eyes, whereas fossorial and aquatic species usually have small eyes. Eyes are degenerate and lie beneath the skin in caecilians and cave-dwelling salamanders; in a few caecilians eyes lie beneath bone. The eyes of most reptiles are large and well developed. The eyes are degenerate only in a few fossorial species and groups. They have disappeared completely, leaving no pigment spot visible externally, in only a few species of scoleophidian snakes.

The structure of the eye is similar in all vertebrates (Fig. 2.19). It is a hollow sphere lined internally with a heavily pigmented sensory layer, the retina. The retina is supported by the sclera, a dense connective tissue sheath forming the outside wall of the eyeball. The cornea is the transparent part of the outer sheath lying over a gap in the retina that allows light to enter the eye. In postmetamorphic amphibians, eyelids and a nictitating membrane slide across the exposed cornea to protect and moisten it. A spherical lens lies behind the cornea and is anchored by a corona of fibers that extend peripherally to the cornea-scleral juncture. The amount of light passing through the lens and onto the retina is regulated by a delicate, pigmented iris lying behind the cornea. Its central opening, the pupil, is opened (dilated) or closed (contracted) by peripherally placed muscles. The eye retains its spherical shape by the presence of fluid, called vitreous humor in the cavity behind the lens and aqueous humor in front of the lens.

Light enters the eye through the iris and is focused on the retina by the lens. The organization of the retina's several layers differs from what might be expected. The sensory or light-registering surfaces are not the innermost surface of the eye. Instead, the innermost layer consists of transmission axons that carry impulses to the optic nerve, and the next layer contains connector neurons that transfer impulses from the adjacent receptor cell layer. The deepest layer contains the pigment cells adjacent to the sclera. The actual receptor surfaces of the sensory cells face inward, not outward toward the incoming light, and against and in the pigment layer. Amphibians have four kinds of light receptors: red and green rods, and single and double cones. The cones are the color receptors that possess specialized pigments sensitive to a narrow range of wavelengths. When light strikes these pigments, their chemical state is changed. Amphibians are the only vertebrates with two types of rods, and the green rods are unique to amphibians. These rods are absent in taxa with degenerate eyes. The visual pigment of the rods is sensitive to all wavelengths of light; hence, rods register only the presence or absence of light.

The eyes of reptiles, except snakes, have a ring of bony plates (scleral ossicles) embedded in the sclera and surrounding the cornea. Pupils range from round to elliptical and are usually oriented vertically, although occasionally they are horizontal is some species. The reptilian eyeball and lens are usually spherical (Fig. 2.19). Rather than moving the lens for accommodation, lens shape is changed by the contraction of radial muscles in the ciliary body encircling the lens. Crocodylians and turtles share a duplex retina (rods and cones) with other vertebrates and possess single and double cones and one type of rod. In squamates, the retina has been modified. Primitive snakes have a simplex retina consisting only of rods; advanced snakes have a duplex retina of cones and rods, although the cones are probably transformed rods. In lizards, the simplex retina contains two or three different types of cones.

Nasal Organs

Olfaction or smelling is performed by bilaterally paired nasal organs and the vomeronasal (Jacobson's) organ (Parsons, 1970). Each nasal organ opens to the exterior through the external naris and internally into the buccal cavity via the choana (internal naris). Between these openings in amphibians is a large olfactory (principal) cavity and several accessory chambers that extend laterally and ventrally; the vomeronasal organ is in one of the accessory chambers. A nasolacrimal duct extends from the anterior corner of each eye to the principal cavity. The surface of the chambers contains support and mucous cells and is lined with ciliated epithelium. The ciliated neuroepithelium occurs in three patches. The largest patch occupies the roof, medial wall, and the anterior end of the principal cavity. A small, protruding patch occurs on the middle of the floor, and another small patch is present in the vomeronasal organ chamber. The neuroepithelium of the principal cavity is innervated by neurons from the olfactory bulb of the brain, and the vomeronasal organ is innervated by a separate olfactory branch. Olfaction is a chemosensory process (Halpern, 1992). The actual receptor site on the cell is unknown but may be either at the base of each cilium or near the cilium's junction with the cell body.

The nasal organs of salamanders are composed of a large main cavity partially divided by a ventrolateral fold. Aquatic salamanders have the simplest and smallest nasal cavities, but they possess large vomeronasal organs. Frogs, in general, have a complex nasal cavity consisting of three chambers and a large vomeronasal organ (Scalia, 1976). Caecilians have simple nasal cavities similar to salamanders but with a major modification, the sensory tentacle. The size, position, and structure of the tentacle vary among different species; however, in all, the tentacle arises from a combination of nasal and orbital tissues as a tubular evagination from the corner of the eye. The tentacle's exterior sheath is flexible but nonretractable. The tentacle proper can be extruded and retracted into its sheath. Odor particles are transported via the nasolacrimal duct to the vomeronasal organ.

In reptiles, each nasal organ consists of an external naris, a vestibule, a nasal cavity proper, a nasopharyngeal duct, and an internal naris (Fig. 2.17). These structures serve as air passages and are lined with nonsensory epithelium. The sensory or olfactory epithelium lies principally on the roof and anterodorsal walls of the nasal cavity. These passages and cavities are variously modified in the different reptilian groups. The vestibule is a short tube in turtles and snakes, and is much longer and often curved in lizards. A concha covered with sensory epithelium projects into the nasal cavity from the lateral wall. *Sphenodon* has a pair of conchae, squamates and crocodylians have one, and turtles have none. The vomeronasal organ is an olfactory structure, used primarily to detect nonaerial, particulate odors. It arises embryologically from the nasal cavity but remains connected to this cavity as well as to the oral cavity only in *Sphenodon*. In squamates, it communicates with the oral cavity by a narrow duct. Odor particles are carried to the vicinity of the duct by the tongue. Well developed in squamates, this organ is absent in crocodylians; in turtles, it lies in the main nasal chamber rather than in a separate chamber.

Internal Sense Organs

The major internal sense organs are the proprioceptor organs embedded in the muscles, tendons, ligaments, and joints. These organs record the tension and stress on the musculoskeletal system and allow the brain to coordinate the movement of limbs and body during locomotor and stationary behaviors. The proprioceptors show a structural diversity from simple nerve endings and netlike endings to specialized corpuscles. Structurally, the proprioceptors of reptiles are similar to those of amphibians.

Taste buds or gustatory organs are present in all amphibians, although they have been little studied and nearly exclusively in frogs. There are two types: papillary organs, located on fungiform papillae on the outer surface of the tongue, and nonpapillary organs, located throughout the buccal cavity, except on the tongue. Each type of taste bud is a composite of receptor and support cells. The buds are highly sensitive to salts, acids, quinine (bitter), and pure water. In many reptiles, taste buds occur on the tongue and scattered in the oral epithelium. Structurally, they appear similar to those of amphibians and share the same sensory responses. In squamates, taste buds are abundant in fleshy-tongued taxa and are greatly reduced or absent in taxa (e.g., most snakes) with heavily keratinized tongue surfaces (Schwenk, 1985; Young, 1997).

HEART AND VASCULAR NETWORK— INTERNAL TRANSPORT

The circulatory system is a transport system that carries nutrients and oxygen to all body tissues and removes waste products and carbon dioxide from them. This system contains four components: blood, the transport medium; vascular and lymphatic vessels, the distribution networks; and the heart, the pump or propulsive mechanism.

Blood

Amphibian blood plasma is a colorless fluid, it contains three major types of blood cells: erythrocytes, leukocytes, and thrombocytes. The blood cells are typically nucleated, although in salamanders a small number of each of the three types lack nuclei. Erythrocytes carry oxygen to and carbon dioxide from the tissues; both gases attach to the respiratory pigment hemoglobin. Erythrocytes vary in size among amphibian species, but, in general, amphibians have the largest erythrocytes known among vertebrates. Leukocytes consist of a variety of cell types, most of which are involved in maintenance duties such as removing cell debris and bacteria or producing antibodies. The thrombocytes serve as clotting agents. Only the erythrocytes are confined to vascular vessels; the other blood cells and the plasma leak through the walls of the vascular vessels and bathe the cells of all tissues. The plasma and cells reenter the vascular vessels directly or collect in the lymphatic vessels that empty into the vascular system.

Blood plasma is colorless or nearly so in most reptiles. A few skinks and crotaline snakes have green or greenish yellow blood. In addition to dissolved salts, proteins, and other physiological compounds, the plasma transports three types of cells: erythrocytes, leukocytes, and thrombocytes, all of which have nuclei in reptiles.

Arterial and Venous Circulation

The vascular vessels form a closed network of ducts that transport the blood. Blood leaves the heart through the arteries that divide into smaller and smaller vessels, the arterioles. The smallest vessels, the capillaries, are only slightly larger than the blood cells flowing through them. Within the capillary beds, the plasma and some leukocytes and thrombocytes leak through to the lymphatic system. Beyond the capillaries, the vessels become progressively larger. Venules, comparable to arterioles in size, lead to the larger veins, which return blood to the heart.

In amphibians, blood leaves the heart through the conus arteriosus (Saint-Aubain, 1985), which soon divides into three aortic arches, the pulmocutaneous arch, the systemic arch, and the carotid arch (Fig. 2.20). The position and number of aortic arches are highly variable in amphibians. The pulmocutaneous arch divides into cutaneous arteries that serve the skin and into pulmonary arteries that lead to the respiratory surfaces where gaseous exchange occurs. The systemic arch curves dorsally and fuses on the midline with its

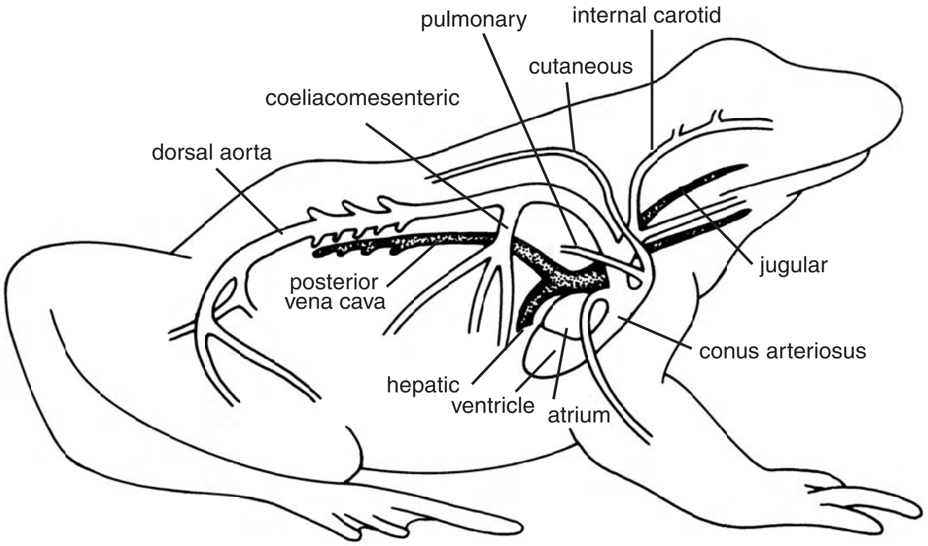


FIGURE 2.20 Lateral view of the circulatory system of a frog. White vessels are arteries; dark ones are veins.

bilateral counterpart to form the dorsal aorta. Vessels that branch from the dorsal aorta as it extends posteriorly provide blood to all viscera and limbs. The branches of the carotid arch carry blood to the tissues and organs of the head and neck. The venous system has a comparable distributional pattern of vessels but in reverse. A pair of common jugular veins drains the numerous veins of the head and neck; the subclavian veins gather blood from the smaller veins of the forelimbs and skin; and the pulmonary veins drain the lungs. A single postcaval vein is the major efferent vessel for the viscera and hindlimbs. All these veins, except the pulmonary vein, empty into the sinus venosus, which opens directly into the heart (Fig. 2.20). The sizes, shapes, and branching patterns within the vascular network are nearly as variable within a taxon as they are between unrelated taxa. The visceral arches of amphibian larvae give rise to the aortic arches of adults, although adults lose the first two arches (I, II). Of the remaining arches, some salamanders retain all, whereas anurans retain three, and caecilians retain two.

The arterial and venous networks of reptiles are similar to that of adult amphibians, but, like amphibians, the reptilian groups differ from each other (Burggren, 1987). For example, the pattern of vessels to and from the trunk of snakes and turtles is not the same. The major trunk vessels leading from the heart and to the viscera, head, and limbs, and those vessels returning the blood to the heart, are more similar among species and groups than they are different.

In reptiles, the pulmonary artery typically arises as a single trunk from the cavum pulmonale of the right ventricle and bifurcates into right and left branches above and in front of the heart (Fig. 2.21). The systemic arteries (aortas) arise separately but side by side from the cavum venosum of the left ventricle. The left systemic artery curves dorsally and bifurcates into a small ductus caroticus and the larger systemic branch. The right systemic artery bifurcates in front of the heart; the cranial branch forms the major carotid network and the systemic branch curves dorsally to join the left systemic branch. This combined aorta (dorsal aorta) extends posteriorly and its branches serve the limbs and the viscera. The major venous vessels are the jugular veins that drain the head and the postcaval vein that receives vessels from the limbs and viscera. The jugular and postcaval trunks join into a common sinus venosus; in turn, it empties into the right atrium.

Lymphatic Network

The lymphatic network is an open system, containing both vessels and open cavities or sinuses within the muscles, in the visceral mesenteries, and beneath the skin. It is a one-way network, collecting the plasma and other blood cells that have leaked out of the capillaries and returning them to the vascular system. The lymph sinuses are the major collection sites, and the subcutaneous sinuses are especially large in frogs. The sinuses are drained by lymphatic vessels that empty into veins. In amphibians and fishes, lymph hearts lie at venous junctions and are contractile structures with valves that prevent backflow and thereby speed the flow of lymph into the veins. Frogs and salamanders have 10 to 20 lymph hearts; the elongate caecilians have more than a hundred.

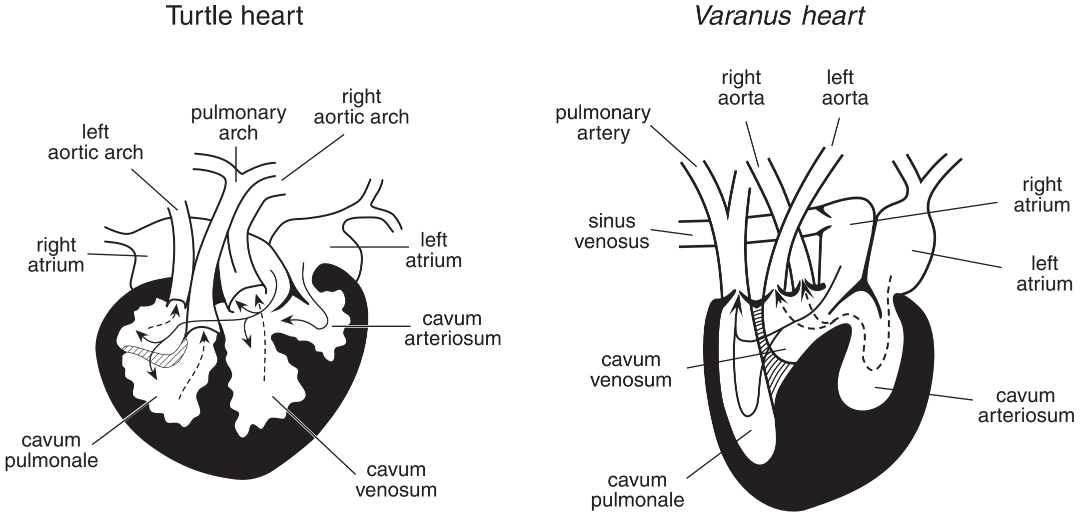


FIGURE 2.21 Heart anatomy of a turtle and a varanid lizard. Shown are diagrammatic ventral views of frontal sections. The arrows indicate only the general pathway of blood flow through the ventricle into the aortic arches. Adapted from Burggren (1987).

The lymphatic system of reptiles is an elaborate drainage network with vessels throughout the body. This network of microvessels gathers plasma (lymph) from throughout the body, and the smaller vessels merge into increasingly larger ones that in turn empty into the main lymphatic trunk vessels and their associated sinuses. The trunk, vessels, and sinuses empty into veins. Major trunks collect plasma from the limbs, head, and viscera, forming a network of vessels that outline the shape of the reptile's body. The occurrence of valves is irregular, and plasma flow can be bidirectional; however, the major flow in all trunks is toward the pericardial sinus and into the venous system. A single pair of lymphatic hearts but no lymph nodes occur in the pelvic area.

Heart

Heart structure is highly variable in amphibians. All possess a three-chambered heart composed of two atria and one ventricle, but the morphology of the chambers and the pattern of blood flow through the chambers vary (Fig. 2.20). The differences are associated with the relative importance of cutaneous and pulmonary respiration. Even differences in an amphibian's physiological state modify the flow pattern—a hibernating frog might have a flow pattern that mixes pulmonary and systemic blood in the ventricle, whereas an active frog does not. The atria are thin-walled sacs separated by an interatrial septum. The sinus venosus empties into the right atrium, and the pulmonary veins empty into the left atrium. Both atria empty into the thick, muscular-walled ventricle, which pumps the blood into the conus arteriosus. Although the ventricle is not divided by a septum, oxygenated and unoxygenated blood can be directed into different arterial pathways. Such segregation is possible owing to the volume and position of the blood in the ventricle, the nature of the ventricular contractions, the spiral fold of the conus arteriosus, the branching pattern of the arteries from the conus, and the relative resistance of the pulmonary and systemic pathways.

There is no single model for a generalized reptilian heart. Heart size, shape, structure, and position are linked to other aspects of each species' anatomy and physiology (Farrell et al., 1998). The animal's physiology is a major determinant of heart structure and function, but phylogeny and behavior also play determining roles. In snakes, heart position is correlated with arboreal, terrestrial, and aquatic habits. Among these variables, three general morphological patterns are recognized.

The typical reptilian heart of turtles and squamates (Fig. 2.21) is three-chambered, possessing two atria and a ventricle with three chambers or cava. From left to right, the cava are called the cava arteriosum, the cava venosum, and the cava pulmonale. The right atrium receives unoxygenated venous blood from the sinus venosus and empties into the cavum venosum of the ventricle. The left atrium receives oxygenated blood from the lungs via the pulmonary veins and empties into the cavum arteriosum. Because the three ventricular cava communicate and the muscular contraction of the ventricle is single-phased, oxygenated and unoxygenated blood mixes and blood exits simultaneously through all arterial trunks. Blood in the cavum pulmonale flows into the pulmonary trunk, and blood in the cavum venosum into the aortas.

Monitor lizards (varanids) possess a higher metabolic rate than other lizards and also have differences in the architecture of the ventricular cava, which communicate with one another (Fig. 2.21). The cavum venosum is small—little more than a narrow channel linking the cavum pulmonale with a greatly enlarged cavum arteriosum. Ventricular contraction is two-phased so that the pumping cycle creates a functionally four-chambered heart. Although mixing of unoxygenated and oxygenated blood can occur and probably does in some circumstances, the cavum pulmonale is isolated during systole (contraction), and unoxygenated blood is pumped from the right atrium to the lungs. Within the crocodylians, the ventricle is divided into separate right and left muscle components. Uniquely, the two aortas in crocodylians arise from different ventricular chambers, the left aorta from the right chamber and the right aorta from the left chamber. This arrangement provides an opportunity for unoxygenated blood to bypass the lungs in special physiological circumstances, such as during diving, by altering the pattern of ventricular contraction (Jones, 1996).

DIGESTIVE AND RESPIRATORY ORGANS—ENERGY ACQUISITION AND PROCESSING

The digestive and pulmonary systems are linked by a common embryological origin, similar functions, and shared passageways. The lungs and respiratory tubes form as an outpocketing of the principal regions. Both systems are intake ports and processors for the fuels needed to sustain life: oxygen for use in respiration, and water and food for use in digestion (see Chapter 6: Water Balance and Gas Exchange and Chapter 10: Foraging Ecology and Diets, respectively).

Digestive Structures

The digestive system of amphibians has two major components, a digestive tube that has specialized regions and various digestive glands. The digestive tube or tract extends from the mouth to the anus, which empties into the cloaca. From beginning to end, the regions are the buccal (oral) cavity, the pharynx, esophagus, stomach, and small and large intestines. The general morphology of these regions is similar within amphibians, although the digestive tracts is short in anurans and long in caecilians.

The mouth opens directly into the buccal cavity and is bordered by flexible, immobile lips. The buccal cavity is continuous posteriorly at the angle of the jaw with the pharynx. The primary palate forms the roof of the buccal cavity, and the tongue lies on its floor. The tongue is variously developed in amphibians. In its least-developed form, the tongue is a small muscular pad lying on a simple hyoid skeleton, as seen in pipid frogs. Some salamanders and many advanced frogs have tongues that can be projected very rapidly for long distances in order to capture prey. These projectile tongues have a more elaborate hyoid skeleton and associated musculature with a glandular pad attached to the muscular base.

Amphibian teeth are typically simple structures; each tooth has an exposed bicuspid crown anchored to a base, or pedicel, in the jaw. Caecilians and a few frogs have unicuspid curved teeth. Salamanders and caecilians have teeth on all the jawbones; most frogs lack teeth on the lower jaw and a few lack teeth on the upper jaw.

The pharynx is the antechamber for directing the food into the esophagus and air into the lungs. A muscular sphincter controls the movement of food in the thin-walled esophagus, and peristaltic movement propels food downward into the stomach. The stomach is an enlarged and expandable region of the digestive tube. Its thick muscular walls and secretory lining initiate the first major digestive breakdown of food. The food bolus passes from the stomach through the pyloric valve into the narrower and thin-walled small intestine. The forepart of the small intestine is the duodenum, which receives the digestive juices from the liver and pancreas. The small intestine of amphibians has only a small amount of internal folding and villi to increase surface area for nutrient absorption. It is continuous with a slightly broader large intestine in caecilians, salamanders, and some frogs. In advanced frogs, a valve separates the large and small intestines. The large intestine empties into the cloaca, which is a sac-like cavity that receives the products and by-products of the digestive, urinary, and reproductive systems. The cloaca exits to the outside through the vent.

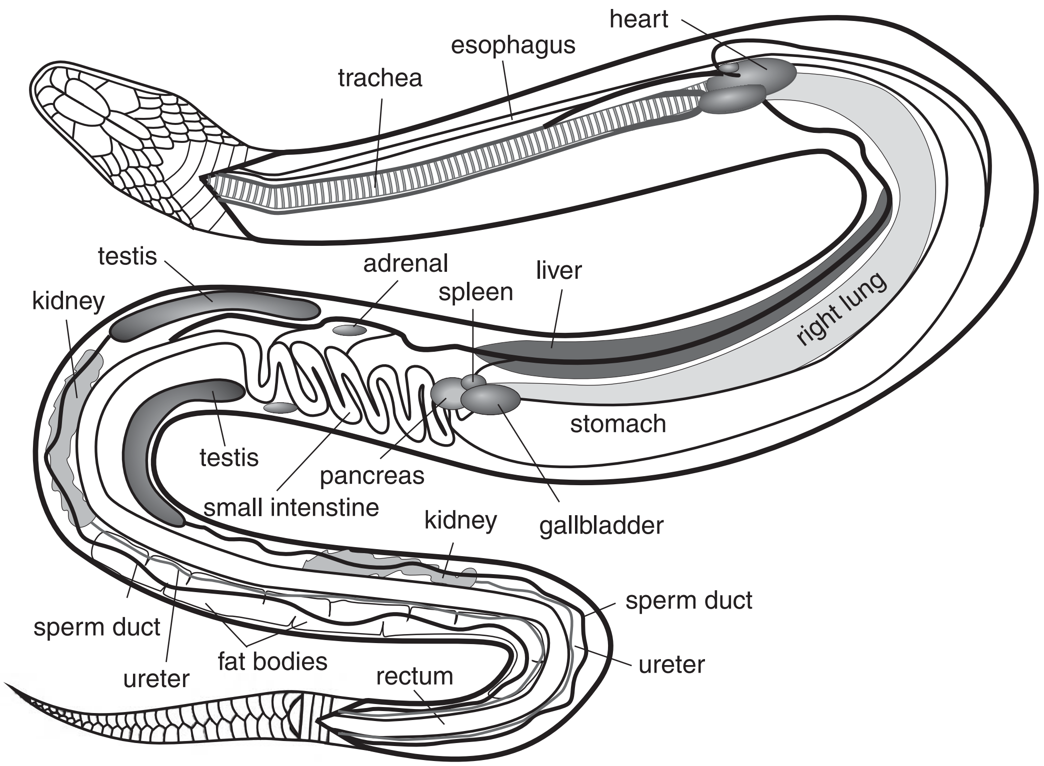


FIGURE 2.22 Visceral anatomy (ventral view) of a generalized male snake.

The mouth of reptiles opens directly into the buccal cavity. The lips bordering the mouth are flexible skin folds, but they are not movable in lepidosaurs. Lips are absent in crocodylians and turtles. Tooth rows on the upper and lower jaws of most reptiles form a continuous border along the internal edge of the mouth. Turtles lack teeth and have keratinous jaw sheaths. In reptiles, teeth typically serve for grasping, piercing, and fragmentation of food items. Only in a few species do the teeth cut and slice (e.g., *Varanus*) or crush (*Dracaena*). A well-developed tongue usually occupies the floor of the mouth. Tongue morphology varies in association with a variety of feeding behaviors; chameleons have projectile tongues, and varanoid lizards and snakes have telescoping tongues. The roof of the buccal cavity is formed by the primary palate. Two pairs of structures open anteriorly in the roof of the buccal cavity; the small Jacobson's organ opens just inside the mouth and is immediately followed by the larger internal nares. The crocodylians have a secondary palate that creates a separate respiratory passage from the internal nares on the primary palate to the beginning of the pharynx. This passage allows air to enter and exit the respiratory system while food is held in the mouth. A few turtles and snakes (aniliids) have developed partial secondary palates.

The pharynx is a small antechamber behind the buccal cavity. A valvular glottis on its floor is the entrance to the trachea. On the rear wall of the pharynx above the glottis, a muscular sphincter controls the opening into the esophagus. The eustachian tubes, one on each side, open onto the roof of the pharynx. Each tube is continuous with the middle-ear chamber to permit the adjustment of air pressure on the tympanum. Middle ears and eustachian tubes are absent in snakes.

The esophagus is a distensible, muscular walled tube of variable length between the buccal cavity and the stomach. In snakes and turtles, the esophagus may be a one-quarter to one-half of the body length (Fig. 2.22). It is proportionately shorter in reptiles with shorter necks. The stomach is a heavy muscular and distensible tube, usually J-shaped and largest in the curved area. The stomach narrows to a thick muscular sphincter, the pylorus or pyloric valve. This valve controls the movement of the food bolus from the stomach into the small intestine. The small intestine is a long narrow tube with little regional differentiation externally or internally; the pancreatic and hepatic ducts empty into its forepart. The transition between the small and large intestine is abrupt. The diameter of the latter is several times larger than the former, and often a small outpocketing, the caecum, lies adjacent to the juncture of the two intestines. The large intestine or colon is a straight or C-shaped tube that empties into the cloaca. The large intestine is the least muscular and most thin-walled structure in the digestive tract (Guard, 1979).

Strictly speaking, the cloaca is part of the digestive tract since it is derived from the embryonic hindgut. A muscular sphincter, the anus, lies between the large intestine and the cloaca. The dorsal portion of the cloaca is the coprodaeum and is the route for the exit of feces. The urodaeum or urogenital sinus is a ventral outpocket of the cloaca and extends a short distance anteriorly and beneath the large intestine. Digestive, urinary, and genital products exit via the vent, a transverse slit in turtles and lepidosaurs and a longitudinal slit in crocodylians.

Digestive Glands

A variety of glands occur within the digestive tract. The lining of the buccal cavity contains unicellular and multicellular glands (Jaeger and Hillman, 1976). The latter secrete mucus that lubricates the surface, and although numerous and widespread in terrestrial amphibians, they are less abundant in aquatic taxa such as pipid frogs and aquatic salamanders. The intermaxillary gland opens in the middle of the palate and secretes a sticky compound that helps prey adhere to the tip of the tongue. Numerous unicellular and multicellular glands are present in the lining of the remainder of the digestive tract; most secrete mucus, and a few secrete digestive enzymes and acid in the stomach.

The liver and pancreas are major secretory structures derived from the embryonic gut that lie astride the stomach and duodendum. The liver is the largest of the digestive glands, serving as a nutrient storage organ and producer of bile. The bile drains from the liver into the gallbladder, and then moves via the bile duct into the duodenum, where it assists in the breakdown of food. The pancreas is a smaller, diffuse gland. It secretes digestive fluids into the duodenum and also produces the hormone insulin.

Similarly, the oral cavity of reptiles contains numerous glands (Kochva, 1978). Small, multicellular mucous glands are a common component of the epithelial lining and compose much of the tissue on the surface of the tongue. Larger aggregations of glandular tissue, both mucous and serous, form five kinds of salivary gland: labial, lingual, sublingual, palatine, and dental. In venomous snakes, the venom glands are modified salivary glands. Mucous glands occur throughout the digestive tract. The stomach lining is largely glandular and has several types of gastric glands. The small intestine has many small glands within its epithelial lining. The liver, usually the largest single organ in the visceral cavity, and pancreas produce secretions that assist in digestion. The pancreas is a smaller, more diffuse structure that lies within the visceral peritoneum.

Respiratory Structures

Lungs

The respiratory passage includes the external nares, olfactory chambers, internal nares, buccopharyngeal cavity, glottis, larynx, trachea, bronchial tubes, and lungs. The glottis, a slitlike opening on the floor of the pharynx, is a valve that controls airflow in and out of the respiratory passages. The glottis opens directly into a boxlike larynx. This voice box occurs in all amphibians but is anatomically most complex in frogs. The larynx exits into the trachea; the latter bifurcates into the bronchi and then into the lungs. Bronchi are absent in all frogs except the pipids. Amphibian lungs are highly vascularized, thin-walled sacs. Internally, they are weakly partitioned by thin septa composed of connective tissue. This weak partitioning and the small size, or even absence, of the lungs emphasizes the use of multiple respiratory surfaces in amphibians. Lung ventilation is triphasic by means of a buccopharyngeal force pump mechanism. Inhalation begins with nares open, glottis closed, and depression of the buccopharyngeal floor, which draws air into this cavity. The glottis then opens, and elastic recoil of the lungs forces the pulmonary air out and over the new air in the buccopharyngeal pocket. The nares close and the buccopharyngeal floor contracts and pumps air into the lungs as the glottis closes to keep air in the lungs under supra-atmospheric pressure. Similar but faster and shallower throat movements occur regularly in frogs and salamanders; these smelling movements rapidly flush air in and out of the olfactory chambers.

Reptiles possess an identical respiratory pathway. Air exits and enters the trachea through the glottis at the rear of the pharynx. The glottis and two or three other cartilages form the larynx, a simple tubular structure in most reptiles. The larynx is the beginning of the trachea, a rigid tube with closely spaced cartilaginous rings within its walls (the rings are incomplete dorsally in squamates). The trachea extends down the neck beneath the esophagus and forks into a pair of bronchi, each of which enters a lung.

Lung structure is variable among reptiles (Fig. 2.23; Perry, 1998). Most lepidosaurs have simple saclike lungs. Each bronchus empties into a large central chamber of the lung. Numerous faveoli (small sacs) radiate outward in all directions, forming a porous wall around the central chamber. The walls of the faveoli are richly supplied with blood and provide the major surface for gaseous exchange. Iguanians have the central chamber of each lung divided by a few large septae. These septae partition the lung into a series of smaller chambers, each of which possesses porous faveolar walls. Varanids, crocodylians, and turtles also have multichambered lungs; a bronchus extends into each lung and subdivides into many bronchioles, each ending in a faveolus. In some lizards, smooth-walled tubes project from the chamber beyond the surface of the lung. No gas exchange occurs in these air sacs; rather the sacs may permit the lizard to hold a larger volume of air. The sacs are used by some species to inflate their body to intimidate predators.

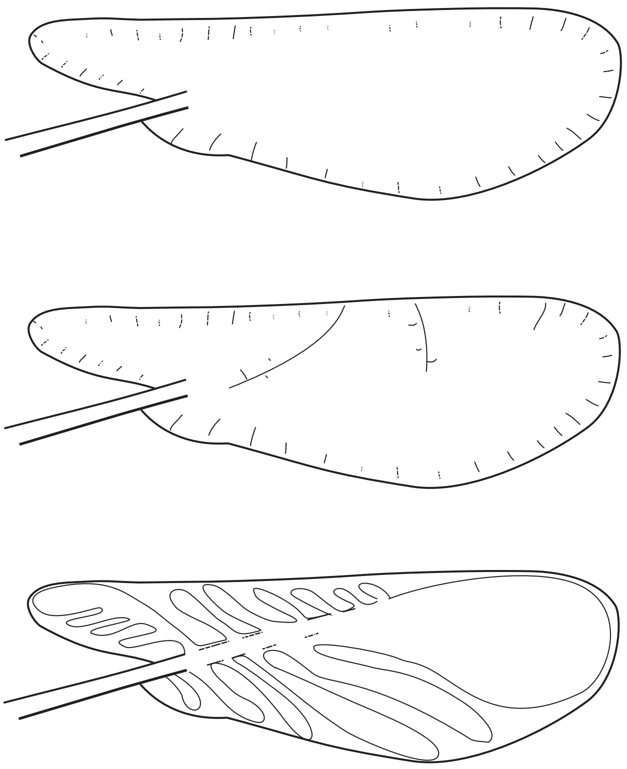


FIGURE 2.23 Internal morphology of generalized reptilian lungs with schematic cross sections of a single-chambered lung (top), a transitional lung (middle), and a multichambered lung (bottom). The central chamber of a single-chambered lung is not divided by a major septum, although small niches are commonly present along the wall. The transitional lung has a central lumen partially divided by large septum. The multichambered lung is partitioned into numerous chambers of various sizes; all chambers communicate with the intrapulmonary bronchus via an airway. Adapted from Perry (1983).

The development of air sacs is even more extensive in snakes because of their highly modified lungs (Wallach, 1998). A single functional right lung and a small, nonfunctional left lung are the common condition (Fig. 2.22). A functional left lung occurs only in a few snakes (e.g., *Loxocemus*), and in these snakes, it is distinctly smaller than the right lung. The trachea and right bronchus extend into the lung and empty into a chamber with a faveoli-filled wall as in most lizards. Snake lungs are typically long, one-half or more of the snake's body length. Usually the posterior one-third or more is an air sac.

Many snakes also possess a tracheal lung. This lung is a vascular, faveoli-dense sac that extends outward from where the tracheal rings are incomplete dorsally; posteriorly, it abuts the right lung. Breathing occurs by the expansion and contraction of the body cavity. Among squamates, the thoracic cavity is enlarged during inhalation by the contraction of the intercostal muscles drawing the ribs forward and upward. Compression of the cavity during exhalation occurs when the muscles relax and the weight of the body wall and adjacent organs squeeze the lungs. In crocodylians, the diaphragm contracts and enlarges the thoracic cavity for inhalation; abdominal muscles contract and drive the liver forward for exhalation. In turtles with rigid shells, the posterior abdominal muscles and several pectoral girdle muscles expand and compress the body cavity for breathing.

Other Respiratory Surfaces

In amphibians, lungs are only one of several respiratory structures. A few caecilians have a small third lung budding off the trachea. The buccopharyngeal cavity is heavily vascularized in many amphibians and is a minor gaseous exchange surface.

Gills are the major respiratory structures in larvae and a few adult salamanders (Warburg et al., 1994). Three pairs of external gills, which develop and project from the outside of the pharyngeal arches, occur in salamanders and caecilians. External and internal gills occur sequentially in anuran larvae; the former arise early, remain largely rudimentary, and are replaced quickly by the latter.

In most adults and larvae, the skin is the major respiratory surface and is highly vascularized. Gaseous exchange in all vertebrates requires a moist surface; drying alters the cell surfaces and prevents diffusion across cell membranes.

Reptiles are dependent upon their lungs for aerial respiration. None of the aquatic species has developed a successful substitute for surfacing and breathing air. Long-term submergence in reptiles is possible owing to a high tolerance to anoxia, a greatly suppressed metabolism, and varying degrees of cutaneous respiration. Softshell turtles are purported to obtain more than 50% of their respiratory needs by cutaneous and buccopharyngeal respiration when submerged, but experimental results of different investigators are conflicting. The accessory cloacal bladders of turtles have also been proposed as auxiliary respiratory structures; however, their walls are smooth and lightly vascularized, unlike most respiratory surfaces.

URINARY AND REPRODUCTIVE ORGANS—WASTE REMOVAL AND PROPAGATION

The urinary and reproductive systems are intimately related in their location along the midline of the dorsal body wall and by a shared evolutionary history. Through generations of vertebrates, the male gonads have usurped the urinary ducts of primitive kidneys for transportation of sperm. Most adult amphibians have opisthonephric kidneys whereas amniotes have metanephric kidneys. The development of these two kidney types is different but both pass through a transient embryonic stage, the mesonephros. In amniotes, ducts from the ancestral opisthonephric kidney system have been usurped by the reproductive system, and the opisthonephric kidney system, including the ducts, has been replaced by the metanephric kidney system and ducts. The structures of each system are paired.

Kidneys and Urinary Ducts

The kidneys remove nitrogenous waste from the blood stream and maintain water balance by regulating the removal or retention of water and salts. The functional unit of the kidney is the nephron or kidney tubule. Each nephron consists of a renal corpuscle and a convoluted tubule of three segments, each of variable length in different species. The corpuscle encloses a ball of capillaries, and most filtration occurs here. Filtration (selective secretion) may also occur in the tubule, but resorption of salts and water to the blood is the major activity as the filtrate passes through the tubule. The tubules of adjacent nephrons empty into collecting ducts, which in turn empty into larger ducts and eventually into the urinary duct that drains each kidney.

Primitively and embryologically, the kidney developed from a ridge of mesomeric tissue along the entire length of body cavity. In modern amphibians, a holonephric kidney exists embryologically but never becomes functional. Instead the functional kidney (pronephros) of embryos and larvae arises from the anterior part of the "holonephric" ridge. The pronephros begins to degenerate as the larva approaches metamorphosis, and a new kidney, the opisthonephros, develops from the posterior part of the ridge. The tubules of the anterior end of the male's opisthonephric kidney take on the additional role of sperm transport. In primitive salamanders, this new role causes the anterior end of the kidney to narrow and the tubules to lose their filtration role. In caecilians, the kidney remains unchanged, and in anurans and advanced salamanders, the kidney shortens into a compact, ellipsoidal organ as a result of the loss of the anterior end. A single urinary duct, the archinephric duct, receives urine from the collecting ducts of each kidney and empties into the cloaca. Two principal patterns characterize urinary drainage in amphibians. Only the archinephric duct drains the kidney in the caecilians and primitive salamanders, whereas in frogs and advanced salamanders, the archinephric duct drains the anterior portion of the kidney and an accessory duct drains the posterior half. The bladder has a single, separate duct, the urethra, that empties into the cloaca; fluids enter and exit the bladder through this duct.

The metanephric kidneys of reptiles vary in size and shape. They are smooth, equal-sized, and nearly spherical in some lizards, and smooth or rugose, elongated cylinders in snakes (Fig. 2.22). The kidneys are lobate spheroids in crocodylians and turtles. In all forms, the kidneys lie side by side on the dorsal body wall in front of the cloaca, and in all, a ureter drains each kidney and empties independently into the cloaca (Fig. 2.24). An elastic-walled urinary bladder is present in turtles and most lizards but absent in snakes and crocodylians. The bladder joins the cloaca through a single median duct, the urethra, through which urine enters and exits.

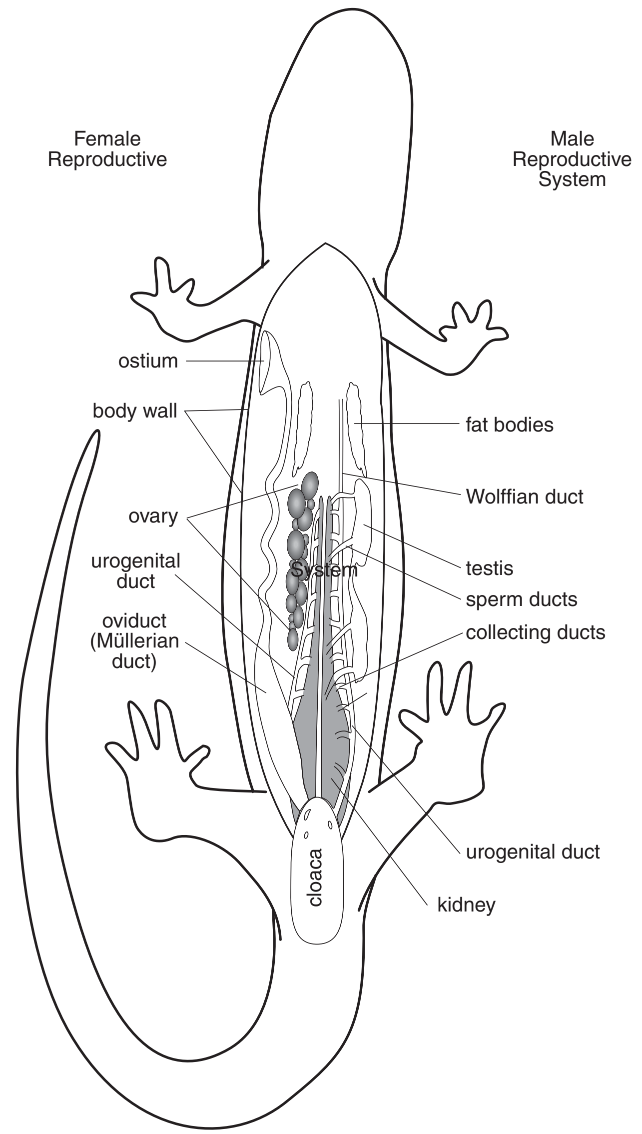


FIGURE 2.24 Ventral view of the reproductive tracts of a female (left side) and male (right side) salamander.

Gonads and Genital Ducts

The female and male gonads, the ovaries and testes, develop from the same embryological organs. The undifferentiated organs arise on the body wall between the middle of the kidneys. Germ cells or gametes migrate into each organ and initiate the reorganization and consolidation of the pregonadal tissue into an external cortex and internal medulla. Later, when sexual differentiation occurs, the cortex is elaborated into an ovary in females, and the medulla into a testis in males.

Structurally, the male and female gonads are quite different. The ovary is a thin-walled sac with the germ cells sandwiched between the inner and outer ovarian walls. The germ cells divide, duplicate themselves, and produce ova. A single layer of follicle cells in the epithelium of the ovarian wall encases each ovum, providing support and nourishment. This unit, the follicle, which consists of the ovum and follicle cells, grows into the ovarian lumen. Numerous developing follicles form the visible portion of the ovaries in gravid females. The testis is a mass of convoluted seminiferous tubules encased in a thin-walled sac. Small amounts of interstitial tissue fill the spaces between the tubules. The developmental cycle (gametogenesis) of the ova and spermatozoa is presented in Chapter 4.

In amphibians, spermatozoa collect in the lumen of the seminiferous tubules and then move sequentially through progressively larger collecting ducts into the kidney collecting ducts before emptying into the archinephric duct. Because of its dual role in urine and sperm transport, the archinephric duct is called the urogenital or Wolffian duct. The oviducts (Müllerian ducts) are paired tubes, one on each side of the dorsal body wall, lateral to each ovary. Each arises *de novo* as a fold of the peritoneum, or in salamanders by a splitting of the archinephric duct. The anterior end of the oviduct remains open as an ostium; ova are shed into the body cavity and move to and through the ostium into the oviduct. The posterior part of the oviduct is expanded into an ovisac which empties into the cloaca; after ovulation, eggs remain briefly in the ovisac prior to amplexus and egg laying. Oviducts form in both males and females, degenerating although not disappearing in many male amphibians, where this nonfunctional duct is called Bidder's duct. Similarly, some males retain a part of the gonadal cortex attached to the anterior end of the testis. This structure, common in bufonids, is Bidder's organ.

In reptiles, a pair of ovaries occupies the same location as the testes of the males, and the right ovary precedes the left in squamates. Each ovary is an aggregation of epithelial cells, connective tissue, nerves, blood vessels, and one or more germinal cell beds encased in an elastic tunic. Depending upon the stage of oogenesis, each ovary can be a small, granular-appearing structure or a large lobular sac filled with spherical or ellipsoidal follicles. An oviduct is adjacent to but not continuous with each ovary. The ostium (mouth) of the oviduct lies beside the anterior part of the ovary and enlarges during ovulation to entrap the ova. The body of the oviduct has an albumin-secreting portion followed by a thicker shell-secreting portion. The oviducts open independently into the urogenital sinus of the cloaca.

The testis is a mass of seminiferous tubules, interstitial cells, and blood vessels encased in a connective tissue sheath. The walls of seminiferous tubules are lined with germinal tissue. The sperm produced by these tubules empties through the efferent duct into the epididymis on the medial face of the testis. The ductuli coalesce into the ductus epididymis that runs to the cloaca as the vas (ductus) deferens. In shape, testes vary from ovoid to spindle-shaped. The testes are usually adjacent to each other, although the right testis lies anteriorly, especially in snakes and most lizards.

All living reptiles have copulatory organs, which are rudimentary in *Sphenodon*. Crocodylians and turtles have a single median penis that originates in the floor of the cloaca. The squamates have a pair of hemipenes, each of which originates at the junction of the cloacal vent and the base of the tail.

ENDOCRINE GLANDS—CHEMICAL REGULATORS AND INITIATORS

The endocrine system comprises numerous glands scattered throughout the body. The glands are an integrative system, initiating and coordinating the body's reactions to internal and external stimuli. Unlike the nervous system, the glands do not communicate directly with one another and their target organs. Instead, they rely on vascular and neural pathways to transmit their chemical messengers. Unlike other organ systems, the endocrine system is a composite of unrelated anatomical structures from other systems; for example, the pituitary of the nervous and digestive systems, the gonads of the reproductive system, or the pancreas of the digestive system. Only a few of the many glands and their functions are mentioned here, and these are described only superficially. The commonality of all endocrine organs is their secretion of one or more chemical messengers, hormones, that stimulate or arrest the action of one or more target organs, including other endocrine glands or tissues. Hormones work both in short-term cycles and continuously to maintain a stable internal environment and in the long term and cyclically to control periodic behaviors, such as reproduction.

Pituitary Gland

The pituitary gland or hypophysis is the master gland of the body. Structurally, it consists of two parts: the neuropophysis, which arises from the ventral portion of the diencephalon, and the adenopophysis, which is derived from the roof of the buccal cavity. The neuropophysis and adenopophysis interdigitate and are joined by neural and vascular connections. The brain receives stimuli that trigger the release of neurohormones by the brain cells. These hormones reach the neuropophysis through blood vessels or secretory axons of neurons ending in the neuropophysis. In turn, the neuropophysis produces hormones that stimulate the adenopophysis (e.g., GnRH, gonadotropin-releasing hormone) or act directly on the target organs (ADH, antidiuretic hormone; MSH, melanophore-stimulating hormone). The adenopophysis secretes six major hormones: adrenocorticotropin, two gonadotropins (FSH, LH), prolactin, somatotropin, and thyrotropin. These hormones control growth, metamorphosis, reproduction, water balance, and a variety of other life processes.

Pineal Complex

The pineal complex consists of a pineal (epiphysis) and a frontal (parapineal) organ, each arising embryologically from the roof of the diencephalon (Fig. 2.17). These two organs are light receptors as well as endocrine glands. As light receptors, they record the presence or absence of light, and as glands they produce and release melatonin. These two functions are associated with cyclic activities, including both daily cycles or circadian rhythms and seasonal cycles. Frogs possess both a pineal organ lying inside the skull and a frontal organ piercing the skull and lying beneath the skin on top of the head. Caecilians and salamanders have only the pineal organ, which may extend upward to, but does not pierce, the skull roof. All reptiles except crocodilians have pineal organs that lie on the brain but do not exit the skull. Some lizards (e.g., iguanians) have pineal organs that pass through the skull and form a parietal eye.

Thyroid and Parathyroid Glands

These two glands are linked because of their shared location in the throat adjacent to the larynx and trachea (Fig. 2.25). Although both arise embryologically as outpocketings of pharyngeal pouches, they have quite dissimilar functions. The parathyroid hormones regulate calcium levels in the blood, and hence control bone growth and remodeling. The thyroid is well known for its accumulation of iodine and the importance of its hormones in controlling development, metamorphosis, and growth. Amphibians typically have a bilobular thyroid and a pair of parathyroids. In reptiles, the thyroid assumes a variety of forms. It is a single, nearly spherical organ in turtles and snakes. In crocodylians, it is an H-shaped, bilobular organ which has a lobe on each side of the trachea connected by a narrow isthmus. Some lizards share this bilobular condition, others have a lobe on each side but no isthmus, and still others have a single median gland. In *Sphenodon*, the gland is transversely elongated. The reptilian parathyroid appears as one or two pair of granular glands, usually at the base of the throat adjacent to the carotid arteries.

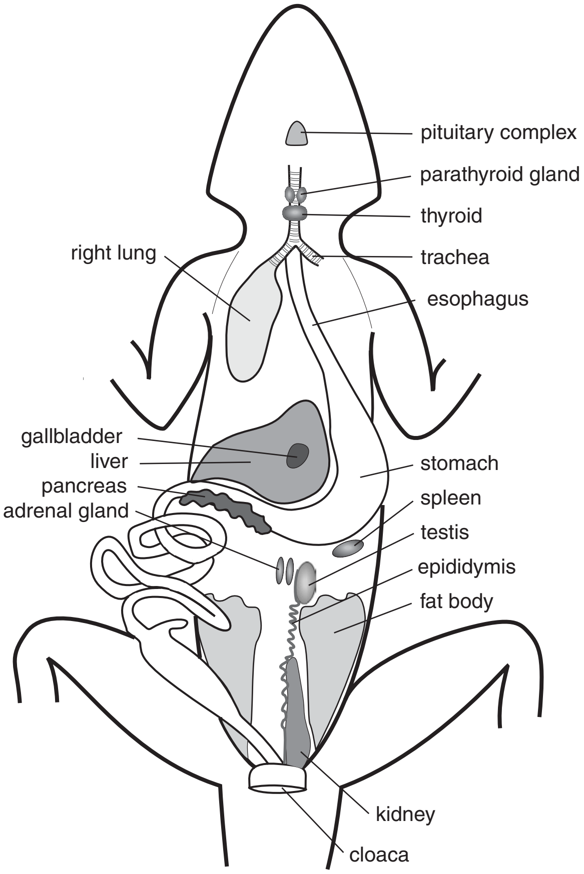


FIGURE 2.25 Schematic lizard showing the location of some digestive and endocrine glands.

Pancreas

The pancreas is composed of both exocrine and endocrine tissues. The exocrine portion secretes digestive enzymes; clusters of cells, the Islets of Langerhans, secrete the hormone insulin. Insulin is critical for regulating carbohydrate metabolism; it stimulates the liver and adipose tissue to remove glucose from the blood stream through glycogen production and fat synthesis, respectively. Insulin facilitates striated muscle activity by increasing the movement of glycogen into the muscle cells. In amphibians, the pancreas is a diffuse gland that lies within the mesentery between the stomach and duodenum. The reptilian pancreas is a compact organ that lies in the mesentery adjacent to the duodenum (Fig. 2.25).

Gonads

Aside from producing gametes, the gonads also produce sex hormones. The maturation and production of gametes are closely regulated by the brain, through the production of hypothalamohypophyseal hormones, and the pituitary, by the production of gonadotropins. In turn, the hormonal response of the gonads influences the secretory cycles of these two organs. In addition to initiating gametogenesis, the gonadotropins stimulate the production of estrogens and androgens, the female and male sex hormones, by gonadal tissues. Estrogens and androgens are steroids, and several closely related estrogens or androgens are produced in each sex. Stimulation and inhibition of the reproductive structures are obvious actions of the sex hormones, but they interact also with a variety of other tissues. They induce the skin to produce secondary sexual characteristics, and they provide a feedback mechanism to the hypothalamic-pituitary complex. Estrogens are produced largely by the follicle cells in the ovarian follicles and the corpus lutea. Androgens are derived principally from the cells of Leydig that lie in the interstitial tissue between the seminiferous tubules. The Sertoli cells also produce minor amounts of androgens.

Adrenals

The adrenals are bilaterally paired glands that lie anterior to the kidneys in reptiles (Fig. 2.25) and elongate glands that lie on the ventral surface of the kidneys in amphibians. Each adrenal is an admixture of two tissues: the interrenal (cortical) cells form the main matrix of the gland and adrenal (medullary) cells form strands and islets within the interrenal matrix. These two tissues have different embryological origins and distinctly different functions. The chromaffin cells produce adrenaline and noradrenaline, both of which affect blood flow to brain, kidney, liver, and striated muscles, mainly during stress reactions. The interrenal tissue produces a variety of steroid hormones. One group of interrenal hormones affects sodium and potassium metabolism, another group affects carbohydrate metabolism, and a third group affects the androgens and reproductive processes.

ADDITIONAL READING

Duellman and Trueb (1986).

Gans and co-editors (1969 et seq.). "Biology of the Reptilia," Vols. 1–4, 6, 11, 14–15, 19 morphology, various publishers.

Hanken, J., and Hall, B. K. (eds.) (1993). "The Skull," Vol. 1–3.

Heatwole, H., and co-editors (1994 et seq.). "Amphibian Biology," Vols. 1 and 3.

REFERENCES

General: Bellairs, 1969; Clarke, 1997; Duellman and Trueb, 1986; Gans and coeditors, 1969 et seq.; Hanken and Hall, 1993 (Vol. 1, Chap. 8; Vol. 2, Chaps. 6, 7); Hayes, 1997a.

Development and Growth: Ova, Sperm, and Fertilization: Wassarman, 1987.

Early Development: Elinson, 1987.

Embryogenesis: Nelsen, 1953; Rugh, 1951.

Morphogenesis: Developing Form and Function: Fox, 1983; Hanken, 1989.

Heterochrony: Reilly et al., 1997.

Embryonic Lifestyles: Protective Barriers: Packard and DeMarco, 1991; Seymour and Bradford, 1995.

Larvae-Free-Living Embryos: Altig and Johnston, 1986, 1989; Orton, 1953; Townsend and Stewart, 1985.

Life in an Egg Shell: Ewert, 1985; Kennett et al., 1993; Packard et al., 1977, 1991; Packard and Packard, 1988; Packard et al., 1982.

Changing Worlds: Metamorphosis: Denver, 1997; Fox, 1986; Hayes, 1997b; Hourdry and Beaumont, 1985; Werner, 1986.

Hatching and Birth: Ewert, 1985; Packard, 1994; Townsend and Stewart, 1985.

Growth: Mechanics of Growth: Andrews, 1982a; Seben, 1987.

Age: Andrews, 1976; Barbault and Rodriques, 1979; Grubb, 1971; Peterson et al., 1983.

Integument: Bechtel and Bechtel, 1991; Elias and Shapiro, 1957; Fox, 1986; Heatwole and Barthalmus, 1994.

Integumentary Structures: Komnick, 1986; Landmann, 1975, 1986; Lillywhite and Maderson, 1982; Quay, 1986; Ruibal and Shoemaker, 1984; Zimmerman and Heatwole, 1990.

Ecdysis: Irish et al., 1988; Maderson, 1965; Maderson et al., 1998.

Coloration: Bagnara, 1986.

Skeleton and Muscles: Head and Hyoid: Bellairs and Kamal, 1981; Edmund, 1969; Frazzetta, 1986; Gaffney, 1979; Haas, 1973; Iordansky, 1973; Oelrich, 1956; Romer, 1956; Trueb, 1973.

Vertebral Column: Gasc, 1981; Hoffstetter and Gasc, 1969; Romer, 1956.

Girdles and Limbs: Burke, 1989; Romer, 1956.

Nerves and Sense Organs: Nervous System: Llinás and Precht, 1976.

Sense Organs: Cutaneous Sense Organs: Catton, 1976; During and Miller, 1979; Landmann, 1975; Lannoo, 1987a,b; Spray, 1976; Whimster, 1990.

Ears: Baird, 1970; Capranica, 1986; Fritzsch and Wake, 1988; Hetherington, 1985; Hetherington et al., 1986; Manley, 1990; Wever, 1978, 1985.

Eyes: Schaeffel and de Queiroz, 1990; Underwood, 1970.

Nasal Organs: Halpern, 1992; Parsons, 1970; Scalia, 1976.

Internal Sense Organs: During and Miller, 1979; Schwenk, 1985.

Heart and Vascular Network: Blood: M.-C. Saint-Girons, 1970.

Arterial and Venous Circulation: Burggren, 1987; Saint-Aubain, 1985; Young, 1988.

Lymphatic Network: Ottaviana and Tazzi, 1977.

Heart: Farrell et al., 1998; Jones, 1996.

Digestive And Respiratory Organs: Digestive Structures: Guard, 1979; Junqueira et al., 1999; Luppa, 1977; Schwenk, 1986; Young, 1997.

Digestive Glands: Jaeger and Hillman, 1976; Kochva, 1978; Komnick, 1986; Miller and Lagios, 1970; Saint-Girons, 1988; Schaffner, 1998.

Respiratory Structures: Lungs: Kinkead, 1997; Perry, 1983, 1998; Ruben et al., 1997 (see Comments, *Science* 237: 45–48); Wallach, 1998.

Other Respiratory Surfaces: Warburg et al., 1994.

Urinary and Reproductive Organs: Kidneys and Urinary Ducts: Fox, 1977.

Gonads and Gonadal Ducts: Fox, 1977.

Endocrine Glands: Pang and Schreibman, 1986.

Pituitary Gland: H. Saint Girons, 1970; Schreibman, 1986.

Pineal Complex: Engbretson, 1992; Quay, 1979; Ralph, 1983.

Thyroid and Parathyroid Glands: Lynn, 1970.

Pancreas: Epple and Brinn, 1986; Miller and Lagios, 1970.

Gonads: Fox, 1970.

Adrenals: Gabe, 1970.

Chapter

3

Evolution of Ancient and Modern Amphibians and Reptiles

Tetrapods adapted first to a shallow water existence and then to a totally terrestrial one. Some taxa later returned to the water (e.g., many turtles). The origin of terrestriality was followed quickly by an eruption of new species with new lifestyles and body forms. As portrayed in Chapter 1, this adaptive radiation was not confined to amphibians and reptiles (that is, strictly the Amphibia and Reptilia clades) but occurred in other ancient tetrapods who left no living descendants. In a general sense, the amphibians had a head start in their diversification but the reptiles were not laggards. By the mid-Permian, the balance had shifted, and amniotes became the dominant group in the number of species and the number of individuals, at least judging by the fossil record. The history of these adaptive radiations is complex and extensive. We offer only a brief introduction to some extinct amphibian and reptilian taxa and an overview of the history of the clades that compose the modern herpetofauna.

HISTORY OF AMPHIBIANS

Radiation among Early Anamniotes

Tetrapods in the Late Devonian were aquatic, but adaptations had appeared that would permit them to become terrestrial (Ahlberg and Milner, 1994). Vegetation completely covered the lowland coastal areas and floodplains, for the plants were no longer confined to water or the margins of streams, lakes, and seas. Herbs and shrubs were the dominant plants, but trees had appeared and perhaps in some places formed forests. Plants were even beginning to invade the upland areas. While some arthropods likely were living their full lives on land, a few vertebrates were, at best, semiaquatic. These early tetrapods (e.g., *Acanthostega*, *Ichthyostega*) lived in the heavily vegetated, shallow water. Their large heads and tooth-filled jaws suggest that they were formidable predators and fed on large prey because they ranged from 0.5 to 1.2 m total length (TL). Their bodies were fusiform and strongly tailed (Fig. 1.6), suggesting that they were capable of fast burst swimming, but they also had short, stout fore- and hindlimbs, perhaps permitting them to "walk" slowly and stalk prey in dense aquatic vegetation. Unlike subsequent tetrapods, all known early tetrapods had more than five digits; *Acanthostega* had eight digits on its forefeet.

Amphibians of the Late Paleozoic

Tetrapods largely disappeared from the fossil record at the end of the Devonian. They next appeared en masse in the Upper Mississippian when fossils representing lowland lake and swamp assemblages reappeared (Ahlberg and Milner, 1994; Milner, 1988). More than a dozen clades are recognized and include several groups of anthracosaurs, at least three amphibian groups, and the enigmatic *Crassigyrinus* (Fig. 3.1). Most of these tetrapods were aquatic, although the lowlands were inhabited by an even greater diversity of plants and plant communities. Amphibians certainly lived there as well. The anthracosaurs *Proterogyrinus* and *Eoherpeton* were large (1 m TL) aquatic predators. The baphetids (= loxommatids) were moderate-sized, reduced-limbed animals, which are known principally from skulls with numerous pointed teeth, some enlarged and fanglike. Baphetids are recognized by an anterior elongation of each orbit that probably housed a large gland. Two other anthracosaur groups, the embolomeres and eoherpetontids, were dominant members of the early tetrapod community. Both groups were mainly aquatic animals. The embolomeres were the largest tetrapods, ranging from 1 to 4 m (TL). All had heavy crocodile-like skulls and short, robust limbs. The limbless aistopodans were delicate eel-like amphibians; none exceeded 70 cm (TL). Presumably they were aquatic and semiaquatic, because their fragile skulls do not match the needs of burrowing animals. The colosteids, possibly basal temnospondyls, were small, aquatic amphibians that had elongated bodies and small, well-developed limbs. The temnospondyl trimerorhachoids included limbed and reduced-limbed forms and likely contained both semiaquatic and aquatic members. They were especially long-lived taxa, appearing in the mid-Mississippian and surviving to the end of the Permian (Fig. 3.2). Edopoids, another temnospondyl group, also persisted through the Carboniferous into the Early Permian. They were larger, more robust amphibians. The earlier edopoids were mainly aquatic forms, but the later ones became increasingly terrestrial.

In the Pennsylvanian, many of the preceding groups were joined by new groups of tetrapods: geophyrostegid and limnoscelid anthracosaurs, eryopoid amphibians, nectrideans (Fig. 3.1), and three groups of microsaurs. This fauna remained moisture dependent and lived

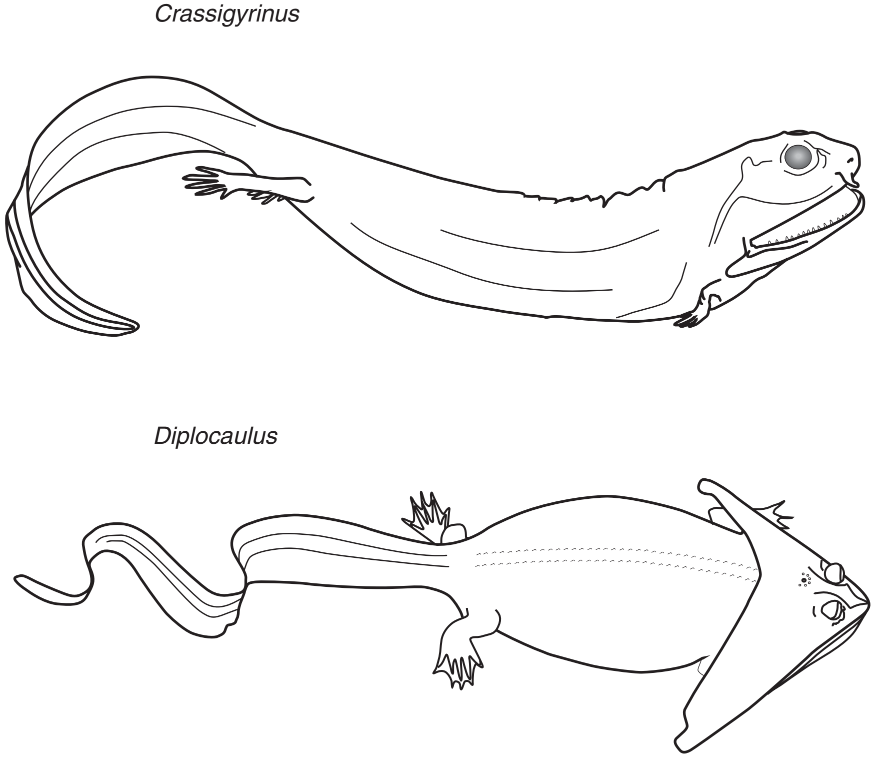


FIGURE 3.1 Paleozoic amphibians, *Crassigyrinus* (group, incertae sedis) and *Diplocaulus* (Nectridea). Adapted from Milner et al. (1986) and Milner (1980).

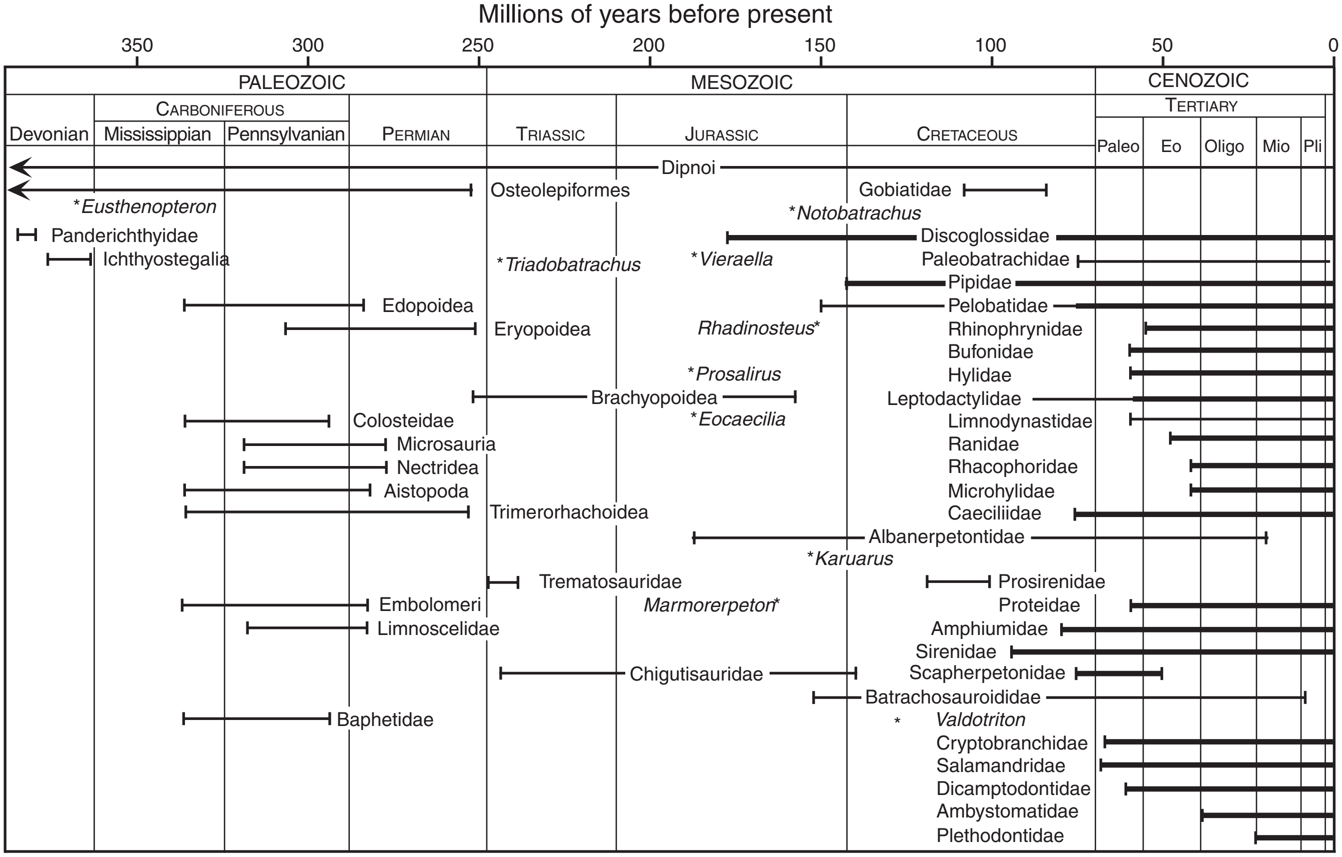


FIGURE 3.2 Geological occurrence of some early tetrapods, including extinct and living amphibians. Abbreviations for Cenozoic epochs are Paleo, Paleocene; Eo, Eocene; Oligo, Oligocene; Mio, Miocene; and Pli, Pliocene. Pleistocene is the narrow, unlabeled epoch on the far right side of the chart.

predominantly in the lowlands. The climate was generally hot and wet and supported diverse and dense plant communities. By this time the uplands also bore a thick plant cover. These tetrapods were primarily aquatic forms, although a few had become terrestrial. For example, the terrestrial limnoscelids were moderate-sized (1–2 m TL), with robust bodies and limbs and long tails. Structurally, they possessed some features that would appear in reptiles. The eryopoids included aquatic to terrestrial, small to large amphibians. The heavy-bodied *Eryops* is characteristic of this group, although it was larger (nearly 2 m TL) than most eryopoids. The nectrideans were moderate-sized, newtlike amphibians, all less than 0.5 m TL. The heads of some were arrow-shaped with large, laterally projecting horns. This head shape appears to be an adaptation to permit the rapid opening of the mouth for suction-gape feeding (Milner, 1980). Other nectrideans had more typically shaped heads with strong dentition for snap-and-grasp feeding. The microsaurs were small (most <50 cm TL), salamander-like tetrapods. They commonly had long bodies and tails, with short limbs. Presumably they were predominantly aquatic and semiaquatic.

Amniotes appeared in the Late Carboniferous (Fig. 3.2). They had already diverged into reptiles and synapsids. Many anamniote groups persisted into the Early Permian, but not beyond. Only the trimerorhachoids and eryopoids survived into the Late Permian, and they were joined by the seymouriamorphs (Fig. 3.3) for most of their Permian tenure. A few small anthracosaurs appeared briefly. The loss of amphibian and anthracosaurian diversity occurred concurrently with the diversification of the amniotes and a shift to an arid climate. Aquatic habitats shrunk and disappeared. Plant cover was reduced, and the drier upland vegetation spread into the lowlands. This changing climate and landscape favored the terrestrial adaptations of the amniotes.

The trimerorhachoids had greatly reduced limbs and were probably highly aquatic. The eryopoids as a group remained diverse in size, body form, and habits (aquatic to terrestrial). The surviving embolomeres had become shallow-water denizens in contrast to their deep-water

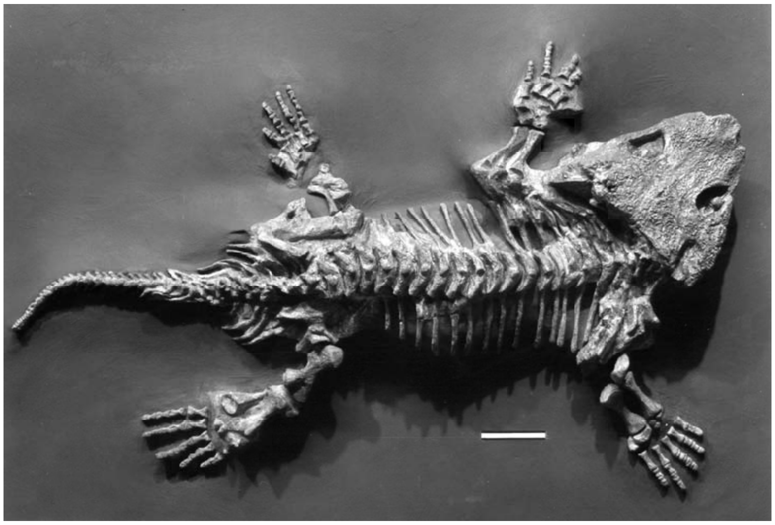


FIGURE 3.3 *Seymouria*, an Early Permian anthracosaur from Texas. Scale bar = 5 cm. Photograph by R. S. Clarke.

ancestors of the Carboniferous. They did not survive beyond the Early Permian. The seymouriamorphs were a much more successful group of semiterrestrial and terrestrial anthracosaurs. Generally, they had large heads with well-developed jaws, robust bodies, and strong limbs.

Amphibians of the Early Mesozoic

In the Triassic, the reptiles and synapsids had become the dominant terrestrial vertebrates. A few anthracosaur groups survived into the earliest Triassic but soon disappeared. In contrast, the amphibians experienced a mini diversity explosion with the appearance of at least seven different groups of presumed temnospondyls, including the first lissamphibian. The radiation included small to large temnospondyls with several groups having species in the 1.5–3 m range (e.g., capitosauroids, chigutisauroids, and metoposaurids) and some mastodonsaurids to 6 m TL. All large species appear to have been highly aquatic and most had crocodile-like body forms. The mastodonsaurids were a short-lived group found only in Lower Triassic sediments of northern Eurasia. The 2–m (TL) trematosaurs were another Lower Triassic taxon with triangular to gharial-like heads; some were marine, an anomaly for amphibians. Three temnospondyl groups (brachyopoids, capitosauroids, and plagiosaurids) occurred throughout the Triassic (Fig. 3.2). Although never common, they persisted throughout this period. The plagiosaurs were peculiar amphibians with broad flattened bodies and heads, and a back armored with numerous small, bony pustules. The brachyopoids were the most diverse group and appeared in the Late Permian and survived into the Lower Jurassic. However, the Chigutisauridae have the record for geological longevity among these ancient temnospondyls, surviving into the Early Cretaceous. Of course, one group of temnospondyls, the Lissamphibia, still survives. The first lissamphibian to appear in the fossil record is the Lower Triassic frog *Triadobatrachus massinoti.* Its occurrence attests to at least an Early Mesozoic divergence among lissamphibians, but then the frogs vanished from the fossil record for another 50 million years, and salamanders would appear before the frogs' reappearance. *Triadobatrachus massinoti* is unquestionably a frog (Fig. 3.4), although it possessed 14 body vertebrae and a short tail of 6 vertebrae. Its pelvic girdle and skull are similar to modern frogs.

History of the Lissamphibia

The origin of the lissamphibians likely occurred in the mid-Permian, and possibly even earlier. The fossil evidence now suggests that the ancestor was a temnospondyl dissorophid (Trueb and Cloutier, 1991b). Presumably, this ancestral stock was composed of small, semiaquatic salamander-like amphibians with external fertilization, a larval developmental stage, and many other physiological and anatomical features shared by today's lissamphibians. No fossils are available to show the timing and manner of divergence of the three modern groups. Often caecilians are depicted as diverging first owing to their extreme structural divergence from frogs and salamanders. But if occurrence of fossils is used as an indicator, frogs diverged first. This issue remains unresolved; however, it is certain that by the

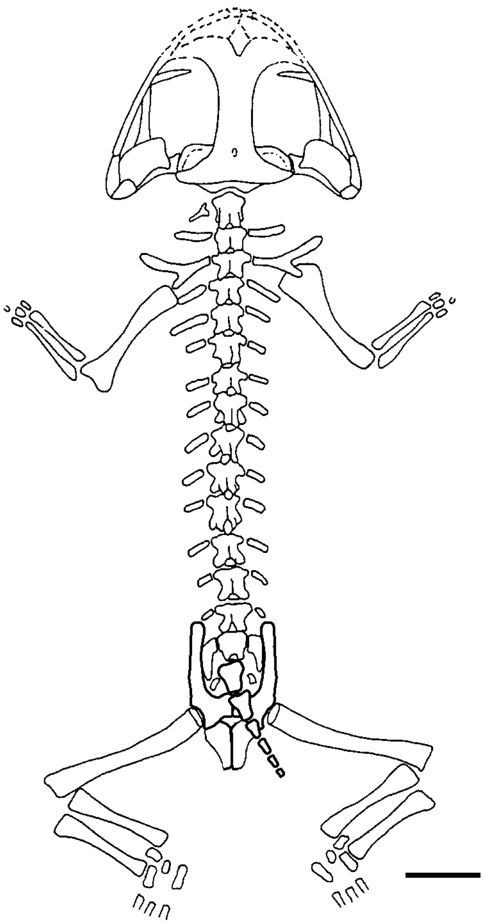


FIGURE 3.4 *Triadobatrachus massinoti*, the earliest known frog, from the Triassic of Madagascar. Adapted as a partial reconstruction from Estes and Reig (1973). Scale bar = 1 cm.

mid-Jurassic, only lissamphibians and chigutisaurids remained of the previously numerous amphibian clades (Fig. 3.2).

Caecilians

Caecilians are poorly represented by fossils (Estes, 1981), and this thin evidence has kept their origin and evolution controversial. Until recently, they were known by a single Paleocene fossil vertebra from Brazil and a Late Cretaceous vertebra from Bolivia. The discovery (Jenkins and Walsh, 1993) of an Early Jurassic caecilian in the southwestern United States is significant because it extends the history of the group deep into the Mesozoic and closer to its potential ancestors of the Upper Permian or Lower Triassic. This caecilian, ***Eocaecilia micropodia*** (Eocaeciliidae), is represented by most of the skeleton, including limb and girdle elements and the skull. The former elements alone demonstrate that it is not an aistopodan, although they do not resolve the question of lissamphibian monophyly. ***E. micropodia***, however, does answer questions on the evolution of skull and limb evolution in the Apoda. The Apoda is the clade (stem-based) encompassing the fossil taxa and the ancestor and all descendants of the extant gymnophionans (Table 3.1).

A single vertebra from each of two South American caecilians and the recent find of four vertebrae from the Upper Cretaceous of the Sudan (Evans et al., 1996) help define the geological and geographic occurrence of caecilians but assist little in understanding their evolutionary history. The Brazilian fossil is most similar to the vertebrae of the African *Geotrypetes* (Caeciliidae) and has been named *Apodops*. If this similarity denotes actual relationship, it provides another example of Gondwanan affinities among African and South American amphibians.

Albanerpetontids

Albanerpetontids are a group of salamander-like lissamphibians that were linked to prosirenid salamanders until recently (McGowan and Evans, 1995). They are moderately abundant as microfossils from Middle Jurassic to Early Miocene deposits of North America, Europe, and Central Asia (Milner, 1994). Although abundant, they are represented largely by disassociated skeletal elements, but even these fragments show albanerpetontids to be very different "salamanders." They possessed a unique

TABLE 3.1 A Hierarchical Classification of the Extant Caecilians (Gymnophiona)

- Gymnophiona
  - Rhinatrematidae
  - Unnamed clade
    - Unnamed clade
      - Ichthyophiidae
      - Uraeotyphlidae
    - Unnamed clade
      - "Caeciliidae"
      - Unnamed clade
        - Unnamed clade
          - Scolecomorphidae
          - "Caeciliidae"
        - Unnamed clade
          - Typhlonectidae
          - "Caeciliidae"

Note: This classification derives from the phylogenetic relationships displayed in Fig. 15.1. Category titles are not assigned to the hierarchical ranks. A name in quotation marks indicates that the group is not monophyletic.

peg-and-socket symphyseal joint in the mandible, a two-part craniovertebral joint, and sculptured osteoderms dorsally from snout to tail. They were small lissamphibians, < 15 cm TL.

The discovery of a complete and fully articulated specimen (*Celtedens*; Fig. 3.5) permitted the recognition of the albanerpetontids as a separate lineage of lissamphibians, likely the sister group of the salamander-frog clade. Albanerpetontids also must have an equally ancient origin in the earliest Triassic or before, and are absent or unrecognized in the fossil record until the Jurassic.

Salamanders

Extant salamanders comprise three clades: sirenoids (Meantes), cryptobranchoids, and salamandroids (Table 3.2). All three clades occur as fossils, and several other clades (e.g., karaurids and prosirenids) are known only from fossils. The extinct and extant salamanders form the Urodela (stem-based clade) with a history extending from the Middle Jurassic, about 165 mybp (Fig. 3.2). Urodelan history (Estes, 1981) is linked mainly to the northern hemisphere (Holarctic) and to the ancient continent of Laurasia; nonetheless, recent fossil salamander discoveries in Africa and South America (Rage et al., 1993) show that the relatively recent dispersal of plethodontids southward is not the first occurrence of salamanders on Gondwanan-derived continents.

TABLE 3.2 A Hierarchical Classification of the Extant Salamanders (Caudata)

- Caudata
  - Meantes/Sirenidae
  - Unnamed clade
    - Cryptobranchoidea
      - Cryptobranchidae
      - Hynobiidae
    - Salamandroidea
      - Unnamed clade
        - Amphiumidae
        - Plethodontidae
      - Rhyacotritonidae
      - Unnamed clade
        - Proteidae
        - Unnamed clade
          - Salamandridae
          - Unnamed clade
            - Ambystomatidae
            - Dicamptodontidae

Note: This classification derives from the phylogenetic relationships displayed in Fig. 16.1 (Larsen and Dimmick, 1993). Category titles are not assigned to the hierarchical ranks.

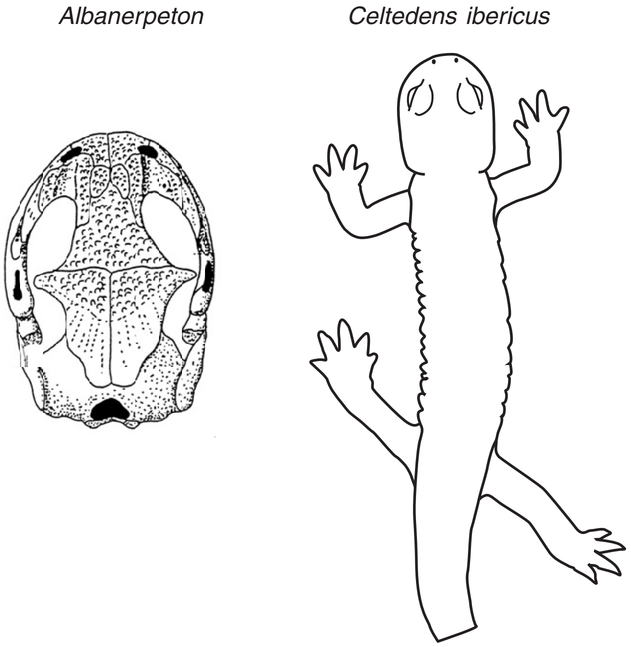


FIGURE 3.5 Albanerpetontidae, salamander-like lissamphibians from the Cretaceous and Tertiary. Skull of *Albanerpeton* and habitus of *Celtedens ibericus*. After Estes and Hofstetter (1976) and as suggested by a skeleton in McGowan and Evans (1995), respectively.

The earliest salamanders are two species of *Marmorerpeton* from a Middle Jurassic deposit in central England (Evans et al., 1998). They were moderate-sized (> 30 cm TL), presumably totally aquatic salamanders. Their relationships are uncertain, in part because they are represented by only a few vertebrae, a humerus, and miscellaneous skull elements. They appear to be related to the extinct scapherpetotids, but they also have some primitive features suggesting a possible sister-group relationship to all other Urodela.

The karaurids are another ancient group of salamanders. They are known presently from a few fossils from the Upper Jurassic of Kazakhstan (Evans and Milner, 1996). The fossil of *Karaurus sharovi* is fortunately nearly complete (Fig 3.6). Its primitive morphology indicates that the karaurids are a sister group of the Caudata. *Karaurus* was small (about 120 mm SVL) and terrestrial judging from its body form and the dermal sculpturing (skin fused to bone) on the skull bones.

The first batrachosauroidids appeared soon after the karaurids in the Late Jurassic (Fig. 3.2), but unlike the latter, they persisted as an occasional member of freshwater assemblages until the Early Pliocene and are

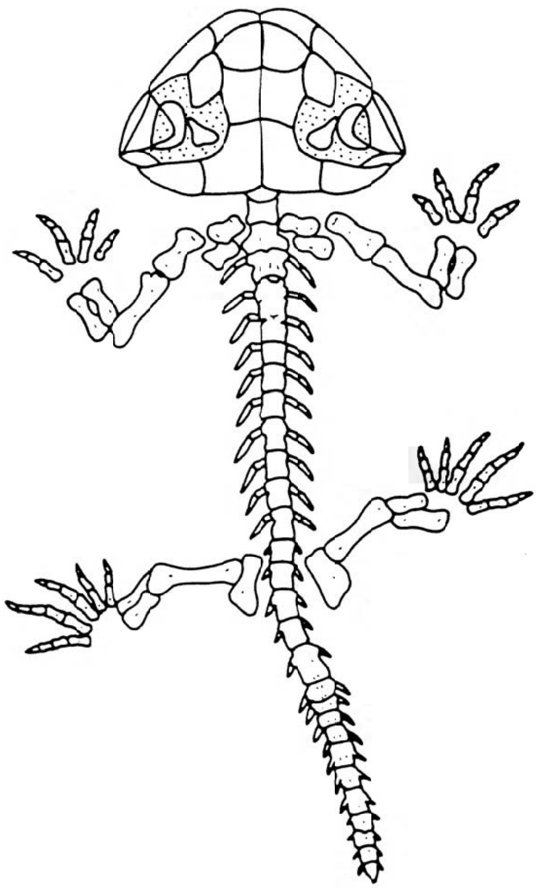


FIGURE 3.6 *Karuarus sharovi* (about 15 cm TL), the earliest known salamander, from the Late Jurassic of Russia. Adapted as a partial reconstruction from Carroll (1988).

found only in North American deposits. They are similar to proteids; however, it is uncertain whether this similarity is related to the retention of a larval morphology as adults (heterochrony) or an indication of phylogenetic relationship. An assortment of other salamander fossils has been found from the Late Jurassic. Most are too fragmentary or incomplete, such as the Wyoming *Comonecturiodes marshi*, to indicate their affinities.

Salamanders are largely absent from Cretaceous deposits until the Late Cretaceous (Evans and Milner, 1996). The exceptions are the batrachosauroidids, prosirenids, and a salamandroid. The prosirenids consists of two species, *Prosiren elinorae* of Texas and *Ramonellus longispinus* of Israel. Both are assumed to share the sirenid habitus of elongate body and presence of only forelimbs. Other characteristics suggest that they are not sirenids, and that they might not even be closely related. The late Lower Cretaceous *Valdotriton* is anatomically a modern salamander and a salamandroid. Because it is represented by six complete skeletons (Evans and Milner, 1996), its proposed inclusion in the salamandroid clade is robust, but it is not a member of any currently named family. It appears ''intermediate'' between the proteids and all other salamandroids (Evans and Milner, 1996).

Two extant families, Amphiumidae and Sirenidae, and the extinct scapherpetonids make their first appearance in the Upper Cretaceous. *Proamphiuma* from a Montana Cretaceous deposit is the first fossil amphiumid. Like many fossils with ''pro'' in their names, *Proamphiuma* is a structural precursor to *Amphiuma* (Paleocene to Recent), and the relationship actually may be ancestor to descendant. The amphiumids have remained a strictly North American group throughout their 60+ million year history.

Sirenids first appeared in the North American Cretaceous as the giant *Habrosaurus*, which survived into the Early Paleocene. This siren looked much like its living relatives, except for specialized shovel-shaped teeth. Other Cretaceous sirenids are *Kababisha humarensi* and *K. sudanensis* from Africa (Evans et al., 1996) and *Notoerpeton bolivianum* from South America (Rage et al., 1993). Another somewhat younger sirenid also occurred in Africa. Sirenids are unknown then until the Middle Eocene when *Siren* appears in North America, where the remainder of the sirenid fossil history is found. *Pseudobranchus* occurred first in Pliocene deposits of Florida.

The extinct scapherpetonids were a group of moderate-sized salamanders living from the Late Cretaceous to the Early Eocene in North America. These salamanders are related to the present day dicamptodontids, and *Scapherpeton* and *Piceoerpeton* share the *Dicamptodon* body form. *Lisserpeton* appears to have had an elongate body and reduced limbs. Interestingly, one species of *Piceoerpeton* occurred on Ellesmere Island within the present Arctic Circle. Fossil dicamptodontids made their first appearance in North America during the Eocene (J. Hutchinson, 1992), but somewhat later than the last scapherpetontid; however, fossil dicamptodontids appeared first in the Upper Paleocene of Europe and again in the Middle Miocene (Rocek, 1994a). Upper Paleocene trackways in western North America are attributed to a dicamptodontid because of the unique bilobate palm impressions. Furthermore, the trackways are associated with a redwood flora, an association occurring today in *Dicamptodon*. Subsequent North American fossil occurrence is in the Middle Miocene.

Other modern salamanders (Cryptobranchidae, Proteidae, and Salamandridae) appeared in the Paleocene (Fig. 3.2). The cryptobranchoid *Cryptobranchus* occurred first in the Paleocene of Saskatchewan and again in the Appalachian and Ozark Pleistocene assemblages (Holman, 1995). *Andrias* has a much more extensive history. The oldest *Andrias* fossils are from the European Upper Oligocene (Rocek, 1994a), and *Andrias* persisted there at least through the Pliocene and in the North American Miocene. Within its present range, *Andrias* has been found only in Japanese Pleistocene deposits. The fossil forms were also giant salamanders, one with a tail length of more than 2 m. The only other salamanders that might have attained such lengths were some fossil sirenids, but it is difficult to confirm because all fossil sirenids are known only from a single or short series of vertebrae. Hynobiidae, the other cryptobranchoid lineage, has no fossil record.

Proteids occurred first in the Late Paleocene of North America and the Middle Miocene of Europe. These fossils represent the extant *Necturus* and *Proteus*, as well as two extinct genera from the Miocene of Europe. All were small, perennibranchiate salamanders (gill-bearing as larvae and adults). Ambystomatids appeared in the Eocene. All fossils have been found in North America, and all appear to be members of the clade *Ambystoma*. They are moderately common in Pleistocene deposits.

Of living salamanders, salamandrids have the most speciose fossil record. Their fossil record contains representatives of 18 genera and more than 50 species. Living genera, such as *Notophthalmus*, extend as far back as the Miocene, *Taricha* and *Triturus* to the Oligocene, and *Salamandra* and *Tylotriton* to the Eocene. The extinct genera derive principally from the Paleocene to the Oligocene. The fossil species of the extinct and extant genera match the extant species in size and body form (e.g., Rocek, 1994a) and probably shared the modern species' diversity of behaviors and ecology.

Today, the plethodontids are the most speciose of the salamanders, and yet they have a meager fossil record. Half a dozen genera are represented, and four of these occur no earlier than the Pleistocene. A few vertebrae attributable to *Aneides* have been found in an Early Miocene deposit in Montana, and a fossil trackway from the Early Pliocene of California has been referred to *Batrachoseps*.

Frogs

The Salientia encompasses all taxa of extinct and living frogs, and the Anura, a crown-group clade, contains the ancestor of all living taxa and its descendant taxa. The "proanurans" is an informal name for the earliest and structurally most primitive frogs. Proanuran taxa include *Triadobatrachus* and other extinct frogs that have sister-group relationships to one another or to the Anura clade; in most instances the relationships are uncertain. The anurans can be divided into three subgroups (Table 3.3, Fig. 17.1): a grade of early frogs, Mesobatrachia, and Neobatrachia. These subgroups appear more or less sequentially and chronologically in the fossil record

TABLE 3.3 A Hierarchical Classification of the Extant Frogs (Anura)

- Salientia
  - *Triadobatrachus*
  - Anura
    - Ascaphidae
      - Leiopelmatidae
        - Bombinatoridae
          - Discoglossidae
            - Mesobatrachia
              - Pelobatoidea
                - Megophryidae
                - Pelobatidae
                - Pelodytidae
              - Pipoidea
                - Rhinophrynidae
                - Pipidae
            - Neobatrachia
              - Allophrynidae
              - Brachycephalidae
              - Bufonidae
              - Heleophrynidae
              - "Leptodactylidae"
              - Limnodynastidae
              - Unnamed clade
                - Myobatrachidae
                - Sooglossidae
              - Rhinodermatidae
              - Unnamed clade
              - Centrolenidae
              - Unnamed clade
                - Hylidae
                - Pseudidae
              - "ranoids"
                - "Arthroleptidae"
                - Dendrobatidae
                - Hemisotidae
                - Hyperoliidae
                - Microhylidae
                - "Ranidae"
                - Rhacophoridae

Note: This classification derives from the phylogenetic relationships displayed in Fig. 17.1 (Ford and Cannatella, 1993). Category titles are not assigned to the hierarchical ranks, and some ranks or nodes are purposefully omitted. A name in quotation marks indicates that the group is not or is questionably monophyletic.

(Fig. 3.2) relative to their branching or cladistic pattern. The first frog fossil derives from Madagascar, and this occurrence has been interpreted as a Gondwanan origin for frogs; however, the next frog fossil was found in North America. Perhaps these two occurrences and the ancientness of the lissamphibians (Milner, 1994) show that the groups giving rise to modern lissamphibians were widespread on the megacontinent of Pangaea. Subsequent fragmentation of this megacontinent could have yielded modern families of both Gondwanan and Laurasian origins.

The fossil record (Sanchiz and Rocek, 1996) reflects a higher diversity of frogs than of salamanders and caecilians, similar to that observed among the modern lissamphibians. Only frogs are known from the Triassic. At least six frog taxa have been found in Jurassic deposits compared to three salamanders and one caecilian. In the Cretaceous (Fig. 3.2), as many clades of salamanders as of frogs occur, and in the Tertiary, the extant families for both salamanders and frogs appear, establishing the diversity seen today.

The first frog is *Triadobatrachus massinoti* from the Early Triassic of Madagascar (Fig. 3.4). Although it had more vertebrae (±20 presacral vertebrae) than later frogs and a short stumpy tail, it was clearly a frog (Estes and Reig, 1973; Rage and Richter, 1989). *T. massinoti* is unlikely to be the ancestor of later frogs; nonetheless, it provides a glimpse of the anatomy of frogs in transition from early temnospondyls to anurans. Its body size of about 10 cm SVL suggests that frog evolution emphasized small size, unlike many other earlier amphibian groups. Only a single fossil exists for this taxon, and it may represent a juvenile of an aquatic form or a metamorphosing individual of a semiterrestrial one.

The next proanuran, *Prosalirus bitis*, derives from the Lower Jurassic (181–184 mybp) of Arizona and from the same deposits as *Eocaecilia*. Its limb and girdle morphology is essentially modern and indicates that *P. bitis* was a jumping frog (Shubin and Jenkins, 1995). The body was truncated, although the actual number of presacral vertebrae is unknown. Similarly its affinities to other Jurassic frogs and extant families are not clear. The Patagonian *Vieraella herbstii* is potentially a contemporary of *P. bitis*; however, its fossil origin has not been precisely dated. Structurally, *V. herbstii* and the later Patagonian *Notobatrachus degustori* are even more modern in occurrence (158–172 mybp; Fig. 3.7). They possess a suite of primitive characteristics, such as nine presacral vertebrae, free ribs, and a partially fused astragalus-calcaneum, all traits shared with *Ascaphus* and *Leiopelma*. As a result, these ancient Patagonian frogs have been considered representatives of the extant Leiopelmatidae. Their similarity is a reflection of primitiveness, not phylogenetic relatedness; they are best considered the sister group to modern anurans (Báez and Basso, 1996). *V. herbstii* was a small frog (about 28 mm SVL); *N. degustori* was much

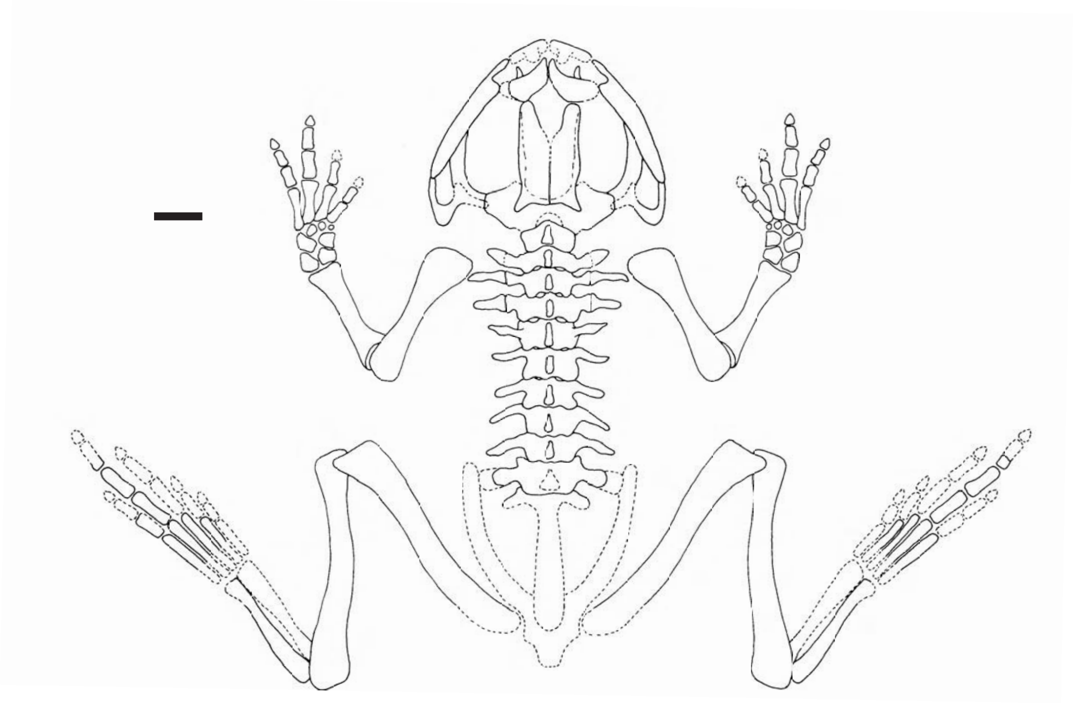


FIGURE 3.7 *Vieraella herbstii*, an ancient frog, from the Jurassic of Patagonia. Scale bar = 2 mm. Adapted from Estes and Reig (1973).

larger (120–150 mm SVL), roughly three times the size of the modern leiopelmatids.

The next appearing group of frogs was the Discoglossidae. Still extant, this conservative group has a history of over 170 million years, having appeared regularly in fossil assemblages during this vast expanse of time (Evans et al., 1990; Prasad and Rage, 1991, 1995). *Eodiscoglossus* appeared in the Late Jurassic of Spain and persisted into the Early Cretaceous. At least skeletally, it seems nearly identical with today's *Discoglossus.* Two other genera appeared in the Late Cretaceous of western North America, and one of them (*Scotiophryne*) survived into the Paleocene. Discoglossids are absent throughout the Eocene; in Europe one discoglossid, *Latonia*, reappeared in the Oligocene (Rocek, 1994b). Modern *Discoglossus* and *Alytes* are found in the European Miocene and Pleistocene, respectively.

The assignment of some taxa to the discoglossid or bombinatorid clades is uncertain owing to the recency of the recognition of these clades and the continued use of the older discoglossid concept by anuran paleontologists. *Bombina* is known since the Early Miocene in Europe. If either *Enneabatrachus* or *Scotiphyrne* are bombinatorids, then this group has a history extending from the late Upper Jurassic or earliest Lower Cretaceous.

Pelobatidae, another modern clade of anatomically conservative frogs, appeared in the Late Jurassic of Asia and North America. The fossil elements from the western North American Morrison Formation cannot be assigned to a particular genus but are unquestionably pelobatids. The next appearance was in the Cretaceous; *Eopelobates* and *Kizylkuma* differ sufficiently from their later-appearing relatives to be placed in a separate clade (Eopelobatinae). *Eopelobates* had a long existence from the Late Cretaceous to the Middle Miocene and an equally broad geographic occurrence from western North America (J. H. Hutchinson, 1992) to temperate Asia and Europe. The eopelobatine species were generally moderate-sized (50–60 mm SVL), terrestrial frogs. They lacked spades on the heels, a prominent characteristic of modern pelobatids, but presumably shared many features of their natural history. The pelobatids or spadefoots appear in the European basal Miocene (*Pelobates*) and the Early Oligocene of North America (*Scaphiopus*). Their modern sister group, the Asian Megophryidae, is unknown as fossils. The related pelodytid frogs had a brief appearance in the Eocene of central Europe and the Miocene of western North America (Henrici, 1994).

Gobiates, a Cretaceous frog from Central Asia, was initially considered a near relative to *Eopelobates*, but it is morphologically quite distinct. It is another basal or proanuran group even though it is presently known only from the mid-Cretaceous (Rocek and Nessov, 1993) and is now recognized as a distinct lineage (Fig. 3.2). *Gobiates* was moderately speciose with about a dozen species.

The recently extinct paleobatrachid frogs (Mesobatrachia) were a long-lived clade. They appeared first in the Upper Cretaceous and went extinct in the early Pleistocene. Throughout their entire history, they were confined to Europe, with one questionable Cretaceous occurrence in North America. Although apparently abundant, they were only moderately speciose with less than two dozen species recognized throughout their 120–million-year history. All paleobatrachids were moderate to small frogs, generally less than 50 mm SVL, and strictly aquatic (Spinar, 1972). They had long, robust hindlimbs and long digits on both the fore- and hindfeet. *Neusibatrachus*, the oldest paleobatrachid, occurred first in the Late Jurassic but then is unknown in the fossil record until the Miocene. *Paleobatrachus* (Fig. 3.8), with 12 species, spanned the Eocene to Pliocene period. Fossils of this taxon are abundant in a series of freshwater deposits in eastern Czech Republic. In this area, volcanic gases apparently poisoned the waters of streams and ponds, periodically causing massive die-offs of all aquatic animals. These gases also stimulated diatom blooms, and the diatom skeletons buried frogs and even tadpoles. Burial was rapid and imprints of soft parts remain to help paleontologists reconstruct the anatomy and life histories of the paleobatrachid frogs.

The paleobatrachids and pipids are sister groups, and all paleobatrachids resembled the modern clawed frogs (*Xenopus*). The pipids did not appear in the fossil record until the Early Cretaceous, but they are more likely ancestors rather than descendants of paleobatrachids. The paleobatrachid's restricted distribution in Europe throughout their history contrasts sharply to the presence of pipids in South America and Africa since the Cretaceous (Báez, 1996). The Upper Jurassic pipoid *Rhadinosteus* may resolve this dilemma. Three definite pipids occurred in the Early Cretaceous of the eastern Mediterranean, suggesting an early radiation of the African pipids. *Xenopus* occurred early in Africa, from the Late Cretaceous of Nigeria and the Oligocene of Libya. It is an amazingly adaptable frog genus and even today it is the most speciose of the pipid clade. The ancient pipids (*Saltenia* and *Shelania*) of the South American Paleocene derive from the southern portion of that continent (Báez and Pugener, 1998). *Shelania* is an especially abundant fossil frog in Patagonian sediments and they are frequently found as complete or near-complete skeletons. These fossils are thus providing valuable insights into the evolution of pipid frogs (Báez and Trueb, 1997).

Although fossorial rather than aquatic, the rhinophrynids are the sister group of the paleobatrachid-pipid

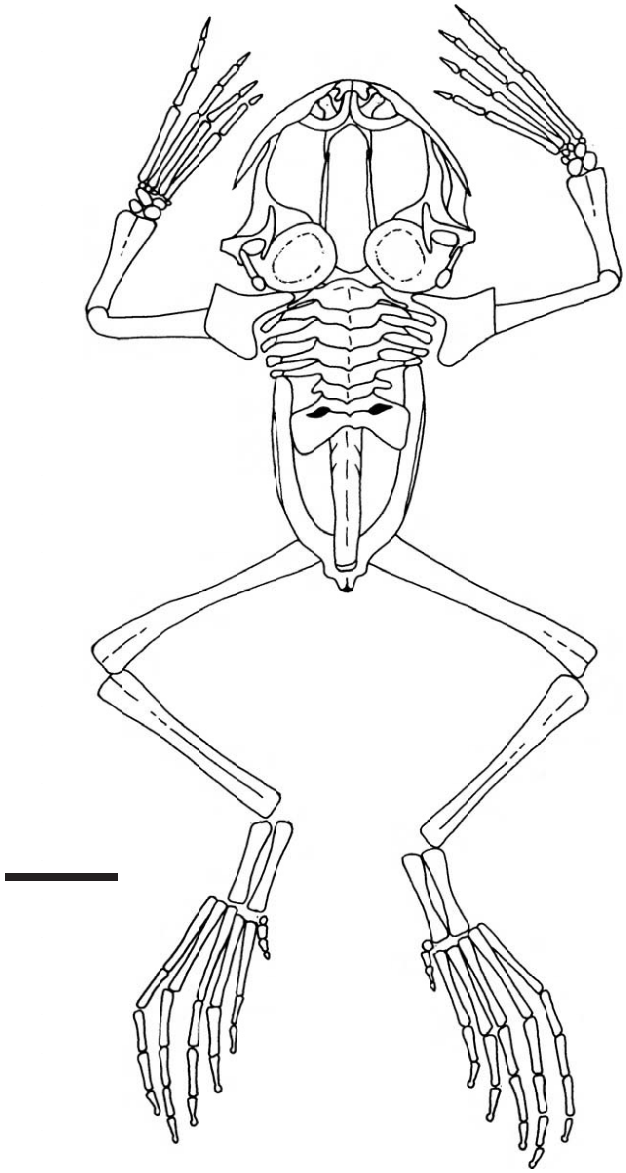


FIGURE 3.8 *Paleobatrachus grandiceps*, a representative of the extinct Paleobatrachidae, from the Oligocene of eastern Europe. Scale bar = 10 mm. Adapted from Estes and Reig (1973).

clade. The first rhinophrynids occurred in the Lower Eocene of western North America. Others occurred in the Oligocene but thereafter disappeared from the fossil record. The Jurassic *Rhadinosteus* represents an early pipoid (Henrici, 1998) and structurally is most similar to the rhinophrynids, likely indicating the divergence of the extant pipoid families.

The advanced frogs (Neobatrachia) also began to appear in the Early Tertiary, even somewhat earlier than rhinophrynids. Surprisingly, considering their present diversity, neobatrachians are neither abundant nor diverse throughout much of the Tertiary. Only in the Pliocene and Pleistocene (Holman, 1995) do they become more common in fossil beds. Excluding fossil records from the Pliocene, only the bufonids, hylids, leptodactylids, limnodynastids, microhylids, ranids, and rhacophorids have Tertiary representatives. Leptodactylids are definitely known from the Upper Cretaceous of South America, and if an Indian fossil's identity is confirmed, hylids will likewise have a Late Cretaceous occurrence. *Bufo* has a nearly continuous record in South America from its first occurrence in the Late Paleocene. It also was present in North America and Europe from the mid-Tertiary onward. No other bufonids are known as fossils. *Hyla* appeared in the Oligocene in North America and in the Miocene in Europe. The only other fossil hyline hylid is *Proacris* from the Miocene of Florida. The Miocene *Australobatrachus* is the first fossil representing pelodryadine hylids and was contemporaneous in the Late Miocene with the still extant *Litoria* (Pledge, 1992; Tyler, 1991a,b). The leptodactylids have a broader and more diverse fossil history, and, although it is mainly New World, leptodactylids occurred in the European Eocene. The ceratophryines were represented in the Miocene of Argentina by *Wawelia*; one Cretaceous leptodactylid is potentially a ceratophryine; the telmatobines are represented by two genera in the Oligocene and Miocene; and a sprinkling of *Eleutherodactylus* and *Leptodactylus* species occur in the Pleistocene. An *Eleutherodactylus* in amber from the Hispaniolan Eocene is an exciting find (Poinar and Cannatella, 1987) because it and its amber-associated biota provide important insights into the early distribution of the Mesoamerican biota and landmass movements. The widespread and diverse ranids are represented in the fossil record only by *Ptychadena* in the Moroccan Miocene and an assortment of nearly 50 species of *Rana* from the Oligocene onward of Europe and the Miocene through Pleistocene of North and Central America.

HISTORY OF REPTILES

The first tetrapod is known from the Late Devonian, the first amphibian from the Middle Mississippian, and the first amniotes from the Middle Pennsylvanian (Fig. 3.9). These first amniotes were *Archaeothyris* (synapsid) and *Hylonomus* and *Paleothyris* (reptiles), showing that the lineages leading to the mammals and modern reptiles were already established in the Late Carboniferous. These three amniotes were small and lizardlike, but structurally quite distinct from modern lizards.

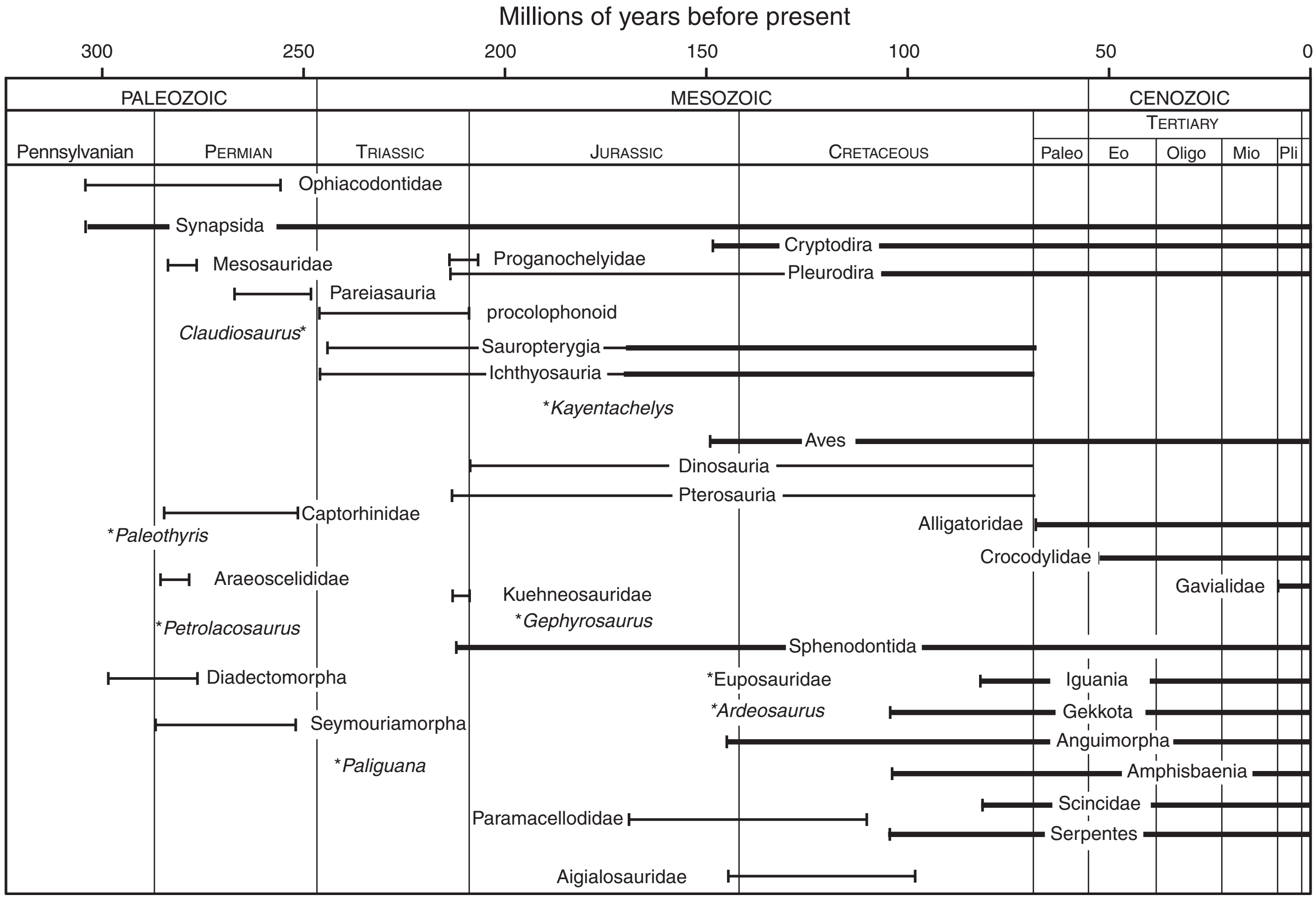


FIGURE 3.9 Geological occurrence of some early anthracosaurs and amniotes, and extinct and living reptiles. Abbreviations for Cenozoic epochs are Paleo, Paleocene; Eo, Eocene; Oligo, Oligocene; Mio, Miocene; and Pli, Pliocene. Pleistocene is the narrow, unlabeled epoch at the far right side of the chart.

Many of the anthracosaurs were aquatic tetrapods (see Chapter 1), although some were definitely terrestrial, e.g., *Proterogyrinus*. Anthracosaurs lived from the Late Devonian into the Late Permian. Thus, the ancestors of the amniotes diverged early in the history of anthracosaurs. The seymouriamorph anthracosaurs (Fig. 3.3) diverged later. Their fossil history begins in the Early Permian at a time when amniotes were beginning to establish their dominance on land. These moderate-sized (25–100 cm TL) tetrapods never became speciose, although their fossil remains are moderately abundant in the Early Permian and indicate that they were definitely terrestrial. The terrestrial seymouriamorphs disappeared in the mid-Permian; the group reappeared at the end of this era as aquatic animals. Another group of anthracosaurs, the diadectomorphs, is structurally more primitive than the early amniotes, although they appeared in the Late Pennsylvanian subsequent to the origin of amniotes (Fig. 3.9). Although primitive in the early occurrence sense, they were specialized tetrapods. *Diadectes* was large (3 m TL) and had a partial secondary palate and molariform cheek teeth, which suggests an herbivorous diet. This group was short lived, as was also an assortment of early reptiles.

Radiation among Early Amniotes

Several contemporaneous taxa of reptiles and synapsids from a buried forest of the Middle Pennsylvanian in Nova Scotia, Canada, are the earliest known amniotes. They apparently lived in hollow, upright trunks of buried trees and were entombed when the forest was periodically flooded. Even though many of the later Paleozoic amniotes were quite large, particularly in comparison to most living reptiles, these taxa (*Archaeothyris*, *Hylonomus*, and *Paleothyris*) were small, approximately 15 cm long (SVL). The explosive radiation of the reptiles was still millions of years away in the future Mesozoic. Nonetheless, amniotes, particularly pelycosaurs (synapsids), began to assume a dominant role in terrestrial vertebrate communities of the Permian.

Protomammals: The Synapsids

Archaeothyris is an ophiacodontid. Ophiacodontids had only a modest history with low diversity, perhaps surviving into the Late Permian; however, they are the basal members and potential ancestors of the pelycosaurs. The pelycosaurs were enormously successful, diversifying into two dozen genera and numerous species in six or more lineages (Hotton et al., 1986); this diverse group represents an evolutionary grade rather than a clade of synapsids. They became the major tetrapods of the Early Permian in both abundance and number of species. The earliest pelycosaurs were small (ca. 30 cm SVL) and lizardlike. They had large heads with big, widely spaced teeth, suggesting that they were effective carnivores of large prey. This basal stock radiated into several groups of medium to large carnivores and at least two groups of herbivores. Two clades, *Edaphosaurus* (herbivorous edaphosaurids) and *Dimetrodon* (carnivorous sphenacotontids), had members that evolved a dorsal "sail" of elongated neural spines on the trunk vertebrae. Both pelycosaurs were large (*Dimetrodon* to >3 m TL). Presumably this sail was a thermoregulation mechanism, and, at least in *Dimetrodon* for which abundant fossils are known, the surface area of the sail scales with body mass, displaying the typical volume-to-area relationship associated with thermoregulation (see Chapter 7). Some other pelycosaurs were varanid-like and probably shared the varanid's agility and carnivory. The pelycosaurs began to disappear in the middle of the Late Permian. Their decline might have been brought about by the success of another early synapsid lineage that gave rise to the therapsid radiation of the Upper Permian. Later in the Triassic, mammals arose within the therapsids.

Paleozoic Reptiles

Many early reptiles have skulls with a solid bony temporal area. The taxa sharing the absence of temporal fenestrae were, at one time, considered to be closely related and called the Anapsida. While this relationship is no longer accepted, "anapsids" remains a vernacular name for early reptiles sharing the anapsid skull. Other clades defined originally on the nature of temporal fenestration persist, for example, Diapsida and Synapsida. Now the two major anapsid groups, the captorhinids and turtles, usually are considered distantly related and classified in the Eureptilia and the Parareptilia, respectively (Fig. 1.10). Only the eureptiles have a fossil presence in the Late Pennsylvanian. *Hylonomus* (Fig. 3.10) and *Paleothyris* (Fig. 1.8) are two of these eureptiles, and a third is *Petrolacosaurus* (Carroll, 1991). *Petrolacosaurus* was a moderate-sized (ca. 40 cm TL) terrestrial reptile, iguanalike with enlarged upper canines. It is typically linked to the short-lived *Araeoscelis* clade (Araeoscelidia) of the Lower Permian. Araeoscelidans are basal diapsids and the sister group to the Sauria. All were lizardlike in head and body proportions, but their limbs were gracile and elongate with fore- and hindlimbs of nearly equal length. Their dentition was simple and indicates a general carnivorous diet.

Thereafter, no other diapsids or saurians are found until *Claudiosaurus* and *Paliguana* of the Upper Permian. These two diapsids were not contemporaries (Fig. 3.9). The former is a long-necked, marine reptile that has been considered a plesiosaur, or at least a basal sauropterygian. Evidence now suggests that the body form of *Claudiosaurus* is independently evolved and that this taxon arose prior to the archosauromorph-lepidosauromorph divergence. *Paliguana* has similarly been linked to a later appearing group, the Squamata. This relationship is uncertain, although *Paliguana* certainly is a diapsid and likely a squamate.

The Captorhinidae represent a primitive group of eureptiles, and some features suggest an origin prior to that of *Paleothyris*. The captorhinids were medium-sized, lizardlike reptiles, although the broad-jowled head was proportionately larger than that of most lizards. The teeth showed regional differentiation with large, pointed incisors in front and double to triple rows of short, cone-shaped teeth in the rear. The bodies were slender and the limbs moderately long, suggesting that they were agile carnivores.

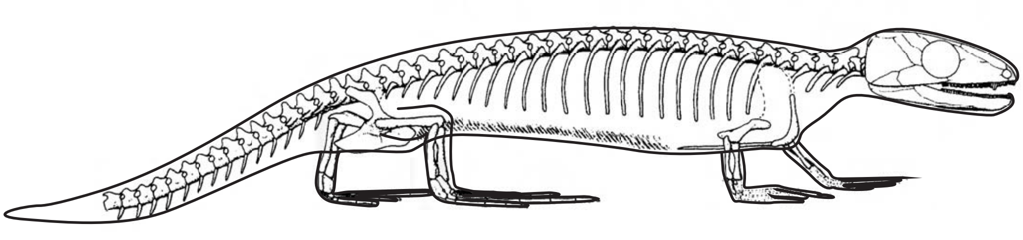


FIGURE 3.10 *Hylonomus lyelli*, the earliest known reptile, from the Early Permian of Nova Scotia. Size is about 42 cm SVL. Adapted from Carroll and Baird (1972).

Several groups of Permian reptiles, the Mesosauridae, Millerettidae, procolophonoids, and Pareiasauria (Fig. 3.11), have proven exceedingly difficult to classify, and for lack of a better name, they were called the parareptiles and presumed to be unrelated. Additional fossils, improved preparation, and new analytical techniques (e.g., Laurin and Reisz, 1995) now indicate that the Parareptilia, excluding Mesosauridae and including the turtles, is a monophyletic clade (Fig. 1.10).

The mesosaurs (Early Permian) were miniature (ca. 1 m TL), marine, gharial-like reptiles. They had long, narrow-snouted skulls, and the long, thin teeth of the upper and lower jaw curved outward and interdigitated when the jaws were closed. Such jaws are excellent for catching fish with a sideward sweep of the head. The body and tail were similarly elongated and the tail laterally compressed for undulatory swimming. Nonetheless, the limbs were well developed, and the hindlimbs and feet were large, perhaps used as rudders.

The parareptiles are a diverse group of small to large reptiles, mainly of Middle Permian to Lower Triassic age. The procolophonoids are strictly Mesozoic, occurring throughout the Triassic. Turtles are a potential sister group of procolophonoids; however, some recent zoologists suggest that turtles are diapsids and not closely related to parareptiles (see Chapter 1). The millerettids were small, lizardlike reptiles. Their small heads and simple conical teeth match the appearance of many iguanians living today, and they probably shared a diet of insects. The pareiasaurs and the procolophonoids were more diverse. The pareiasaurs were the giants of the parareptiles with some taxa to 3 m (TL) (Fig. 3.11). They had large barrel-shaped bodies, elephantine limbs, and proportionately small, broad-jawed heads capped with thick bone and numerous projections. The teeth were closely spaced with laterally compressed leaf-shaped crowns. By all indications, the pareiasaurs were slow, lumbering herbivores. The procolophonoids were small to medium-sized lizardlike reptiles. Their stocky bodies, short limbs, and broad-jowled heads gave them the appearance of modern *Uromastyx* or *Sauromalus*, and they may have shared the herbivorous habits of these extant lizards. Unlike the pareiasaurs, their widely spaced, thick, bulbous-crowned teeth were probably used for crushing rather than mincing. Procolophonoids may have contained the ancestors of turtles. This suggestion had been discredited, but a recent discovery of numerous complete skeletons of *Owenetta* shows that this diminutive reptile of the Late Permian shares many features with the oldest known turtle, *Proganochelys.*

Like *Claudiosaurus*, *Eunotosaurus* represents another enigmatic Permian reptile. This small (20 cm SVL) lizardlike creature from the Middle Permian was once considered the link between the basal reptiles and turtles because it possessed eight pairs of broadly expanded ribs on the trunk. However, the pectoral girdle lays external to the ribs, and the skull is strongly divergent from the cranial morphology of any early turtles.

Age of Reptiles—Radiation in the Mesozoic

Reptiles dominate the fossil beds of the Mesozoic. They are both the most numerous and the largest fossils. This richness reflects the diversity of Mesozoic reptiles and their amazingly broad radiation (McGowan, 1991). They were the dominant terrestrial and aerial animals, and although not the dominant marine ones, many were

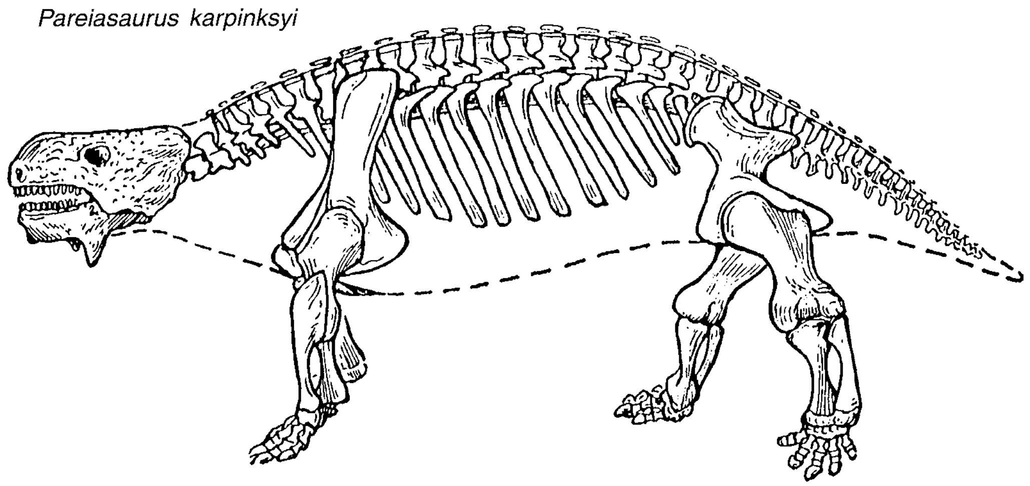


FIGURE 3.11 *Pareiasaurus karpinksyi*, a pareiasaur from the Late Permian of Russia (about 3 m TL). Adapted from Gregory (1951).

major marine predators. The following summaries touch only briefly on this diversity.

Marine Reptiles

The sauropterygians and ichthyosaurs are a presumed clade (Euryapsida) of marine reptiles, whose origin has been uncertain until recently. Evidence now suggests that these exclusively Mesozoic reptiles diverged early from the saurian line (Rieppel, 1993) prior to the origin of the lepidosauromorphs and archosauromorphs (Fig. 1.11). The sauropterygians were immensely successful aquatic reptiles that appeared early in the Triassic and remained abundant until the end of the Cretaceous. The sauropterygians consist of two distinct but related groups, the placodonts (Middle and Upper Triassic) and the ‘‘plesiosaurs’’ in the broadest sense. The placodonts, although presumably aquatic, did not have a strongly aquatic-designed habitus. They had short, broad heads, stout bodies, and long, laterally compressed tails. Their limbs were short and well developed with a terrestrial manus and pes anatomy. Most were 1–2 m TL, and some had dermal carapaces resembling turtle shells. The broad heads and tooth morphology suggest herbivory or a diet of shelled invertebrates, gathered in coastal and shallow-water environments. The ‘‘plesiosaurs’’ had a body form unlike that of any other aquatic tetrapods (Fig. 3.12). Although streamlined, the body was large and stocky with a long, flexible neck and large flipperlike limbs. The Triassic nothosaurs were small to moderate-sized (20 cm to 4 m TL) reptiles with the tail being one-third to nearly one-half of the total length. This body form suggests that they swam by undulatory movements of the tail and posterior half of the body, using the limbs as rudders. The subsequent plesiosaurs appeared in the mid-Triassic and were abundant in the Jurassic through the Middle Cretaceous. They were generally large creatures from 10 to 13 m in total length. The body was barrel-shaped with a short tail, less than body length, and very large flipperlike limbs. In one group, the neck was very long, ending in a tiny head, and in another group the neck was shorter with a large, elongated head. They swam with their limbs rather than through body and tail undulation. How they swam is uncertain. The two most likely possibilities are aquatic flight like penguins and seaturtles whose limbs move in a figure eight stroke as in flying birds, or with the more paddlelike stroke of seals (Tarsitano and Riess, 1982).

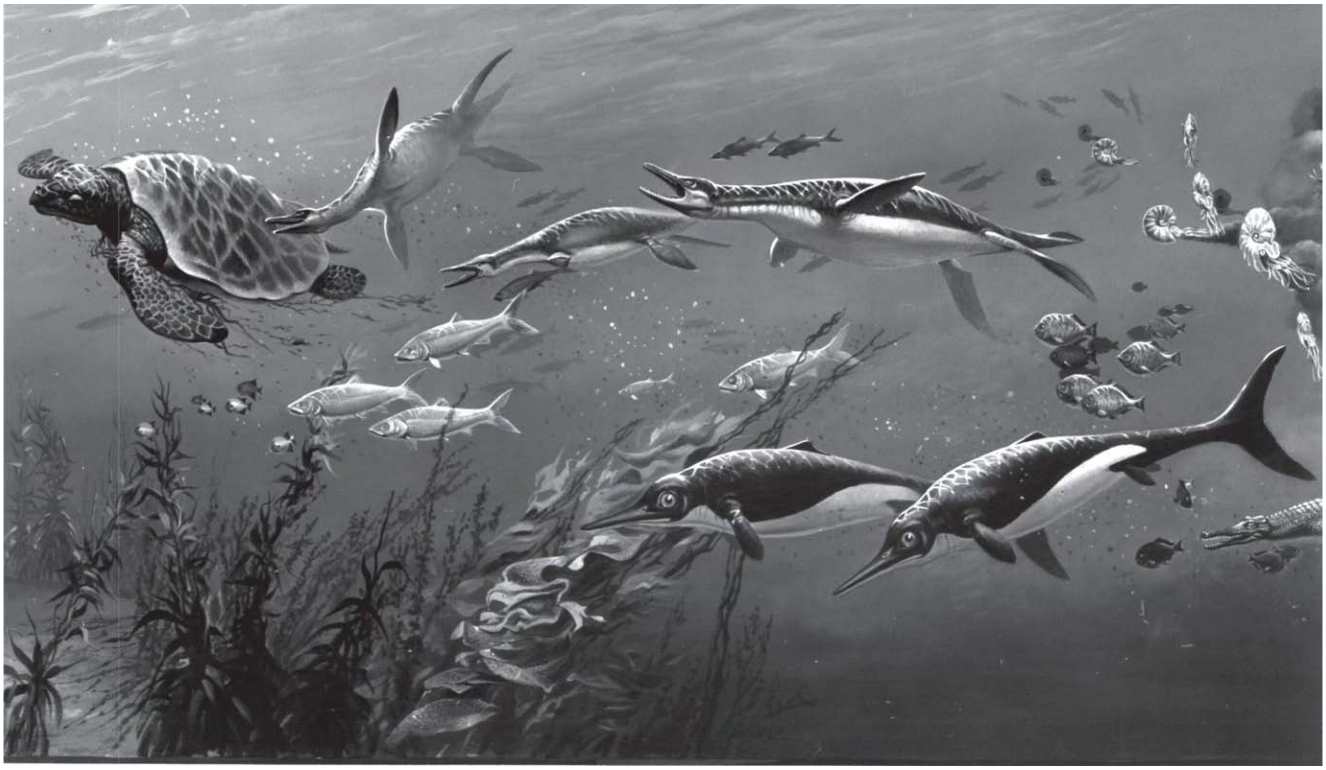


FIGURE 3.12 Some Mesozoic marine reptiles (from upper left, clockwise): *Protostega* (cryptodiran chelonioid; Late Cretaceous), *Dolichorhychops* (pliosaurid plesiosaur; L. Cret.), and *Stegoptergius* (ichythyosaur; L. Cret.). From *Into the Swim Again*, courtesy of the National Museum of Natural History, Smithsonian Institution.

No matter how they swam, they were probably excellent and fast swimmers.

The ichthyosaurs were also a successful group of marine reptiles (McGowan, 1991), although they declined greatly in abundance in the Early Cretaceous and disappeared by the mid-Cretaceous. As their name implies, the ichthyosaurs were fishlike reptiles (Fig. 3.12), with body forms matching those of today's faster swimmers—mackerel and tunas. They ranged in size from about 1.5 to 15 m. Their fishlike form and the presence of fetuses within the body cavity of some individuals attest to their viviparity (live-bearing). Most other Mesozoic marine reptiles probably were oviparous and had to struggle ashore like modern seaturtles to deposit their eggs.

Among the early crocodyliforms, several groups became highly aquatic (Hua and Buffetaut, 1997) and perhaps totally so. The most specialized group was the metriorhynchids (Middle Jurassic to Lower Cretaceous). At least 15 species have been recognized. All were about 3 m long with heavy, streamlined heads, bodies, and tails. The tail had a sharklike downward bend at its tip (heterocercal), and the limbs were flippers. The head was long-snouted and strongly toothed. By all appearances, they were excellent swimmers and successful fish predators. Other marine crocodyliformes included the teleosaurids (Fig. 3.13; late Lower Jurassic to early Lower Cretaceous), dyrosaurids (Middle Cretaceous to Eocene), and a few more Mesozoic families of brief geologic occurrence. These taxa were more typically crocodilian in appearance, although with a tendency toward streamlining and reduction of dorsal armoring.

In the Middle Cretaceous, the first marine turtles appeared. They already had streamlined shells and flipper forelimbs, indicating a much earlier origin. Three clades are evident in these seaturtles, the Cheloniidae, Protostegidae, and Dermochelyidae (Hirayama, 1997). Cheloniids and protostegids were moderately abundant and widespread throughout the Upper Cretaceous and had a modest radiation. The protostegid *Archelon ischyros* was the largest of the seaturtles and had a carapace length of nearly 3 m. Today's giants, the dermochelyids, did not appear until late in the Cretaceous.

A lineage of aquatic lizards split early from the evolutionary line leading to the extant varanoid groups. The dolichosaurs (Middle to Late Cretaceous) were long-necked plesiosaur-like lizards that displayed little

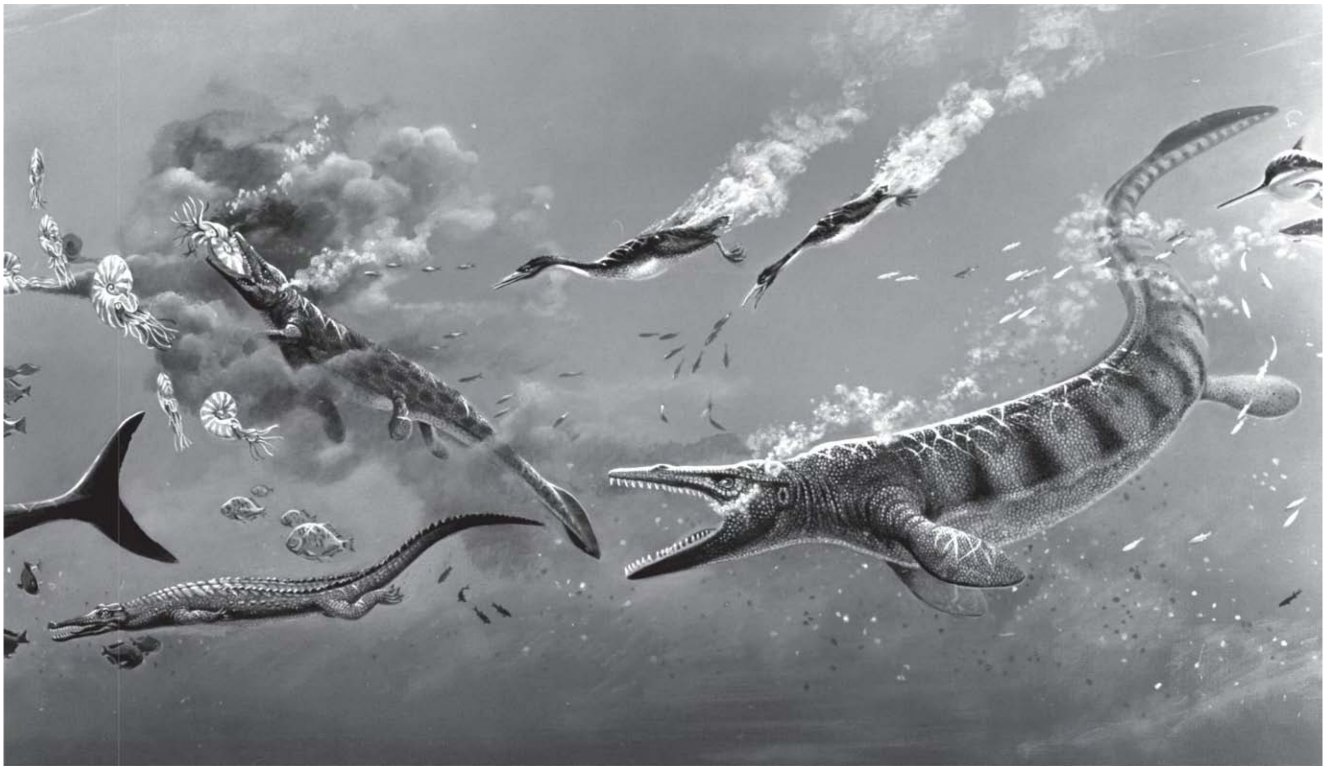


FIGURE 3.13 Some Mesozoic marine reptiles (from upper left, clockwise): *Clidates* (mosasaur; Late Cretaceous), *Hesperornis* (bird; L. Cret.), *Tylosaurus* (mosasaur: L. Cret.), and *Stenoeosaurus* (teleosaurid crocodyliform; Late Jurassic). From *Into The Swim Again*, courtesy of the National Museum of Natural History, Smithsonian Institution.

diversity. Their relationship to the mosasaurs is unclear. The earliest mosasaurs were the small (1–2.5 m TL) aigialosaurs, monitor-like in general appearance, although they had shorter necks, reduced but not structurally reorganized limbs, and a laterally compressed, heterocercal tail. They lived in the Late Jurassic to Middle Cretaceous seas. The Late Cretaceous mosasaurs (Fig. 3.13) had a moderate adaptive radiation that produced a variety of different sizes and feeding morphologies (e.g., at least 16 different body forms are recognized). These body forms remained somewhat lizardlike, even though the mosasaurs were highly aquatic animals. The head was elongate and narrow, joined by a short neck to an elongate trunk and tail. Their limbs were modified into flippers by a shortening of the pro- and epipodial elements and an elongation (i.e., hyperphalangy) of the meso- and metapodial elements and phalanges. The sinuous body and tail were both used in undulatory swimming, with flippers serving as rudders. Terrestrial locomotion would have been most difficult; nonetheless, they were likely oviparous and females would have had to come ashore to lay eggs. This difficult task was compounded further by their size, as the smallest genus was 2.5 m (TL) and the largest reached nearly 12.5 m. Some mosasaurs were surface creatures; others probably dove regularly to depths of several hundred meters for food (Martin and Rothschild, 1989). All were carnivorous predators.

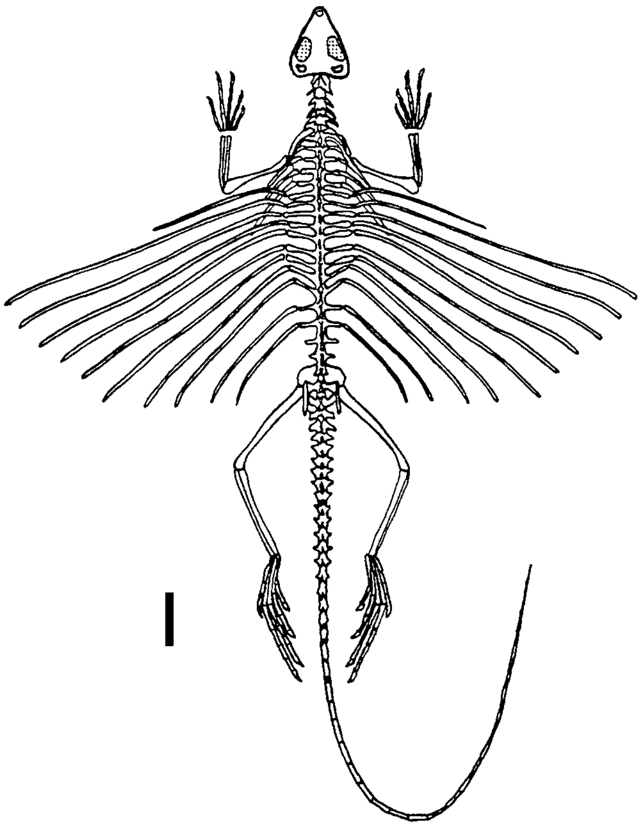


FIGURE 3.14 *Kuehneosaurus*, an ancient diapsid glider, from the late Upper Triassic. Scale bar = 4 cm. Adapted from Robinson, in Romer (1966).

Gliders and Fliers

Most airborne animals develop flight surfaces by modifying anterior appendages or by stretching membranes between anterior and posterior appendages. Several groups of diapsid reptiles independently modified their ribs and associated muscles to form an airfoil. This ribcage adaptation is unique to diapsids and exists today in *Draco*, a group of Indomalaysian agamids (Fig. 3.14). The thoracic ribs are greatly elongated and for more than one-half of their length are free of the body cavity and attached to each other by a thin web of skin (Colbert, 1967). Limbs are well developed, and *Draco* can run nimbly up and down tree trunks, with the elongated ribs folded tightly against the body. When pursued, they jump into the air; the elongated ribs unfold like a fan and create an airfoil that allows them to glide long distances at a gentle angle of descent.

The first flying reptile appeared in the Late Permian. *Coelurosauravus* was a moderately large diapsid (ca. 18 cm SVL) with membranes arising from each side of the trunk creating an airfoil of nearly 30 cm width. The original description suggested that this airfoil was supported by the ribcage as in *Draco*; however, subsequent examinations show the airfoil to be supported by dermal rods that would have appeared dracolike in glide-flight (Frey et al., 1997). Although highly specialized as a glider, *Coelurosauravus* possessed many primitive diapsid features and is a basal member of the neodiapsid clade.

The Late Triassic kuehneosaurids were also gliders (Colbert, 1967). They had ribcage airfoils like that of *Draco*. They are an early divergent lineage and the sister group of the lepidosaurs. Another Late Triassic glider, *Sharovipteryx*, had large membranes extending from each hindlimb to the base of the tail and perhaps small ones from the forelimbs to the trunk, creating a stealth-bomber profile with a long, thin tail projecting posteriorly (Gans et al., 1987). *Sharovipteryx* is a small (<10 cm SVL) diapsid of uncertain affinities.

The typical vertebrate airfoil of modified forelimb wings was used for flight by two groups of ornithodiran archosaurs—pterosaurs and birds. Both of these aerial reptiles were capable of self-propulsive, "flapping" flight. Some proponents, however, still argue for only gliding flight in pterosaurs. The pterosaurs developed a membranous wing that stretched from the posterior edge of the forelimb to the body. The proximal skeletal elements were shortened and robust for the attachment of flight muscles. Most of the wing's span attached to a greatly elongated fourth digit, that is, elongation of metacarpal IV and especially the phalanges, each of which was longer than the humerus. The birds modified their specialized scales (feathers) to produce an airfoil surface. The forelimb provided the support for the feathers and the anterior edge of the airfoil. In birds, the humerus is short, and the radius and ulna elongate, along with elongate metacarpals and phalanges of the first three digits.

The pterosaurs appeared in the Late Triassic as full-winged fliers and persisted as a group throughout the remainder of the Mesozoic (Benton, 1997a). Nearly a hundred species of pterosaurs are recognized—from small species (15 cm wingspan) to the aerial giants *Pteranodon* (7 m wingspan) and *Quetzalcoatlus* (11–12 m wingspan). This variety in size was matched by a variety of shapes and feeding habits, including scavengers, insectivores, piscivores, carnivores, and even filter-feeders. Their distant cousins, the birds, did not appear until the Late Jurassic (*Archaeopteryx*), and bird diversity either remained low throughout the remainder of the Mesozoic or, alternatively, only a few kinds were fossilized.

The present controversy concerning the origin of birds from within dinosaurs or from other and earlier archosauromorphs is based on how flight evolved. The nondinosaur proponents suggest flight arose from gliding down; in contrast, the dinosaur proponents advocate that flight arose from running and jumping up. The gliding-down advocates point to the small forelimbs of the proposed dinosaur-bird ancestors and the low probability of such limbs becoming wings. The running-jumping advocates note that limb evolution can proceed in either direction and feathers were present to provide lift.

Archosauromorphs

The archosaurs, the so-called "Ruling Reptiles" of the Mesozoic, are a monophyletic group still with a major presence today, that is, the crocodilians and birds. Indeed these two groups represent the two major clades of archosaurs: crocodylotarsi and ornithodirans. The former includes a diverse group of crocodilians and relatives; the latter contains the dinosaurs, pterosaurs, and their relatives. The divergence of these two groups is evident by the Middle Triassic.

The rhynchosaurs, proterosuchids, erythrosuchids, and *Euparkeria* were early offshoots of the diapsid lineage that led to the archosaurs. They show a sequential alteration of the skeleton toward the archosaurian mode and a trend toward increasing size. Proterosuchids (Late Permian to Early Triassic) were moderate-sized, varanid-like reptiles with a sprawling gait. The erythrosuchids, present from the Early to Middle Triassic, were large (ca. 5 m), heavy-bodied reptiles with the beginnings of a more erect limb posture and the archosaurian triradiate pelvic girdle. *Euparkeria* interrupts the size trend as it was less than 1 m TL; further it likely was quadrapedal, walking on all four limbs.

Euparkeria, from the Early Triassic, is variously considered the most primitive or the sister group of archosaurs. It appeared much like a short-necked monitor lizard and is the first of this clade with dermal bony armor, a trait that occurs in numerous subsequent archosaurs. Of the archosaurian lineages, the crocodylotarsians radiated broadly beginning in the Middle Triassic. The ornithodirans, that is, pterosaurs and dinosaurs, do not appear until later, with the first definite dinosaur fossils from the Triassic–Jurassic boundary. These first fossils contain representatives of three taxa, and all three were lightweight, bipedal saurischian dinosaurs, demonstrating that the saurischian–ornithischian divergence had occurred (Benton, 1997b). The diversity of dinosaurs was great (Parrish, 1997). They ranged in all sizes from 1 to 25 m (TL) and had an enormous variety of shapes. They had equally varied diets and occupied a wide range of habitats. Because this diversity and their evolution are so broadly covered elsewhere, that literature is recommended to the reader.

The Crocodylotarsi includes a large number of families, most of which possessed a general crocodilian body form that was variously modified (Buffetaut, 1989; Russell and Wu, 1997). The diversity of this group does not match that of the ornithodiran archosaurs; nonetheless, nearly two dozen families and numerous species are known from the Mesozoic. Until recently, the classification emphasized levels (grades) of specialization or divergence from the basic pseudosuchian stock. These grades, such as the protosuchian (Fig. 3.15) or mesosuchian, contained multiple groups. That classification is now being replaced by monophyletic groupings; however, the new classification is not yet firmly established, in part because the fragmentary nature of some of the extinct species and genera does not permit reliable determination of relationships.

The phytosaurs from the Late Triassic are the most primitive crocodylotarsians and an early offshoot of the main crocodilian lineage. They were 2–4 m (TL), gharial-like animals; however, their teeth were small and remained inside the mouth when closed, and their nostrils were on a raised bony mound at the base of a long, narrow snout. The aetosaurs of the Late Triassic are another early evolutionary side branch. They had a small, piglike head (Fig. 3.15) on a heavily armor-plated crocodilian body and tail. Their small, leaf-shaped teeth suggest a herbivorous diet, which would make them the earliest herbivorous archosaurs.

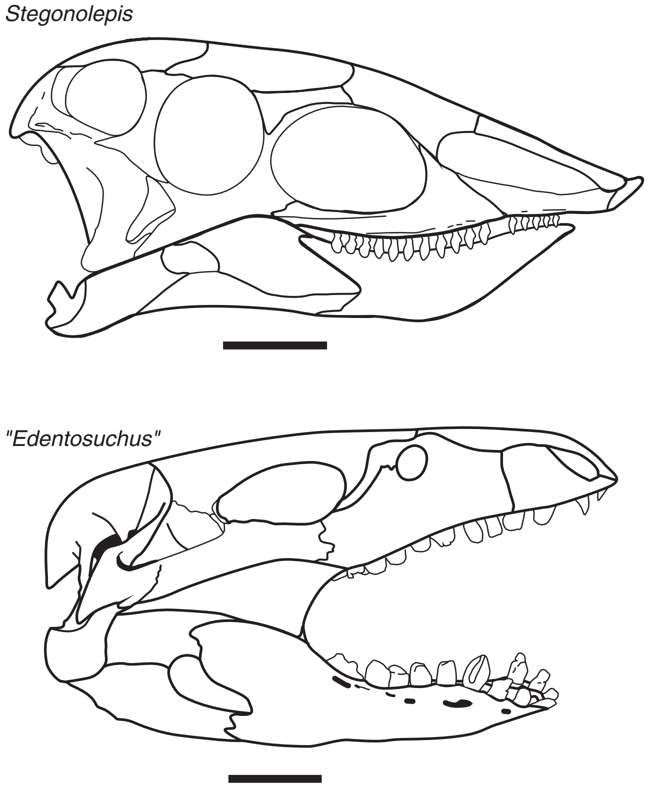


FIGURE 3.15 Cranial structure of ancient crocodilians: the aetosaur *Stegonolepis* (above) of the Upper Triassic and an unnamed *Edentosuchus*-like protosuchid of the Early Jurassic. Scale bar = 1 cm. Adapted from Walker (1961) and Seus et al. (1994), respectively.

Several other divergent groups appeared and disappeared in the Triassic. The main crocodilian clade, Crocodyliformes, was represented by a few subclades (e.g., teleosaurids; Fig. 3.13) in the Early Jurassic, but the diversity of this group did not arise until the Late Jurassic and Early Cretaceous (Russell and Wu, 1997). The low Jurassic diversity results from the presence of only a few terrestrial and freshwater fossil deposits, the habitats in which crocodyliforms were radiating. A marine radiation of crocodyliforms is evident from the late Lower Jurassic to the Middle Cretaceous (Hua and Buffetaut, 1997), and one group, the dyrosaurs, persisted into the mid-Tertiary. All were highly aquatic. The teleosaurids from the Early Jurassic to the Early Cretaceous were gharial-like crocodyliforms (1–9.5 m TL) of estuarine and near-shore habitats. The forelimbs of the teleosaurids were greatly reduced and swimming probably was accomplished through the undulatory movement of the body and tail. The hindlimbs remained large and likely served as rudders. Another lineage included the monstrous (>11 m TL), semiaquatic *Sarcosuchus*, an Early Cretaceous pholidosaurid. Other members of this marine radiation were metriorhynchids and *Pelagosaurus*.

The neosuchians, the lineage leading to the modern crocodilians, consist of much more than the sole surviving Crocodylia and include several Cretaceous groups, such as *Bernissartia*, a small alligator-like, mollusivorous form. The Crocodylia, the modern crocodilian clade, presumably arose in the Early Cretaceous. Members of the extant families did not appear until the Late Cretaceous, and they have been the prominent semiaquatic crocodylians since then (see "History of Extant Reptiles" below). A few species became terrestrial, and the pristichampsines developed hooflike feet.

Extinct Lepidosauromorphs

The lepidosauromorphs are the second major diapsid lineage. The first appearance of this group occurs in the Late Permian. The Younginiformes, including *Youngina*, *Acerosodontosaurus*, and Tangsauridae, are basal members of this early radiation that survived into the Early Triassic. *Youngina* was a slender diapsid that would have been easily mistaken for many modern lizards and was likely an agile, terrestrial insectivore. The tangsaurids were similar but had laterally compressed tails and probably an aquatic lifestyle. Another group of Upper Permian–Lower Triassic lepidosauromorphs includes *Paliguana*, *Saurosternon*, and *Palaeagama*; the relationships of these eolacertilians are uncertain and debated. They were medium-sized (<20 cm TL) lizardlike diapsids.

Thereafter, the lepidosauromorphs are largely absent from the fossil record until the Late Triassic (Benton, 1994) when the Sphenodontida and the kuehneosaurids appeared (Fig. 3.9). Kuehneosauridae is the sister group to the Lepidosauria (Fig. 1.13). Kuehneosaurids (Fig. 3.14) and the eolacertilians are similar in size.

The first sphenodontidan was *Brachyrhinodon taylori* from the Upper Triassic of Virginia and a likely contemporary of the first kuehneosaurid. Sphenodontidans were never an exceptionally diverse group, and most appeared much like the living tuataras, *Sphenodon*. The exception is a small group of aquatic genera, the pleurosaurines, which have elongated bodies and tails, and usually a barracuda-like head (Fig. 3.16). A sphenodontidan mini-radiation occurred from the Late Triassic to the Late Jurassic, during which this group was moderately abundant (Benton, 1997a). Thereafter, the fossil presence of sphenodontidans declined through the Cretaceous, and no Tertiary forms have been found.

Lepidosaurs that are unquestionably squamates do not appear until the Middle Jurassic (Fig. 3.9; Evans and Milner, 1994). The Paramacellodidae, which are often considered scincomorphs, had a broad history from the Middle Jurassic into the Middle Cretaceous (Evans, 1993, 1994). Four other presumably more

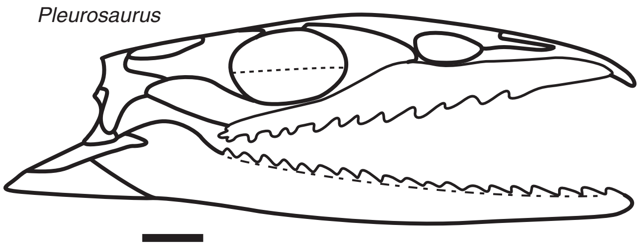


FIGURE 3.16 Cranial structure of the marine sphenodontidan *Pleurosaurus* from the Late Jurassic. Scale bar = 1 cm. Adapted from Carroll and Wild (1994).

basal squamate clades, Ardeosauridae, Bavarisauridae, Dorsetisauridae, and Euposauridae, appeared in the Late Jurassic and apparently all became extinct in the Early Cretaceous. The ardeosaurids contain three genera, *Ardeosaurus*, *Eichstaettisaurus*, and *Yabeinosaurus*, which appear geckolike in some features and have been considered gekkotans. This gekkotan relationship is now questioned. The bavarisaurids contain two genera, *Bavarisaurus* and *Palaeolacerta*, and similarly share some features with gekkotans. The other two families have been linked with extant lizard families, but these relationships also are uncertain. The euposaurids resemble agamids, but other evidence suggests that they are sphenodontidans. The dorsetisaurids resemble anguimorphs although not convincingly so. The Early Cretaceous *Scandnesia* is another basal squamate, whose affinities lie basal to the Iguania and possibly with *Eichstaettisaurus* (Evans and Barbadillo, 1998).

Not all Upper Jurassic squamates are of uncertain affinities (Rieppel, 1994). *Parviraptor estesi* is a medium-sized anguimorph (ca. 15 cm SVL) and appears to be the sister group of the varanoids (Fig. 21.1). The Cretaceous marine lizards (aigialosaurids, mosasaurs, and others) are strikingly similar to the varanoids, and this similarity includes a number of derived traits that are shared, thus attesting to a close relationship (Fig. 21.1). The Necrosauridae, occurring from the Early Cretaceous to the Oligocene, also possess some uniquely varanoid traits and have been proposed as a sister group of the helodermatids.

Aside from the preceding fossil representatives, the extant squamate families lack a fossil presence until the Middle Cretaceous or later (Estes, 1983a,b; Kardong, 1997). These taxa are discussed in the following section.

History of Extant Reptiles

Crocodylians

The Crocodylia, as now defined, is a clade consisting of the ancestor of extant crocodilians and all its descendants (Norell, 1989). Members of this clade, vernacularly the crocodylians, appeared first in the Late Cretaceous, although no members of the extant families occur in the fossil record until the Tertiary (Fig. 3.9; Brochu, 1999; Markwick, 1997). The older and broader definition of Crocodylia (Steel, 1973) included protosuchians, eusuchians, and other groups, and extended their history into the Lower Jurassic (Russell and Wu, 1997; Wu et al., 1996b). A few members of these older clades survived into the mid-Tertiary (Brochu, 1997b); however, the Tertiary belongs to the crocodylians. The higher clades (gavialoids, alligatoroids, and crocodyloids) include many fossil taxa and these reveal a Cretaceous divergence of gavialoids from the other crocodylians (Table 3.4).

Gavialis has only a Pliocene and Recent occurrence (Brochu, 1997a). Extinct gharial or gavialoid fossils occur in the Late Cretaceous and were geographically widespread. Taxa occurred in North America (Cretaceous to Pliocene), South America (Oligocene to Pliocene; Gasparini, 1996), Europe (Oligocene to Miocene), Australia (Pliocene), and southern Asia (Eocene to Recent). All possessed the long, narrow snout associated with a specialized diet of fish. Most extinct gharial species equaled the size of the living species, but a Pliocene *Gavialis* from India apparently reached total lengths of 15–18 m.

The *Borealosuchus* clade and the pristichampsines are sister groups to the alligatoroid–crocodyloid clade, and both likely arose in Late Cretaceous. *Borealosuchus* were broad-snouted and alligator-like. They appeared at the end of the Cretaceous and survived into the Paleocene of

TABLE 3.4 A Hierarchical Classification of the Extant Crocodilians (Crocodylia)

- Reptilia
  - Diapsida
    - Archosauria
      - Crocodylotarsi
        - Crocodyliformes
          - Crocodylia
            - Gavialoidea
              - Gavialidae
            - Unnamed clade
              - Alligatoroidea
                - Alligatoridae
              - Crocodyloidea
                - Crocodylidae

Note: This classification derives from the phylogenetic relationships proposed in Brochu (1997a,b). Category titles are not assigned to the hierarchical ranks.

North America and Europe. The pristichampsines must also have arisen in the Cretaceous; however, they appeared only briefly in the Middle Eocene of Europe. They were peculiar crocodylians with heavy dorsal and lateral armor and hooflike terminal phalanges.

The earliest alligatoroid (Brochu, 1999; Wu et al., 1996a) and crocodyloid fossils (Norell et al., 1994) are also Late Cretaceous. The Cretaceous alligatoroids include *Brachychampsa* and *Stangerochampsa*. Several other lineages arose and disappeared in the Early Tertiary. The alligatorines appeared first in the Early Oligocene, although the group certainly arose much earlier because the caiman lineage was present in the Early Tertiary (Brochu, 1999) and was represented by *Eocaiman* from the Middle Paleocene to the Middle Miocene and by nettosuchids from the mid-Eocene to the Pliocene of South America. The nettosuchids had a unique jaw articulation and typically a broad, elongate snout. Their ducklike snout suggests a mud-noodling behavior for buried prey. *Melanosuchus* and *Caiman* appear only in the Neotropic Late Miocene and Pleistocene, respectively. In contrast, *Alligator* ranges from the Early Oligocene to the present in North America and Asia.

Crocodyloids similarly had a moderate diversity in the Late Cretaceous and Early Tertiary; the crocodylids first appeared in the lowest Eocene. The tomostomines occurred in the Middle Eocene of Egypt and China, then intermittently in northern Africa (Tchernov, 1986) and Europe from the Oligocene to the Middle Miocene, and then not again until the Late Pliocene in Asia. All shared the narrow, elongate skull. The crocodylines include a variety of lineages of which the "true" *Crocodylus* is only of recent origin from the Pliocene to the present. The Australian–New Caledonian Tertiary crocodylids appear to represent a separate evolutionary stock, the mekosuchines, that likely were displaced in the Pleistocene by the arrival of *Crocodylus* from Asia. The mekosuchines had a variety of body and head forms, ranging from narrow elongate skulls like gharials to short, broad-headed species (Willis, 1997). *Quinkana* was pristichampsine-like in having hooflike terminal phalanges. *Mekosuchus* survived into the Recent era in New Caledonia and apparently was hunted to extinction by the first humans to arrive there.

Turtles

Turtles have a good fossil record (Mlynarski, 1976). Their bony shells are durable structures—in life and in death. The history of turtles extends back nearly 220–210 mybp to the Late Triassic where the most primitive turtle, *Proganochelys*, occurred (Gaffney, 1990). *Proganochelys quenstedti* was unquestionably a turtle (Fig. 3.17). Osteoderms were present and the axial skeleton was modified into a true shell: the ribs and vertebrae were fused to dermal bones to form a carapace, and some pectoral girdle elements and dermal bones fused to form a plastron. *P. quenstedti* also possessed a number of early amniote characteristics that were lost in later turtles. Teeth were present on the palatines but absent from the upper and lower jaws. It had a large carapace with a length of 90 cm (CL), and it was a semiaquatic turtle, well protected by its bony shell and bony neck spines (Fig. 3.17). *P. quenstedti* is not a "transitional" turtle; rather, it is the sister-group taxa to the pleurodire–cryptodire clade, Casichelydia (Table 3.5; Fig. 18.2).

A pleurodire, *Proterochersis*, was contemporaneous and sympatric in Europe with *Proganochelys* (Gaffney, 1986). It was somewhat smaller (ca. 50 cm CL) and likely terrestrial. The pelvic girdle was fused to the plastron, indicating that it was the earliest pleurodire and confirming that the divergence of cryptodires and pleurodires had occurred. Two other contemporaries are *Australochelys* from the Late Triassic–Early Jurassic of Africa and South America and *Paleochersis* from the Late Triassic of Africa and South America (Gaffney, 1986; Gaffney and Kitching, 1994). All subsequent fossil turtles are either cryptodires or pleurodires.

After *Proterochersis*, pleurodires are absent until the brief appearance of *Platychelys* in the Late Jurassic. Pleurodires do not occur again until the Early Cretaceous, but from then to the present, they are represented in many fossil faunas, particularly those of the Southern Hemisphere. Although now confined to the southern continents, a few pleurodires occurred in the Northern Hemisphere at least through the Miocene (Tong et al., 1998). Some Tertiary pleurodires were marine or estuarine and reached the size of modern seaturtles, although they did not develop the habitus and locomotor mode of the cryptodiran seaturtles. Chelids do not appear until the Oligocene or Miocene and only in South America and Australia. In contrast, the fossil history of the extant pelomedusoids begins in the Early Cretaceous (Meylan, 1996). Pelomedusid sidenecks occur first in the Late Cretaceous, with all subsequent fossils confined to Africa. Podocnemids had a much broader distribution in Africa (Late Cretaceous to Eocene), southern Asia (Late Cretaceous to Pliocene–Pleistocene), Europe (Eocene), and South America (Late Cretaceous onward).

The oldest turtle in North America and the first cryptodire is *Kayentachelys aprix* from the late Early Jurassic (185 mybp) of western North America (Gaffney et al., 1987). It was a moderate-sized (30 cm CL), semiterrestrial turtle. Structurally, *K. aprix* was a cryptodire, although it possessed a number of features not seen in modern turtles, such as small teeth on the roof of the mouth. Thereafter, fossil cryptodires are absent until the appearance of the Pleisochelyidae and Pleurosternidae in

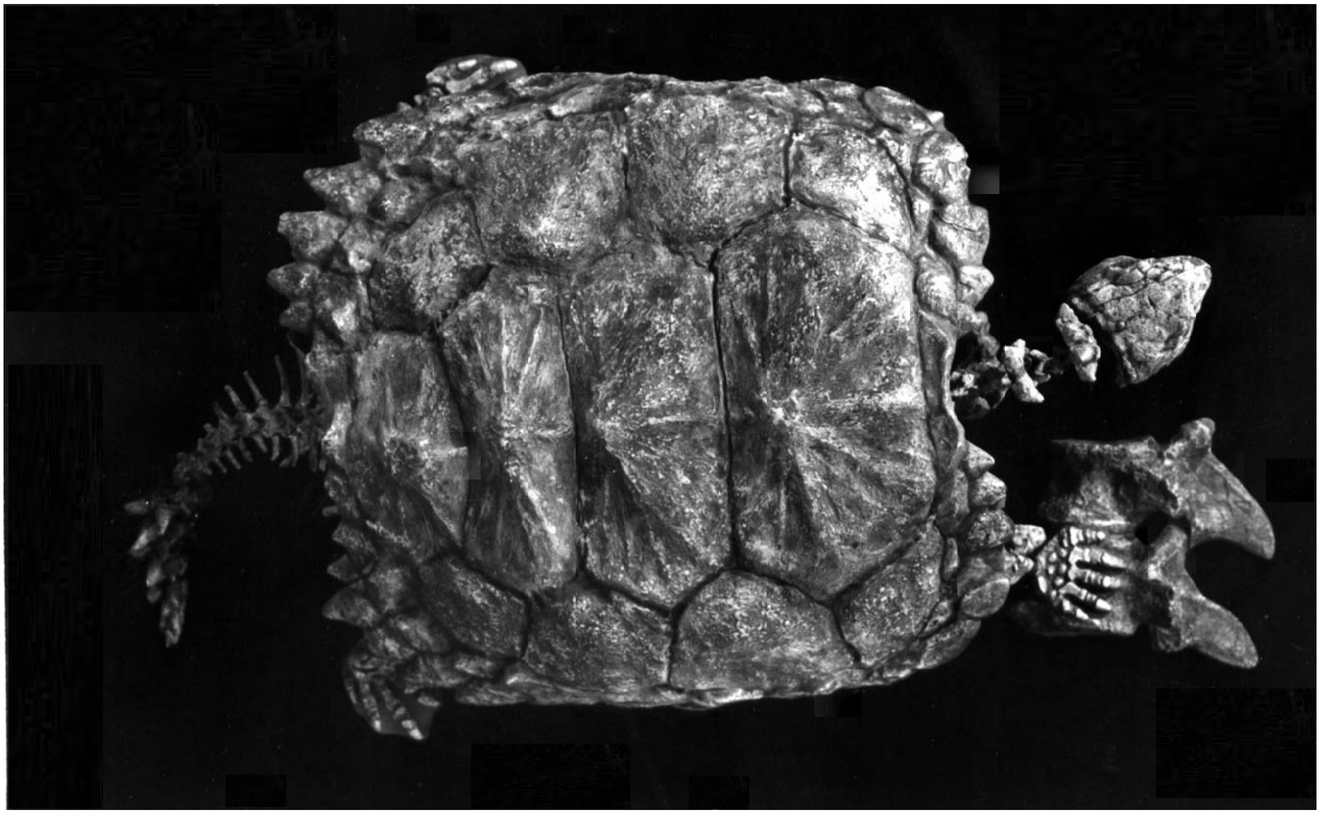


FIGURE 3.17 *Proganochelys quenstedti*, the most ancient turtle, from the Lower Triassic of Germany (approximately 15 cm CL). From Gaffney (1990), courtesy of the American Museum of Natural History.

the lower Late Jurassic; subsequently, cryptodires remained part of the reptilian fauna. Both fossil families contained moderate-sized, aquatic turtles, and neither is related to any of the later-appearing turtle groups. Pleurosternids are the sister group to all subsequent cryptodires. The pleisochelyids are structurally more advanced turtles and the sister group to the meiolaniids and all extant groups of cryptodires. In origin, the baenoids likely arose between the pleurosternids and pleisochelyids; however, the first fossil baenids did not appear until the Middle Cretaceous and persisted into the mid-Tertiary. These heavy-shelled, moderate-sized turtles were strictly North American and probably aquatic to semiaquatic.

Extant or recently extinct clades of cryptodires began to appear in the Cretaceous. The meiolaniids arose prior to the origin of the chelydrids, yet neither has the temporal depth of the chelonioids, which appeared early in the Lower Cretaceous. The meiolaniids or horned tortoises do not occur in the fossil record (Australia and South America) until the Eocene and probably survived into prehistoric times (Gaffney, 1991). Most were large (1 m CL), high-dome-shelled species. They had large heads with a bizarre arrangement of horns or spines projecting from the posterior margin of the skull. The first fossil of chelydrids (*Chelydropsis*) occurred in the Oligocene (Gaffney and Schleich, 1994), and the first snapping turtles, *Chelydra* and *Macrochelys*, in the Miocene.

The oldest known seaturtle, *Santanachelys gaffneyi*, derives from the Middle Cretaceous (ca. 112 mybp). *S. gaffneyi* was a large (1.5 m CL), protostegid seaturtle (Hirayama, 1998). It and other protostegids possessed all the typical features that are seen in extant seaturtles, such as streamlined shells and forelimb flippers. They are the sister group to the extant leatherback seaturtles but probably did have keratinous scutes on their shells. The leatherbacks (Dermochelyidae) did not appear until the Eocene and thereafter experienced a modest radiation of several genera and a dozen species. The other group of chelonioids includes the typical hard-shelled seaturtles, which, depending on whose opinion is followed, include the toxochelyids, osteopygids, and cheloniids, or just the cheloniids, including all the preceding as subfamilies. The toxochelyids and osteopygids appeared near the end of the Cretaceous (Hirayama, 1997); the former did not survive into the Tertiary, and the latter persisted into the Oligocene. The extant cheloniid genera likely

TABLE 3.5 A Hierarchical Classification of the Extant Turtles (Testudines)

- Testudines
  - Pleurodira
    - Chelidae
    - Pelomedusoides
      - Pelomedusidae
      - Podocnemididae
  - Cryptodira
    - Chelydridae
    - Procoelocryptodira
      - Chelonioidea
        - Cheloniidae
        - Dermochelyidae
      - Chelomacryptodira
        - Trionychoidea
          - Carettochelyidae
          - Trionychidae
        - Kinosternoidae
          - Dermatemydidae
          - Kinosternidae
      - Testudinoidea
        - Emydidae
        - Testudinoidae
          - Bataguridae
          - Testudinidae

Note: This classification derives from the phylogenetic relationships displayed in Fig. 18.2 and presented in Shaffer et al. (1997, Table 1). Category titles are not assigned to the hierarchical ranks.

arose in the Late Miocene, although fossils identified as *Chelonia* and *Caretta* have been reported from Eocene and Oligocene sediments.

The trionychoids (Gardner et al., 1995) and testudinoids also occur in the Cretaceous, although only the trionychids are represented by extant genera. Fossils of batagurid–testudinoid might be incorrectly identified, thereby shifting the first appearance of the testudinoids to the Eocene. The modern genera of these turtles began to appear in the Miocene, concurrently with the disappearance of the Early Tertiary genera, although a few of the latter remained into the Pliocene.

Lepidosaurs

Sphenodon guentheri and *Sphenodon punctatus* are the only surviving members of an old (220+ million years), conservative lineage. Although this clade extends deep in time, *Sphenodon* has no fossil presence beyond subrecent records, and with few fragmentary exceptions, the sphenodontidans disappear from the fossil record after the Late Cretaceous.

In contrast, the geological history of the extant squamate families and near relatives (Estes, 1983a,b) begins in the Late Jurassic (ca. 150 mybp), and squamate diversity is evident in the Late Cretaceous (ca. 70–65 mybp; Fig. 3.9, Tables 3.6 and 3.7). Even though the assignment of Middle Jurassic squamates to modern taxa is debated, the numerous groups of Cretaceous squamates and the structural similarity of Jurassic squamates (Evans and Chure, 1998) to them argue for a mid-Mesozoic or earlier radiation. The chronology of first geological occurrence (Gao and Hou, 1995; Evans, 1993, 1995; Kardong, 1997) is Iguanidae (Middle Cretaceous, 98–94 mybp), Agamidae (Late Cretaceous, 98–94 mybp), Chamaeleonidae (Middle Miocene, 20–15 mybp), Xantusiidae (Middle Paleocene, 62–60 mybp), Gekkonidae (Middle Cretaceous, 112–100 mybp), Amphisbaenidae (Late Paleocene, 56–54 mybp), Rhineuridae (Early Eocene, 52–50 mybp), Lacertidae (Eocene, 45–40 mybp), Teiidae (Late Cretaceous, 82–72 mybp), Cordylidae (Oligocene, 36–34 mybp), Scincidae (Late Cretaceous, 88–84 mybp), Anguidae (Late Cretaceous, 98–94 mybp), Xenosauridae (Middle Cretaceous, 98–94 mybp), Helodermatidae (Late Cretaceous, 98–94 mybp), Varanidae (Late Cretaceous, 98–94 mybp), Typhlopidae (Eocene 50–45 mybp), Aniliidae (Cretaceous, 98–94 mybp), Boidae (Early Eocene, 52–48 mybp), Trophidophiidae (Eocene, 52–40 mybp), Acrochordidae (Miocene, 20–10 mybp), Viperidae (Middle Miocene, 20–15 mybp), Colubridae (Oligocene, 35–30 mybp), and Elapidae (Early Miocene, 24–20 mybp).

The broader hierarchical groupings, such as Iguania, Scleroglossa, and Anguimorpha, have earlier occurrences than the families listed above because these clades encompass species of uncertain familial assignment and those of extinct families. Few Cretaceous squamates represent recent genera and species, or even subfamilies, and as noted in the section on "Extinct Lepidosauromorphs," most Jurassic and Lower Cretaceous squamates have debatable relationships to modern families and higher clades. This situation is highlighted by the presumed Cretaceous iguanid *Pristiguana* and the agamid *Priscagama*, both of which are likely correctly placed (Evans, 1995), but their primitive or generalized nature has made even an Iguania assignment suspect. Furthermore, Iguania are cladistically basal to Gekkota and Anguimorpha (Evans, 1994); yet unquestionable gekkotans and anguimorphs occur earlier in the fossil record (Fig. 20.2).

The transition from Cretaceous squamate fauna to a modern one begins in the early Tertiary with a mix of extant and extinct genera and a few extinct subfamilies or

TABLE 3.6 A Hierarchical Classification of the Extant Lepidosauria, Exclusive of Snakes

- Lepidosauria
  - Sphenodontida
    - Sphenodontidae
  - Squamata
    - Iguania
      - Iguanidae
      - Acrodonta
        - Agamidae
        - Chamaeleonidae
    - Scleroglossa
      - Nyctisaura
        - Xantusiidae
        - Unnamed clade
          - Gekkota
            - Gekkonidae
          - Annulata
            - Dibamidae
            - Amphisbaenia
              - Amphisbaenidae
              - Bipedidae
              - Rhineuridae
              - Trogonophidae
      - Autarchoglossa
        - Lacertiformes
          - Lacertidae
          - Teioidea
            - Teiidae
            - Gymnophthalmidae
        - Diploglossa
          - Cordylidae
          - Scincidae
          - Anguimorpha
            - Anguidae
            - Unnamed clade
              - Xenosauridae
              - Varanoidea
                - Helodermatidae
              - Thecoglossa
                - Varanidae
                - Pythonomorpha
                  - mosasaurs
                  - Serpentes

Note: The squamate classification derives from the phylogenetic relationships displayed in Fig. 20.2. Category titles are not assigned to the hierarchical ranks.

TABLE 3.7 A Hierarchical Classification of the Extant Snakes

- Serpentes
  - Scolecophidia
    - Leptotyphlopidae
    - Unnamed clade
      - Anomalepididae
      - Typhlopidae
  - Alethinophidia
    - Unnamed clade
      - Anomochilidae
        - Uropeltidae
          - Cylindrophiidae
            - Aniliidae
              - Xenopeltidae
              - Unnamed clade
                - Loxocemidae
                - Unnamed clade
                  - Boidae
                  - Pythonidae
                  - Unnamed clade
                    - Bolyeriidae
                    - Unnamed clade
                      - Trophidophiidae
                      - Caenophidia
                        - Acrochordidae
                        - colubroids
                          - Viperidae
                          - Unnamed clade
                            - Atractaspididae
                            - "Colubridae"
                            - Elapidae

Note: This classification derives from the phylogenetic relationships displayed in Fig. 21.1. It is a continuation of the classification in Table 3.6. Category titles are not assigned to the hierarchical ranks.

families. Extant genera become prominent in the Miocene, although extinct ones are still numerous. By the Pliocene, modern squamate genera and even a few extant species compose more than 90% of the fauna. Nonetheless, a few ancient taxa linger into the latest Tertiary or Quaternary. A spectacular example is the Australian varanid *Megalania*, a huge goanna. Its average size was about 1.5–1.6 m (SVL), but some individuals reached total lengths of nearly 7 m (4–4.5 m SVL). These giants, probably weighing more than 600 kg, must have been formidable predators, equivalent to lions or tigers.

The earliest presumed iguanian is represented by a dorsal skull fragment from the Middle Cretaceous of Central Asia. Even though it appears unquestionably iguanian, the fossil lacks characteristics for familial assignment. Fossils from the Late Cretaceous sites in the Gobi Desert (Gao and Hou, 1995) and western North America represent four or more genera of Iguanidae and the same for the Agamidae. These iguanids appear most similar to modern crotaphytines. Iguanids occur subsequently in most Tertiary periods, with the first definite iguanine, *Armandisaurus*, from the Lower Miocene of New Mexico (Norell and de Queiroz, 1991), although the *Aciprion* fragment from the Late Eocene may also be an iguanine. While the precise status of *Pristiguana* from the Brazilian Cretaceous (Albino, 1996) remains unclear, *Priscagama* and others, such as *Mimeosaurus* and *Flaviagama*, are certainly agamids. Agamids also appear regularly, if not abundantly, in most Tertiary periods. Leiolepidines appear in Early Eocene deposits in Central Asia (Averianov and Danilov, 1996), and Australian Miocene deposits contain both extant and extinct agamid genera. Chamaeleonids are definitely known from the European and African Miocene, and questionably from the Chinese Paleocene.

Hoburogecko from the Middle Cretaceous of Mongolia is the first gekkotan (Gao and Nessov, 1997). Gekkotans are not abundant or frequent as fossils. Furthermore the assignment of pre-Pliocene fossil gekkotans to the currently recognized subfamilies is difficult. Their presumed sister group, the Annulata, has a much older and more extensive record.

Xantusiidae are the proposed sister group to the Gekkota-Annulata clade. Xantusiids appeared in the Middle Paleocene as the primitive *Palaeoxantusia*, which persisted into the Eocene. Modern *Xantusia* appeared first in the Late Miocene.

The first amphisbaenian is the Middle Cretaceous *Hodzhakulia* from Central Asia (Gao, 1997). Although represented only by maxillary and dentary fragments, these bones possess adequate features to confirm its amphisbaenian identity. The more complete *Sineoamphisbaena* was found recently in a Late Cretaceous deposit of Mongolia (Wu et al., 1997a,b). Its skull and the presence of forelimbs show a primitive amphisbaenian and suggest that this taxon is the sister group to all other amphisbaenians. The next amphisbaenian was a shovel-headed form, *Oligodontosaurus*, from the Late Paleocene of western North America. Although similar to rhineurids, which appeared first in the Early Eocene of the American West, *Oligodontosaurus* had a distinct jaw structure and is placed in its own lineage. The rhineurids are abundant in the Oligocene of the American West and are remarkably similar to the single species surviving today in Florida. *Hyporhina*, another Oligocene shovel-nosed amphisbaenian from the West, represents another lineage. It is probable that these shovel-headed lineages compose a single monophyletic group. The amphisbaenids have a fossil history beginning in the Late Eocene.

The lacertiforms contain two families with a fossil history, although that of the Lacertidae is poor with a spotty history from the Eocene onward. In contrast, the Teiidae have a longer history. Fossil teiines and tupinambines occurred first in the Late Cretaceous (Denton and O'Neill, 1997; Sullivan and Estes, 1997), and concurrently with the polyglyphanodontines. The latter are structurally very similar to extant *Dicrodon* and *Teius*, although more primitive in some features. The polyglyphanodontines were moderately diverse and abundant and occurred in western North America and Central Asia (Alifanov, 1993). In spite of their abundance, they disappeared after the Cretaceous.

The "scincomorphs," the cordylids and scincids, have a modest fossil history. The former has an uncertain occurrence in the Late Cretaceous of western North America; these Cretaceous fossils are inadequate for taxonomic designation, although they possess enough traits to indicate their familial assignment. The next cordylid occurrences were in the Oligocene of France and the Miocene of Kenya. A fossil jaw from the Lower Cretaceous of Spain has been identified as a scincid, although definite scincid fossils are confirmed only from Late Cretaceous assemblages of western North America. Scincids did not appear again until the Oligocene in North America and the Miocene in Asia and Australia.

The anguimorphs, represented by *Parviraptor estesi*, occurred in the Upper Jurassic (Evans, 1994), but the first anguid was the Late Cretaceous glyptosaurine *Odaxosaurus* from the American West. Glyptosaurines were heavy-bodied, broad-headed lizards with an armor of tubercular sculptured osteoderms covering the head and body (see Fig. 3.18). This group, common through the early Tertiary of Eurasia and North America, disappeared in the Middle Miocene. The anguines appeared first in the Middle Eocene of the Northern Hemisphere.

The Xenosauridae, another basal group of anguimorphs, is the sister group to the varanoids. Xenosaurids occurred in the Middle Cretaceous of Central Asia, and in the Late Cretaceous and Upper Paleocene to Lower Eocene of western North American. Thereafter, they disappeared from the fossil record and today occur as one species in China and four or more species in Mexico.

Varanoids are broadly and abundantly present in the fossil record owing to the great diversity that encompasses snakes, mosasaurs, aigailosaurs, helodermatids, necrosaurids, and varanids. The mosasaurs and aigailosaurs were briefly reviewed above in the section on "Marine Reptiles." The Necrosauridae includes an assortment of primitive terrestrial varanoids whose history extended from the Late Cretaceous to the Eocene of

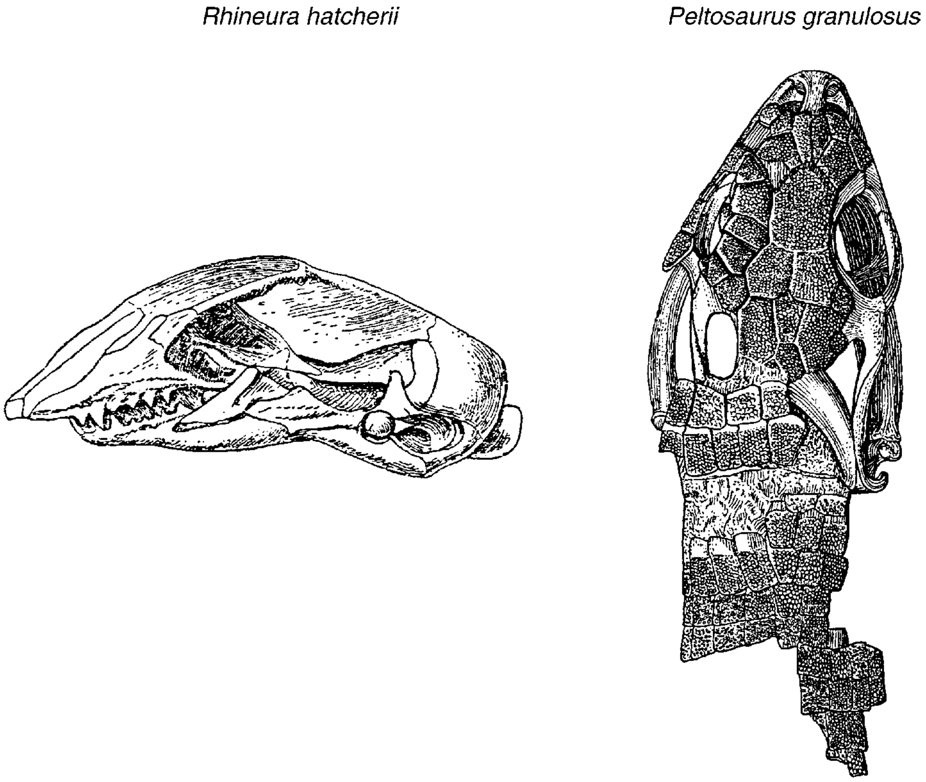


FIGURE 3.18 Skulls of two extinct taxa of North American lizards: Middle Oligocene wormlizard *Rhineura hatcherii* (left; lateral view) and Middle Oligocene glyptosaurine *Peltosaurus granulosus* (right; dorsal view). Adapted from Gilmore (1928).

North America (Cifelli and Nydam, 1995) and to the Oligocene of Eurasia. Helodermatids have a much more extensive history than their modern distribution and diversity indicate. *Paraderma bogerti* was one of two or three Upper Cretaceous beaded lizards in North American. These early helodermatids and the Mongolian *Estesia* (Norell and Gao, 1997) possessed grooved teeth, suggesting that venom has long been a prey-capture mechanism for these lizards. Later records of helodermatids derive from the Eocene and Oligocene of Europe, the Oligocene and Miocene of south-central North America, and Pleistocene records from the American southwest desert. The earliest varanid is *Palaeosaniwa canadensis* from the Late Cretaceous of Alberta. The Mongolian Late Cretaceous also had several lizards that may be varanids. Subsequently, the varanid *Saniwa* occurred in the Late Paleocene to the Oligocene of North America and Europe, and *Iberovaranus* in the Spanish Miocene. The first known *Varanus* derives from the Lower Miocene of Kenya (Clos, 1995), and subsequent *Varanus* fossils occur within the distribution of the extant varanids.

Whether the snakes arose from the varanoid ancestor or a deeper anguimorph one, they appeared in the fossil record (Rage, 1984, 1987) as early as the iguanians. Presently, the oldest known snake (Rage and Richter, 1994) is represented by two vertebrae from the Early Cretaceous (127–121 mybp). Although two vertebrae might seem an inadequate base on which to recognize a snake, snake vertebrae have several unique features that easily separate them from other squamates, and yet they retain features that are typical lepidosaurian. The vertebrae alone are, however, inadequate to determine the relationship of this fossil to other snakes. *Lapparentophis defrennei* from the Middle Cretaceous (100–96 mybp) is known only from three trunk vertebrae. *L. defrennei* is an alethinophidian and presumably was a terrestrial snake. Two other snakes of equal antiquity, *Simoliophis* and *Pouitella*, are apparently not closely related to one another or to *Lapparentophis*, other than being primitive snakes. These three snake genera also do not seem to be related to any of the living families of snakes, and they or their descendants do not occur later in time; however, determination of relationships and habits on the basis of a few vertebrae is risky.

Pachyrhachis was recognized as a peculiar long-bodied varanoid of the Middle Cretaceous. It had small limbs and was apparently marine, but aspects of its skull and vertebrae were snakelike. The initial discoverer proposed that it was a mosasaur or relative of a mosasaur; however, when reexamined, it was declared to be a limbed snake and the sister group to all subsequent snakes (Caldwell and Lee, 1997). This proposition remains controversial (Zaher, 1998); nevertheless, *Pachyrhachis* supports the origin of snakes from a varanoid ancestor.

Other snakes appeared in the Late Cretaceous. One of these, *Coniophis*, was initially considered an aniliid; however, it might be a boid. *Gigantophis* and *Madtsoia* were large snakes equal in size to the largest extant boids and initially considered a lineage within boids. As a group, madtsoiids are Gondwanan and occur in fossil assemblages from Australia (Early Eocene to Pleistocene), Madagascar (Cretaceous), Africa (Cretaceous to Late Eocene), and South America (Cretaceous to Early Eocene); recently, one was discovered in a Spanish Cretaceous deposit (Rage, 1996). In Australia, the madtsoiids (*Wonambi*, *Yurlunggur*, and several undescribed taxa) were a major group of snakes throughout the Tertiary (Scanlon, 1992). Was their disappearance linked to an increasing diversity of pythons in the Late Tertiary and Quaternary?

The unique *Dinilysia* (Dinilysiidae; Fig. 3.19) is known only from the Late Cretaceous of Patagonia; it was also a large snake, roughly equal in size and appearance to *Boa constrictor.* It is one of the rare fossil snake finds consisting of a nearly complete skull and part of the vertebral column. In spite of the completeness of its skeleton, the relationships of *Dinilysia* remain uncertain, although it appears to be an alethinophidian.

Additional booids (a vernacular label for alethinophidian snakes that are not caenophidians) appeared in the Early Tertiary and seemed to be the dominant snakes through the Eocene. Apparently climatic events caused major snake extinctions at the Eocene–Oligocene boundary. Snake diversity remained low through the Oligocene, and dominance in the snake faunas shifted to the caenophidians. Some of the booids were related to modern species. *Charina brevispondylus* from the Middle Eocene of Wyoming, for example, is the sister species of *Charina trivirgata*. A variety of boines and erycines were present in the Eocene. *Coniophis* also occurred in the Eocene of North America and Europe and was accompanied by other aniliids. Scolecophidians have an extremely poor fossil history. Only a few fossils have been found and the earliest are from the Eocene. These fossils have been assigned tentatively to the typhlopids.

The first caenophidians appear in the Eocene (Sullivan and Holman, 1997) and include acrochordoid and colubroid relatives. These caenophidians include extinct families and genera, none with clear affinities to modern taxa. The Oligocene presented the first colubrids, for example, "*Coluber*" and *Texasophis.* Thereafter, colubrids occur with increasing frequency. Acrochordids appeared first in the Middle Miocene, but two earlier Paleocene and Eocene fossils are of a related but extinct group. The first elapid was the European *Palaeonaja* from the Early Miocene; subsequently in the Miocene, elapids occurred in Eurasia and North America. The viperids also appeared first in the Miocene. As with lizards, fossil snake faunas become increasingly modern in appearance through the Pliocene (Parmley and Holman, 1995), and by the Middle Pleistocene, most snake faunas are composed solely of modern taxa (Holman, 1995).

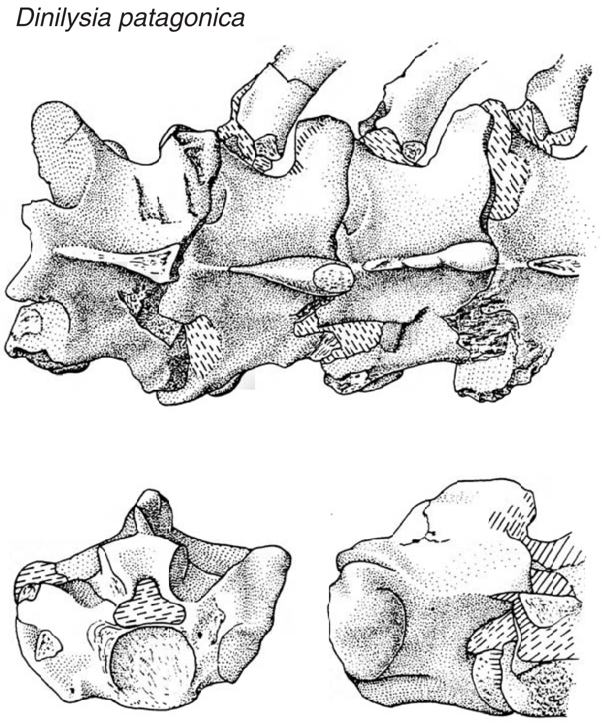


FIGURE 3.19 Trunk vertebrae from the Upper Cretaceous snake *Dinilysia patagonica*: dorsal view of a series of four vertebrae (top), and anterior view (bottom left) and lateral view (bottom right) of individual vertebrae. Adapted from Rage and Albino (1989).

ADDITIONAL READING

Ahlberg, P. E., and Milner, A. R. (1994). The origin and the early diversification of tetrapods. *Nature* **368:** 507–514.

Benton, M. J. (1997a). "Vertebrate Paleontology," 2nd ed. Chapman & Hall, London.

Carroll, R. L. (1988). "Vertebrate Paleontology and Evolution." W. H. Freeman & Co., New York.

Farlow, J. O., and Brett-Surman, M. K., Eds. (1997). "The Complete Dinosaur." Indiana Univ. Press, Bloomington.

REFERENCES

General: Benton, 1997a; Carroll, 1988.

Amphibians of the Late Paleozoic: Ahlberg and Milner, 1994; Milner, 1980, 1988, 1993.

Amphibians of the Early Mesozoic: Milner, 1994; Milner et al., 1986.

History of Lissamphibia: Caecilians: Estes, 1981; Evans et al., 1996; Jenkins and Walsh, 1993; Rage, 1986.

Albanerpetontids: McGowan and Evans, 1995; Milner, 1994.

Salamanders: Estes, 1981; Evans and Milner, 1994, 1996; Evans et al., 1988, 1996; Holman, 1995; Hutchinson, 1992; Rage et al., 1993; Rocek, 1994a.

Frogs: Báez, 1996; Báez and Basso, 1996; Báez and Pugener, 1998; Báez and Trueb, 1997; Estes and Reig, 1973; Evans and Milner, 1993; Evans et al., 1990; Henrici, 1994, 1998; Holman, 1995; Hutchinson, 1992; Milner, 1994; Pledge, 1992; Poinar and Cannatella, 1987; Prasad and Rage, 1991, 1995; Rage and Rocek, 1989; Rocek, 1994b; Rocek and Lamaud, 1995; Rocek and Nessov, 1993; Sánchiz and Rocek, 1996; Shubin and Jenkins, 1995; Spinar, 1972; Tyler, 1991a,b.

Radiation among Early Amniotes: Protomammals: The Synapsids: Hotton et al., 1986.

Paleozoic Reptiles: Benton, 1991; Carroll, 1991; Laurin and Reisz, 1995.

Age of Reptiles: Marine Reptiles: Hirayama, 1997; Hua and Buffetaut, 1997; Martin and Rothschild, 1989; McGowan, 1991; Rieppel, 1993; Tarsitano and Riess, 1982.

Gliders and Fliers: Colbert, 1967; Frey et al., 1997; Gans et al., 1987.

Archosauromorphs: Benton, 1997b; Buffetaut, 1989; Parrish, 1997; Russell and Wu, 1997.

Extinct Lepidosauromorphs: Benton, 1994, 1997a; Estes, 1983a,b; Evans, 1993, 1994; Evans and Barbadillo, 1998; Evans and Milner, 1994; Kardong, 1997; Rieppel, 1994.

History of Extant Reptiles: Crocodylians: Brochu, 1997a,b, 1999; Buffetaut, 1989; Gasparini, 1996; Markwick, 1998; Norell, 1989; Norell et al., 1994; Russell and Wu, 1997; Steel, 1973; Tchernov, 1986; Willis, 1997; Wu et al., 1996a,b.

Turtles: Gaffney, 1986, 1990, 1991; Gaffney et al., 1987; Gaffney and Kitching, 1994; Gaffney and Schleich, 1994; Gardner et al., 1995; Hirayama, 1997, 1998; Meylan, 1996; Mlynarski, 1976; Tong et al., 1998.

Lepidosaurs: Albino, 1996; Alifanov, 1996; Averianov and Danilov, 1996; Caldwell and Lee, 1997; Cifelli and Nydam, 1995; Clos, 1995; Denton and O'Neill, 1997; Estes, 1983a,b; Evans, 1993, 1994, 1995; Evans and Chure, 1998; Gao, 1997; Gao and Hou, 1995; Gao and Nessov, 1998; Holman, 1995; Kardong, 1997; Norell and de Queiroz, 1991; Parmley and Holman, 1995; Rage, 1984, 1987, 1996; Rage and Richter, 1994; Scanlon, 1992; Sullivan and Estes, 1997; Sullivan and Holman, 1997; Wu et al., 1997a,b; Zaher, 1998.

Part II

REPRODUCTION AND LIFE HISTORIES

> *Evolution places heavy emphasis on reproduction, for the way an organism reproduces affects profoundly its contribution to future generations.*
>
> S. C. Stearns, 1976

The ability of organisms to reproduce and send their genes into future generations is a key feature that separates living from nonliving things. Sexual reproduction provides the raw material on which natural selection operates: variation among individuals. Organisms cannot predict the environment of their offspring; consequently, the production of numerous, slightly different offspring that results from reshuffling genes during reproduction provides the opportunity for the adaptation to changing environments. Individuals best able to survive and reproduce given the abiotic and biotic environments at the time will have the most descendants in the next generation.

Amphibians and reptiles have evolved diverse solutions to enhance their reproductive output and survival of their offspring. Fertilization can occur inside or outside the body of the female and development can be direct or indirect. These and other characteristics define the *modes of reproduction*. The location of fertilization and the site of development play important roles in both. Amphibians display a spectacular diversity of reproductive modes. Their complex life history, which includes a larval stage, seemingly has allowed them to experiment with reproduction, and many of these reproductive experiments have proved successful, that is, evolutionarily viable. Reptilian reproduction is much less diverse and includes only two major modes: oviparity, the deposition of eggs, and viviparity, the birth of fully formed individuals. Although most amphibians and reptiles reproduce sexually, some species consist entirely of females that reproduce asexually. In some cases, males are necessary in the reproductive process but their genes are not. Parental care is widespread in amphibians and reptiles, varying from attendance of eggs to protection of juveniles well after hatching.

Chapter

4

Modes of Reproduction and Parental Care

The transition from a totally aquatic life to living at least part of the time on land presented a major challenge in vertebrate evolution and led to an explosion of reproductive adaptations. Because external fertilization was the ancestral condition of the first amphibians, standing water was required for reproduction. The evolution of internal fertilization allowed some amphibians independence from standing water for breeding. Direct development (no free-living larval stage) or attendance of eggs in moist microhabitats permitted development away from water. The evolution of the amniotic egg characterized one lineage of tetrapod vertebrates, the Amniota (reptiles and mammals). Amniotic structures allow respiration and storage of nitrogenous waste within the egg, making it possible for development to occur on land in ‘‘dry,’’ although not desiccating, egg deposition sites. These factors, among others, ultimately led to the successful and broad diversification of tetrapod vertebrates.

GAMETOGENESIS AND FERTILIZATION

In most amphibians and reptiles, two sexes, a female and a male, are necessary for reproduction, although there are remarkable exceptions (see ‘‘Sexual versus Asexual Reproduction’’ below). Each sex must be reproductively ready when the opposite sex is ready. This timing has internal controls but ultimately is coordinated directly or indirectly by the environment, for example, changing temperatures or photoperiods. Internal preparation begins with the production and release of hormones and other associated physiological changes. Gametogenesis, the production of the sex cells or gametes (ova in females and sperm in males), is the major feature of internal reproductive preparations. This process is similar in all vertebrates, where the division and growth of gametes within the females’ ovaries and males’ testes are triggered by hormones. In addition to gamete production, the gonads produce hormones that feed back on the brain, the pituitary, and other organs, and ultimately influence the physiology and behavior of reproduction.

Gamete Structure and Production

Male gametes or spermatozoa are produced by cells (spermatogonia) in the seminiferous tubules of the testes during spermatogenesis (Fig. 4.1). Primary spermatogonia undergo several mitotic divisions to produce primary spermatocytes, and these cells undergo two meiotic divisions to produce spermatids. Differentiation of the spermatids produces spermatozoa that receive nutrition from Sertoli cells. Each spermatozoon is a highly modified cell with three sections: a head, a midpiece packed with mitochondria for the cell's energy needs, and a filamentous tail for locomotion. The head contains the cell nucleus capped by an acrosome. The acrosome produces proteolytic enzymes that digest the egg capsule and allow the spermatozoon to penetrate into an egg. Among amphibians, spermatozoan morphology is highly variable. Salamanders may have a barb on the acrosome; in anurans, primitive lineages have two tail filaments (flagella), whereas species in other lineages may have one or two filaments, or one filament only (Fouquette and Delahoussaye, 1977). Although the spermatozoa of many reptiles have been described (Newton and Trauth, 1992), thorough examination of variation in sperm morphology has not been made in a phylogenetic context.

In females, the gametes or ova are produced in the ovary (Fig. 4.2). Oogenesis is similar to spermatogenesis in males. Primordial gonocytes occur in capsules of nonsex cells known as follicles, which are located in the wall of the ovary. Primordial gonocytes divide by mitosis to produce oogonia (cells that will produce eggs). Each oogonium undergoes two mitotic divisions and enlarges to produce a primary oocyte, which then undergoes two meiotic divisions. The first meiotic division produces a secondary oocyte and the first polar body, a nonfunctional cell; the second meiotic division produces the ovum and a secondary polar body. Each oogonium thus yields only one ovum. Nutrients accumulate in the cytoplasm of the ovum by a process known as vitellogenesis. These nutrients, primarily phosphoproteins and lipids, will become the yolk (Follett and Redshaw, 1974).

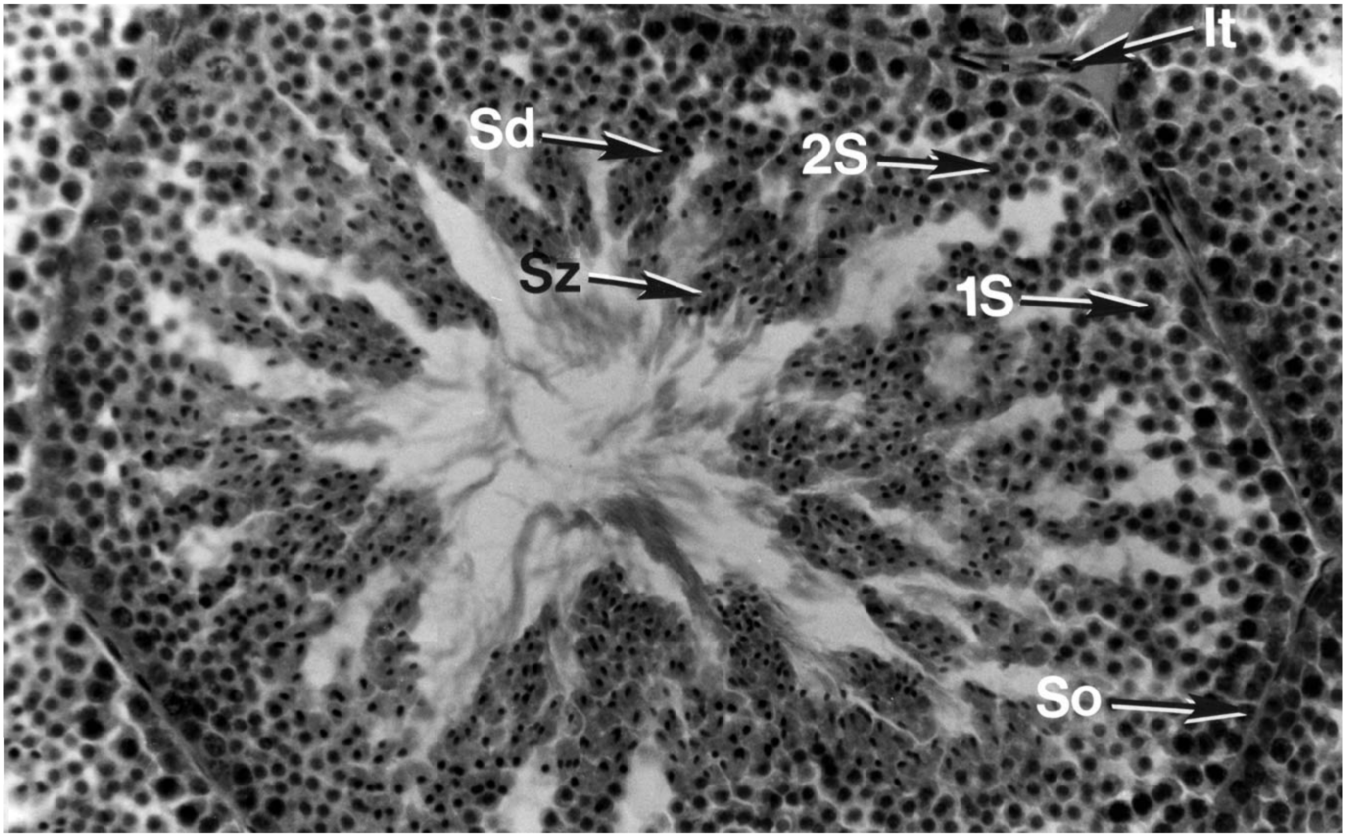


FIGURE 4.1 Spermatogenesis. Cross section through the seminiferous tubule of the skink *Carlia bicarinata*. Abbreviations are 1S, primary spermatocyte; 2S, secondary spermatocyte; It, interstitial tissue; Sz, spermatozoon; Sd, spermatid; and So, spermatogonium. Photograph by M. Barber.

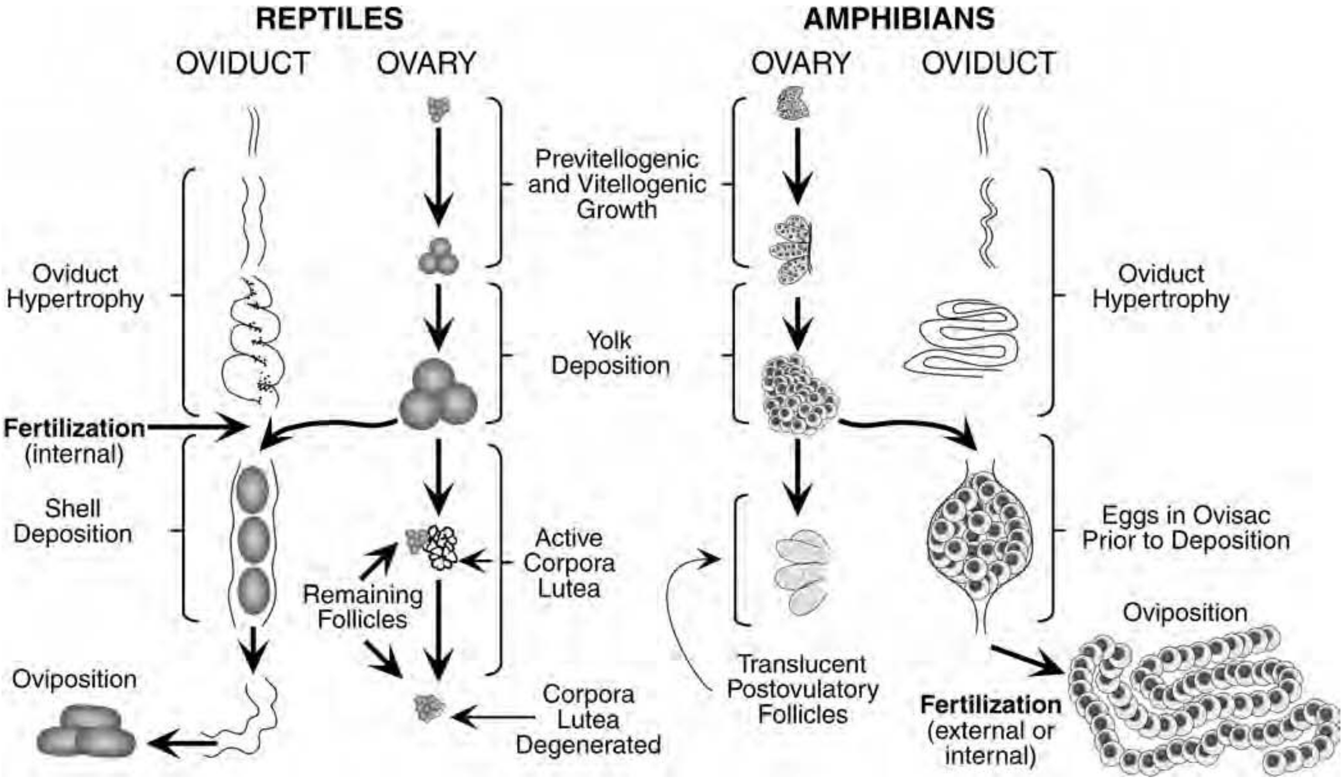


FIGURE 4.2 Development of eggs in amphibians and reptiles. Fertilization occurs internally in all reptiles after eggs are ovulated into the oviducts. Fertilization occurs externally in most amphibians. Corpora lutea are often prominent in reptiles but rare in amphibians. Following production of the clutch, the process is repeated as unused ovarian follicles mobilize lipids for production of the subsequent clutch. Subsequent clutches may be produced within the same season or in the following season depending upon species and the environment.

During vitellogenesis in amphibians and reptiles, lipids are mobilized from fat stores throughout the body, carried through the bloodstream to the liver, converted into vitellogenin, and delivered and transferred to the ova.

At metamorphosis, the number of nonvitellogenic oocytes in the ovary of a female amphibian begins to increase rapidly, and evidence from studies on the toad *Bufo bufo* indicates that the total number of oocytes to be used during the lifetime of the female is reached early in the juvenile stage. *Bufo bufo* may produce from 30,000 to 40,000 oocytes during this time (Jørgensen, 1992); presumably, species producing smaller clutches of eggs have fewer nonvitellogenic oocytes.

Vitellogenic growth and maintenance of the small oocytes are initiated by the hormone gonadotropin and signal the beginning of an ovarian cycle. In mature amphibians, the ovaries contain a set of small, nonvitellogenic oocytes that are not responsive to gonadotropin and a set of larger oocytes that are responsive to gonadotropin. Apparently, once vitellogenesis begins for one set of oocytes, intraovarian regulatory mechanisms prevent additional small oocytes from responding to gonadotropin (Jørgensen, 1992).

In all amphibians, fat bodies are discrete structures located adjacent to the gonads. The complex relationship between the gonads and fat bodies has been debated for many years. Experimental evidence regarding the role of fat bodies is contradictory. In many species, fat bodies are large in juvenile females and in those females with ovaries undergoing vitellogenesis. Other species, however, show no correlation between fat body size and the ovarian cycle. In reptiles, vitellogenin is selectively absorbed (during a process called pinocytosis) by oocytes and enzymatically converted to yolk platelet proteins (lipovitilin, phosvitin). The first phase of vitellogenesis is usually slow with little observable growth in the ova. During the last phase of vitellogenesis, ovum growth is rapid. Prior to ovulation (release of ova from the ovaries), a mature ovum is 10–100 times its original size.

In both amphibians and reptiles, ovulation occurs when the follicular and ovarian walls rupture, releasing ova into the body cavity where they migrate into the infundibulum of each oviduct. In most amphibians, the postovulatory follicles exist only for a short time and do not secrete hormones. In viviparous amphibians and reptiles, walls of the follicle transform into corpora lutea (Fig. 4.3). The corpora lutea produce progesterone, and this hormone prevents the expulsion of developing embryos.

As ova pass through the oviduct, protective membranes are deposited around them. In amphibians, the ovum is already enclosed in a vitelline membrane that was produced by the ovary. Continuing their oviductal passage, each ovum is coated with layers of mucoproteins and mucopolysaccharides. The number of layers or capsules around the ovum is species specific. In some salamanders, the egg consists of as many as eight capsules around the ovum. Anurans typically have fewer capsules than salamanders. Amphibian eggs are anamniotic because they lack the extraembryonic membranes characteristic of reptiles and mammals (Fig. 4.4; also see Chapter 2).

In egg-laying reptiles, the ovum is ultimately encased in a durable and resistant shell. While in the upper portion of the oviduct, the ovum is sequentially coated with albumin and several thin layers of protein fibers. The fiber layer is impregnated with calcite crystals in crocodilians and squamates, and argonite crystals in turtles. Shortly after ovulation and fertilization (12 hours or less in *Sceloporus woodi*; Palmer et al., 1993), endometrial glands in the oviduct produce the proteinaceous fibers that constitute the support structure of the eggshell (Fig. 4.5).

Shell structure varies considerably among species of oviparous reptiles, but all shells provide at least some protection from desiccation and entry of small organisms. During development, in both viviparous and oviparous reptiles, three extraembryonic membranes, the allantois, amnion, and chorion, develop during embryogenesis. These structures characterize the amniotic egg of reptiles and mammals. The allantois serves as a respiratory surface for the developing embryo and storage sac for nitrogenous wastes (Fig. 4.4).

Fertilization—Transfer and Fusion of Gametes

Fertilization occurs when a spermatozoon and an ovum unite to form a diploid zygote. External fertilization

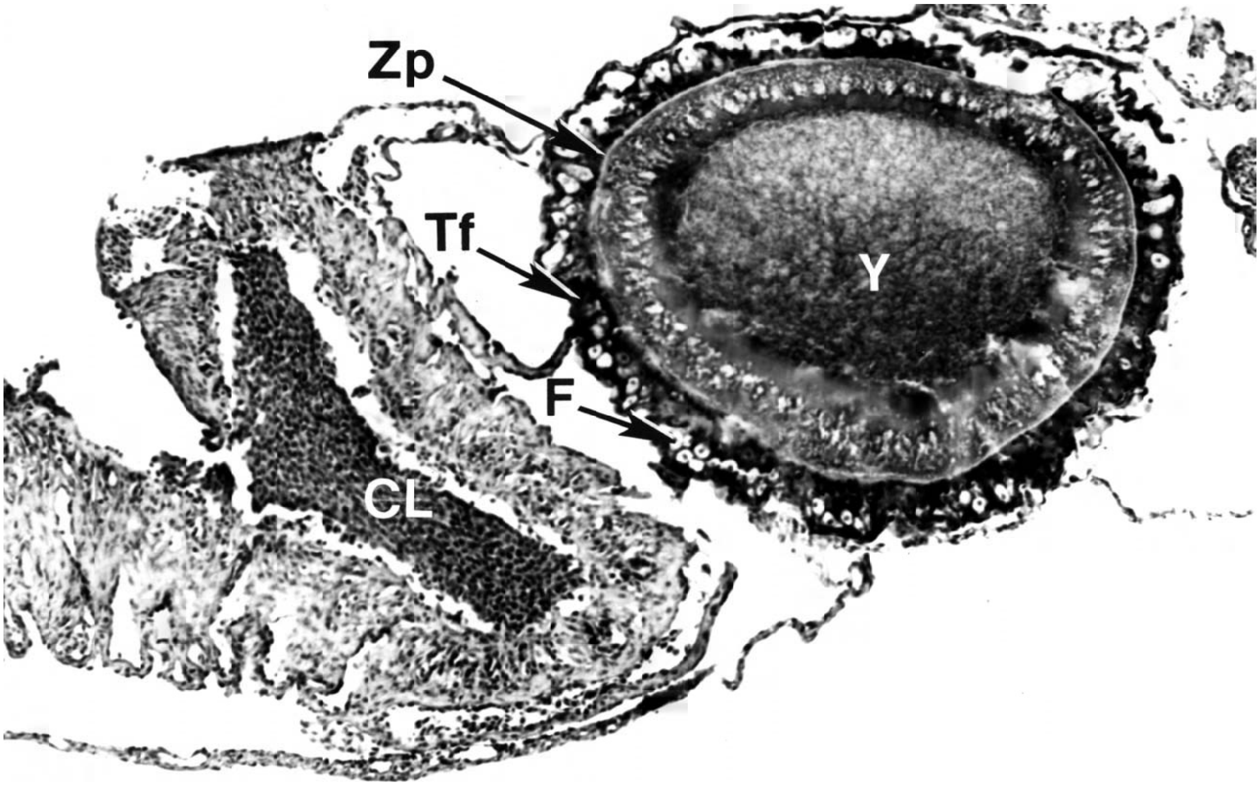


FIGURE 4.3 Oogenesis. Cross section through the ovary of the skink *Carlia bicarinata*, showing a corpus luteum (left) and a maturing follicle (right) with its ovum. Abbreviations are CL, corpus luteum; F, follicular cells; Tf, theca folliculi; Y, yolk; and Zp, zona pellucida. Photograph by D. Schmidt.

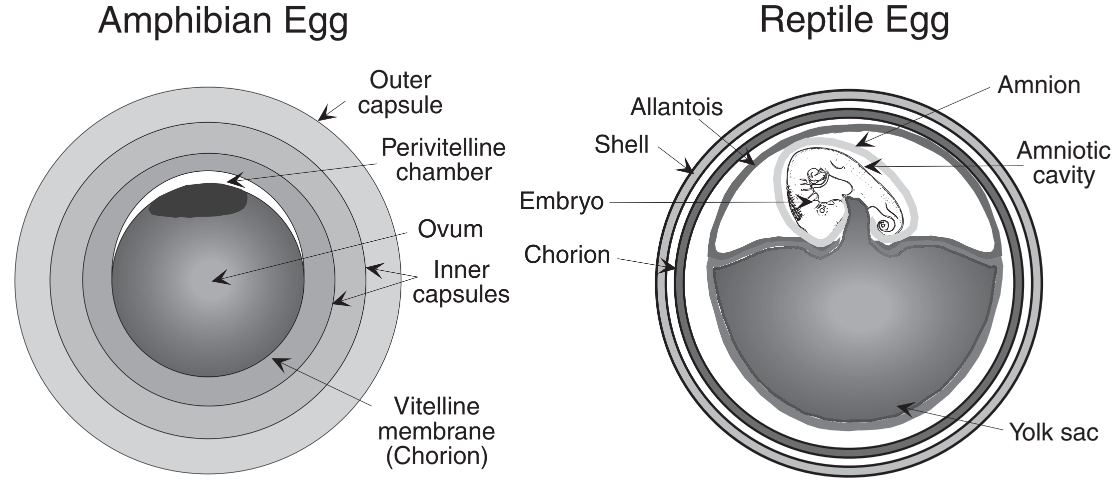


FIGURE 4.4 Comparison of anatomy of the anamniotic amphibian egg and the amniotic reptile egg.

occurs when this union occurs outside the bodies of the male and female, and internal fertilization when the union occurs within the female's body, almost always in the oviducts.

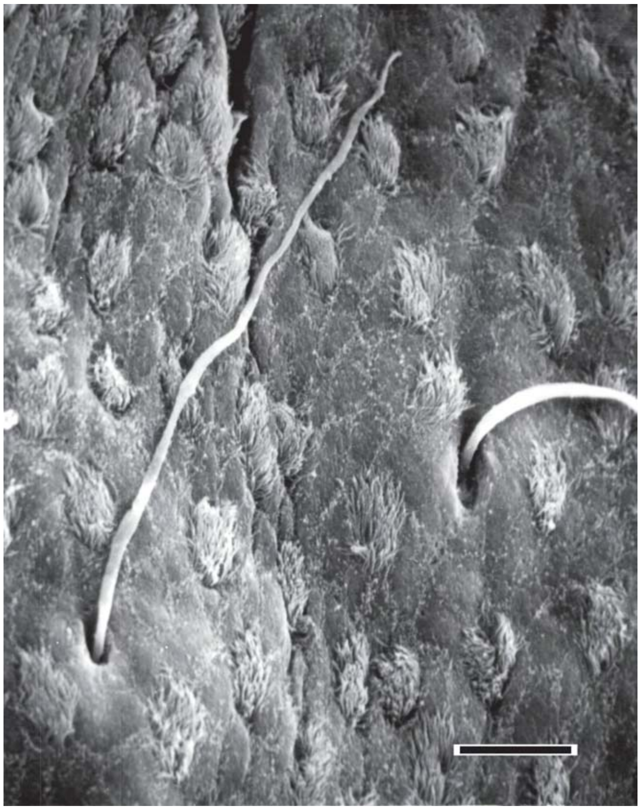


FIGURE 4.5 Wall of the oviduct of the lizard *Sceloporus woodi* during shell production. Two proteinaceous fibers are emerging from the endometrial glands of the oviduct. Scale bar = 5 m. Adapted from Palmer et al. (1993).

Males produce millions of tiny spermatozoa, whereas females produce relatively few eggs. Even though the eggs of some amphibians are small, they are orders of magnitude larger than spermatozoa. During mating, many sperm can reach the surface of an egg but only one will penetrate the cell membrane of the ovum and fertilize it. When sperm first arrive at the egg, a few adhere to the surface. Enzymes produced by the acrosome digest a tiny hole in the egg capsules, bringing the sperm head into contact with the plasma membrane. The enzymes break down receptors binding the sperm pronucleus to the surface of the egg, and the sperm pronucleus moves into the cytoplasm of the ovum. In response to the entry of the sperm pronucleus, the vitelline membrane separates and elevates, lifting all other sperm from the ovum's surface. As the successful sperm pronucleus moves to the ovum pronucleus, the ovum pronucleus completes its final meiotic division. The fusion of the two pronuclei is the final act of fertilization and restores the diploid (2N) condition to the fertilized ovum, which is thereafter called the zygote. The zygote soon begins development via typical cell division—mitosis. Embryonic development continues in externally fertilized eggs, but after development to a gastrula stage, developmental arrest occurs in internally fertilized eggs. Salamanders are unusual because they have polyspermic fertilization, in which more than one sperm pronucleus enters the ovum's cytoplasm, but only one sperm pronucleus fuses with the egg pronucleus.

Reproductive Behaviors Associated with Mating

Courtship and mating behaviors vary greatly among species of amphibians and reptiles. Vocal (auditory), visual, tactile, or chemical signals used during courtship not only bring individuals together for reproductive purposes but also provide opportunities for mate choice. Reproductive behaviors are influenced by hormones. Males, but not always females, have mature gametes when mating occurs. In females of some species, sperm may be stored and used to fertilize eggs long after mating.

Sperm is transferred to females in a variety of ways. In most frogs and cryptobranchoid salamanders, external fertilization is the rule; the male releases sperm on the eggs as they exit from the female's cloaca. In frogs, the male grasps the female so that his cloaca is positioned just above the female's cloaca. This behavior is called amplexus, and the exact positioning of the male with respect to the female varies among species (Fig. 4.6). In salamanders with external fertilization, amplexus can occur, or the male can follow the female and deposit his sperm directly on the egg mass during or after deposition.

A few frogs, including *Ascaphus*, *Mertensophryne*, two species of *Eleutherodactylus*, and four species of *Nectophrynoides*, all salamandroid salamanders, and all reptiles have internal fertilization. Internal fertilization usually requires morphological structures to deliver sperm, and complex mating rituals often are found in these species. All frogs with internal fertilization except *Ascaphus* and *Mertensophryne* use cloacal apposition to transfer sperm. Although the tuatara *Sphenodon* has rudimentary hemipenes, cloacal apposition is used to transfer sperm. Males of other reptiles, the frogs *Ascaphus* and *Mertensophryne*, and caecilians have intromittent organs that deposit sperm into the cloaca adjacent to the oviductal openings. The male reproductive structure of caecilians, the phallodeum, is a pouch in the cloacal wall that is everted into the female's cloaca through a combination of muscular contractions and vascular hydraulic pressure and is withdrawn by a retractor muscle. The intromittent organ in *Ascaphus* is modified from the cloaca; vascularization of the tissue permits engorgement of the organ with blood, facilitating deposition of sperm into the female's cloaca. Males of salamanders with internal fertilization produce spermatophores that are deposited externally. The spermatophore consists of a proteinaceous pedestal capped by a sperm packet; the structure is produced from secretions of various glands in the male's cloaca. Male salamanders have elaborate courtships that rely on secretions from various types of glands to stimulate females to

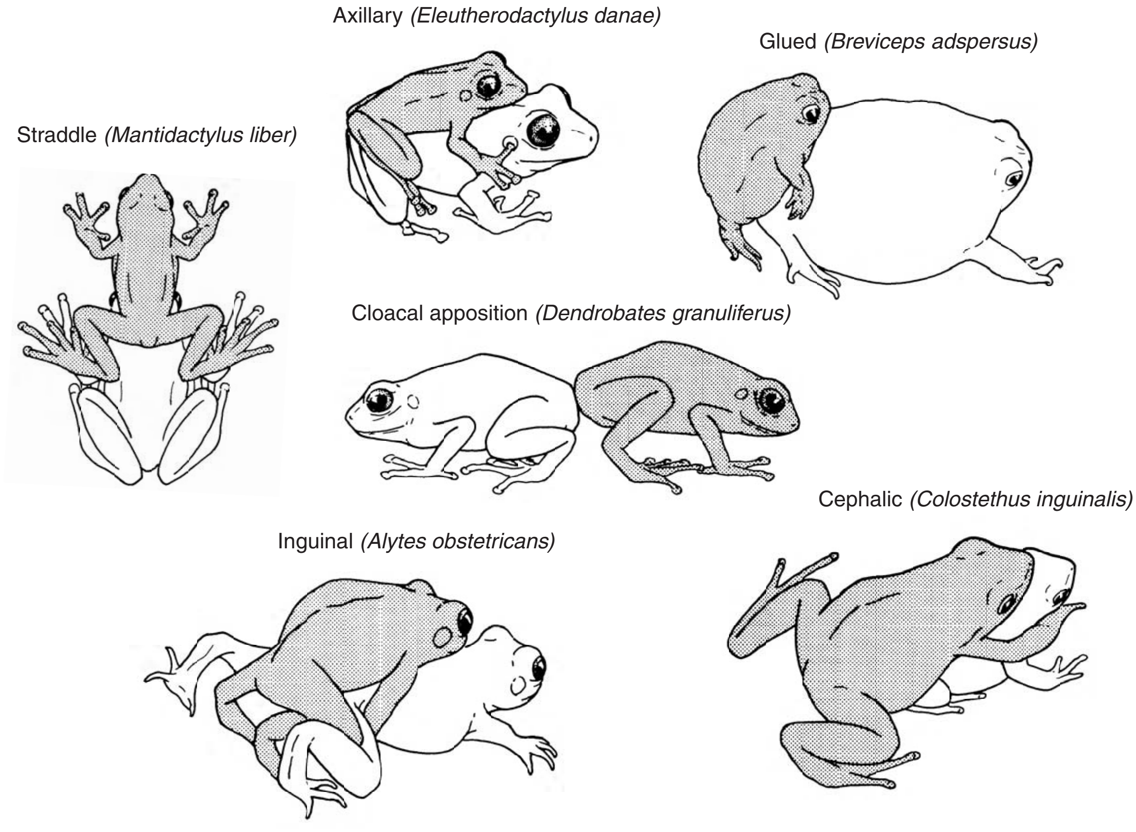


FIGURE 4.6 Positions used by frogs during amplexus. Adapted from Duellman and Trueb (1986).

move over the spermatophores and pick up the sperm packets with the lips of the cloaca (Fig. 4.7). In turtles and crocodilians, a penis of spongy connective tissue becomes erect and retracts depending on vascular pressure; it is structurally similar to and probably homologous with the mammalian penis. Hemipenes are used for intromission in male squamates. These structures consist of two pouches located in the base of the tail that are everted from openings in the posterior part of the cloaca by vascular pressure. Hemipenes of squamates are not homologous with intromittent organs of turtles and crocodilians. Usually only one hemipenis is everted and used during copulation. A retractor muscle withdraws the hemipenis following copulation.

In reptiles, fertilization occurs in the upper portion of the oviducts prior to egg deposition. Fertilization also occurs in the upper portion of the oviducts in caecilians. In contrast, fertilization occurs in the cloaca in salamanders. The exact timing of fertilization varies among species. It can occur immediately after copulation (most lizards) or be delayed (salamanders, turtles, and snakes) for a few hours to years after copulation. Sperm storage structures, which occur in salamanders, turtles, and squamates, facilitate retention of sperm for long periods of time. Delayed fertilization permits females to mate with more than one male, and can result in multiple paternity among the resulting offspring (see Chapter 9).

The sperm storage structure in salamanders, the spermatheca, is located in the roof of the cloaca. The spermatheca is composed of either simple tubes, each of which opens independently into the cloaca, or a cluster of tubules that open by a common duct into the main cloacal chamber. The stored sperm are expelled by muscular contraction as the eggs enter from the oviducts. Sperm storage tubules typically do not unite to form a common duct in reptiles. They are confined to the upper-middle section of the oviducts between the infundibulum and the shell-secreting area in turtles and to the base of infundibulum and lower end of the shell-secreting area in squamates. Because of their location in squamates, their function for long-term storage of sperm has been questioned. The mechanism for expelling sperm from the tubules is unknown.

REPRODUCTIVE MODES

To survive and grow, embryos of amphibians and reptiles must have a supply of nutrients; these are provided in a variety of ways. Embryos of oviparous amphibians and reptiles receive all of their fetal nutrition from yolk within the egg. In viviparous species, nutrition can be provided entirely by yolk, by oviductal secretions, or by a

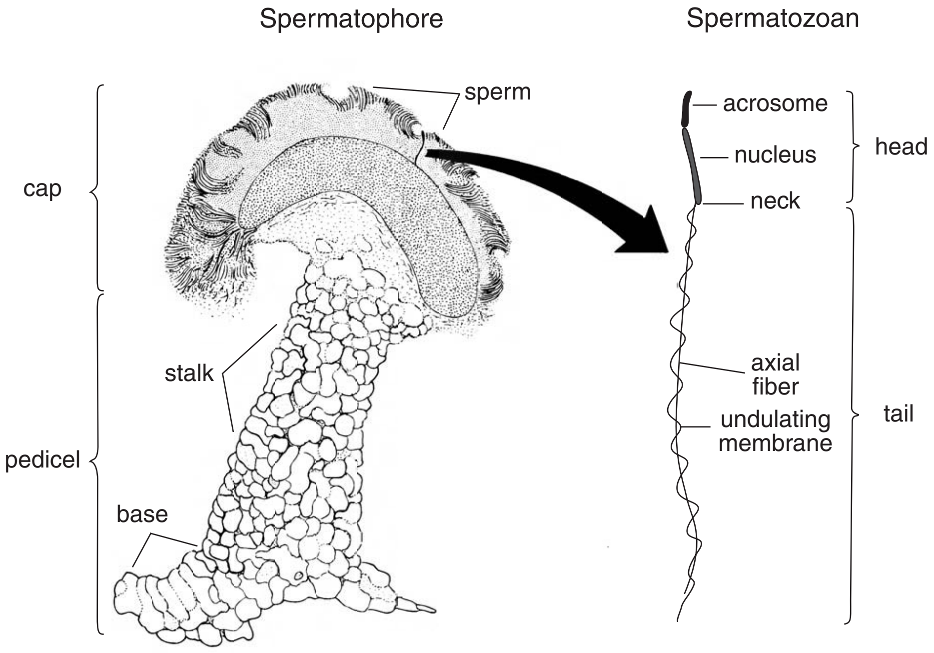


FIGURE 4.7 Diagrammatic representations of a spermatophore and a single spermatozoan of the salamander *Ambystoma texanum*. Sperm are located on the periphery of the cap of the spermatophore. The sperm heads point outward and tails are directed inward. Adapted from Kardong (1992).

complex placenta. The types of embryonic and fetal nutrition have a specific terminology. Lecithotrophy (lecitho = yolk; trophy = food) is the provision of all nutrients necessary for hatching or birth from the yolk of the egg. Matrotrophy (matro = mother) is the provision of at least some nutrients by the mother, and many different types have been identified (Table 4.1). Patrotrophy (patro = father) is provision of some nutrients by the father. These terms are used in this and related chapters.

Amphibians

The reproductive mode in amphibians is defined by a combination of characteristics, including breeding site, clutch structure, location of egg deposition (terrestrial or aquatic), larval development site, and parental care, if present (Salthe, 1969; Salthe and Duellman, 1973). This complex suite of characters is needed because of the rich diversity of reproductive behaviors and life histories among anurans. In contrast, caecilian and salamander reproductive modes are less diverse, although no less complex and interesting.

The ancestral reproductive mode in amphibians is assumed to include external fertilization, oviparity, and no parental care (Duellman and Trueb, 1986; Wake, 1992a). Within salamanders and frogs, some species have external fertilization and some internal fertilization, although the latter is rare in frogs. Caecilians are the exception because all known species have internal fertilization. Oviparity is the rule, with a few exceptions, in salamanders and frogs, and about one-half of caecilians. Parental care in caecilians and salamanders includes egg attendance. Parental care is more diverse in frogs, and has been reported in about 6% of the known species (Duellman and Trueb, 1986; Crump, 1995). The three groups of amphibians will be discussed individually because of the major differences in their reproductive modes (Table 4.2).

Caecilians

Because of the fossorial and secretive nature of caecilians, less is known about their reproduction and life history than either frogs or salamanders. All male caecilians have a copulatory organ, the phallodeum, and presumably all have internal fertilization. More than one-half of the caecilian species are viviparous (Wake, 1993b). In these species, development occurs in the oviduct, and some form of maternal nutrition is provided. Fully metamorphosed young caecilians are eventually born, although the duration of pregnancy is known for only a few species. The remainder of the species are oviparous, depositing eggs on land. The oviparous species either have direct development or eggs hatch and the free-living larvae enter water to complete their development.

Viviparity in caecilians has evolved at least twice, once in an Old World lineage and once in a New World lineage (Wake, 1993b). As in other viviparous amphibians, the number and size of ova of these species are smaller than those in oviparous species; egg size is from 1 to 2 mm in diameter, and egg number is from 10 to 50 (Wake,

TABLE 4.1 Fetal Nutritional Adaptations in Amphibians and Reptiles

Nutritional pattern	Definition	Occurrence
Lecithotrophy	All nutrients for development to hatching or birth contained in egg as yolk when it is ovulated	All amphibians and reptiles that deposit eggs and viviparous species in which there is no matrotrophy
Matrotrophy	Some or all nutrients for developing fetuses provided by female during gestation	
Oophagy	Developing fetuses feed on sibling ova	Only known in *Salamandra atra*
Adelphophagy	Developing fetuses feed on developing siblings (also called uterine cannibalism)	May occur in *S. atra*
Histophagy	Developing embryos feed on maternal secretions	Some viviparous caecilians, frogs, and salamanders
Histotrophy	Developing fetuses absorb maternal secretions	May occur through large saclike gills in typhlonectid caecilians and through fine papillae around the mouths of *Nectophrynoides occidentalis*
Placentotrophy	Developing embryos receive nutrients from the mother by placental transfer	Squamate reptiles with a placenta
Patrotrophy	Male provides some nutrients for developing tadpoles	Tadpoles carried in vocal sacs of *Rhinoderma darwinii* may absorb nutrients from male

Note: Individual species can utilize more than one nutritional adaptation. Three other types of matrotrophy occur in fishes but are not shown. Adapted in part from Blackburn et al. (1985).

TABLE 4.2 Reproductive Modes in Amphibians and Reptiles

Amphibians

Caecilians

- I. Fertilization internal
  - A. Oviparity
    - 1. Eggs terrestrial; development direct
    - 2. Eggs terrestrial; development indirect (larvae)
  - B. Viviparity
    - 1. Birth and neonates terrestrial
    - 2. Birth and neonates aquatic

Salamanders

- I. Fertilization external
  - A. Oviparity
    - 1. Eggs aquatic; development indirect, larvae aquatic
- II. Fertilization internal
  - A. Oviparity
    - 1. Eggs aquatic; development indirect, larvae aquatic
    - 2. Eggs terrestrial; development indirect, larvae aquatic
    - 3. Eggs terrestrial; development indirect, larvae terrestrial and nonfeeding
    - 4. Eggs terrestrial; development direct
  - B. Viviparity
    - 1. Birth and neonates terrestrial
      - a. lecithotrophy
      - b. matrotrophy
        - 1. oviductal histophagy
        - 2. oophagy or adelphophagy

Frogs

- I. Eggs aquatic
  - A. Eggs deposited in water
    - 1. Eggs and feeding tadpoles in lentic water
    - 2. Eggs and feeding tadpoles in lotic waters
    - 3. Eggs and feeding tadpoles in natural or constructed basins; subsequent to flooding, tadpoles in natural ponds or streams.
    - 4. Eggs and feeding tadpoles in water in tree holes or aerial plants
    - 5. Eggs and nonfeeding tadpoles in water-filled depressions
    - 6. Eggs and nonfeeding tadpoles in water in tree holes or aerial plants
    - 7. Eggs deposited in stream and swallowed by female; eggs and tadpoles complete development in stomach of female
  - B. Eggs in foam nest
    - 8. Foam nest on pond, larvae feed in pond
    - 9. Foam nest in pool, larvae feed in stream
  - C. Eggs embedded in dorsum of aquatic female
    - 10. Eggs hatch into feeding tadpoles in ponds
    - 11. Eggs hatch into froglets
- II. Eggs terrestrial or arboreal
  - D. Eggs on ground or in burrows
    - 12. Eggs and early tadpoles in excavated nest; subsequent to flooding, feeding tadpoles in stream or pond
    - 13. Eggs on ground or rock above water or in depression or excavated nest; upon hatching, feeding tadpoles move to water
    - 14. Eggs hatch into tadpoles that are carried to water by adult
    - 15. Eggs hatch into nonfeeding tadpoles that complete their development in nest
    - 16. Eggs hatch into nonfeeding tadpoles that complete their development on dorsum or in pouches of adult
    - 17. Eggs hatch into froglets
  - E. Eggs arboreal
    - 18. Eggs hatch into tadpoles that drop into ponds or streams
    - 19. Eggs hatch into tadpoles that drop into water-filled cavities in trees
    - 20. Eggs hatch into froglets
  - F. Eggs in foam nest
    - 21. Nest in burrow; subsequent to flooding, feeding tadpoles in stream or pond
    - 22. Nest in burrow; nonfeeding tadpoles complete development in nest
    - 23. Nest arboreal; tadpoles drop into ponds or streams
  - G. Eggs carried by adult
    - 24. Eggs carried on legs of male; feeding tadpoles in ponds
    - 25. Eggs carried in dorsal pouch of female; feeding tadpoles in ponds
    - 26. Eggs carried on dorsum or in dorsal pouch of female; nonfeeding tadpoles in bromeliads
    - 27. Eggs carried on dorsum or in dorsal pouch of female; direct development into froglets
- III. Eggs retained in oviducts
  - H. Viviparity—fetal nutrition either lecithotrophic or matrotrophic via histophagy

Reptiles

Crocodylians

- I. Fertilization internal
  - A. Oviparity
    - 1. Parental care, none
    - 2. Parental care, nest and hatchling attendance

Turtles

- I. Fertilization internal
  - A. Oviparity
    - 1. Parental care, none

(*continues*)

TABLE 4.2 (*continued*)

Tuataras
- I. Fertilization internal
  - A. Oviparity
    - 1. Parental care, none

Lizards and snakes
- I. Fertilization internal
  - A. Oviparity
    - 1. Parental care, none
    - 2. Parental care, nest attendance
  - B. Viviparity
    - 1. Strictly placentotrophy; level of nutrient acquisition from predominantly lecithotrophy to near total matrotrophy
      - a. lecithotrophy
      - b. matrotrophy

Note: Terminology with respect to fetal nutrition follows Blackburn et al. (1985). All oviparity involves lecithotrophic nutrition. Amphibian modes are modified from Duellman and Trueb (1986).

1993b). Initially, development is fueled by the yolk, but the yolk is soon exhausted and the fetus switches to matrotrophy. The fetus has a specialized dentition that allows it to scrape nutrient-rich secretions from the walls of the oviduct. This type of maternal nourishment is known as histophagy (Table 4.1) and is evidenced by the presence of the oviductal epithelial cells and secretion in the mouths and pharynges of the fetuses. The fetal dentition is lost at birth and replaced by the typical caecilian dentition of juveniles and adults.

The ovarian cycle and oviductal morphology are known in only a few species of caecilians (Wake, 1993b). The gestation period is approximately 11 months in one species, *Dermophis mexicanus* (Wake, 1980). Corpora lutea are large in pregnant females of the few species that have been studied. Corresponding high levels of progesterone are found in the blood, and, as in other vertebrates, the production of progesterone by the corpora lutea apparently functions to prevent expulsion of the fetuses prior to birth. Proliferation of the epithelial layer of the oviduct begins about the second or third month of pregnancy (Wake, 1980). The content of the secretion changes throughout the gestation period; initially the contents are mainly free amino acids and carbohydrates that gradually become rich in lipids near the end of gestation.

Oviparous species of caecilians have free-living larvae or direct development. Ovum size of species with free-living larvae ranges from 8 to 10 mm, the largest among all reproductive modes. Oviparous species with direct development have eggs ranging in size from 3 to 6 mm; the size of these eggs contrasts with those of oviparous salamanders and frogs, in which direct-developing species have the largest eggs with greater amounts of yolk than species with free-living larvae. Clutch size in oviparous species ranges from 6 to 50 eggs. Larval caecilians of oviparous species do not have specialized dentition. The teeth are fewer in number but otherwise the same as postmetamorphic adult dentition. The length of the larval stage is unknown for most species, but in some Old World taxa, the larval period is about one year (Wake, 1992a).

Gill structure of the viviparous typhlonectidids differs from the free-living larval caecilians that have the typical triramous gills of other larval lissamphibians (Fig. 4.8). Typhlonectid gills are large saclike structures. They appear to function as pseudoplacentas, allowing gas and nutrient exchange between the parent and fetus (Delsol et al., 1981, 1983, 1986). These gills are lost soon after birth.

Salamanders

The basal lineages of salamanders (Hynobiidae, Cryptobranchidae, and presumably the Sirenidae) have external fertilization. All other salamanders have internal fertilization. Hynobiid salamanders deposit paired egg sacs, which are then fertilized by the male. Clutch size in one species varied from 24 to 109 (Kusano, 1980). Cryptobranchids deposit paired strings of eggs (Nickerson and May, 1973). Reproduction has not been observed in the four sirenid species. Two nests of *Siren intermedia* had 206 and 362 eggs, each attended by a female (Godley, 1983). Studies of oviductal anatomy of the two species of *Siren* revealed no sperm in the oviducts (Sever et al., 1996a). The absence of a sperm storage organ and of spermatozoa in the oviducts at the time of oviposition provides strong evidence that external fertilization occurs in sirenids. In all other salamanders, eggs are fertilized as they pass through the oviduct by sperm held in sperm storage structures, and in all species studied, sperm are found in the spermathecae prior to and after oviposition.

All other lineages of salamanders (Salamandroidea) have internal fertilization by means of the male spermatophore. No salamanders have intromittent organs. Instead, cloacal glands secrete substances that form a spermatophore. During elaborate courtship rituals, the male induces the female to follow him. With the female behind him, he deposits a spermatophore on his path, and as the female passes over the spermatophore, she pauses and picks it up with her cloacal lips. Sperm are then stored in the female's spermatheca, a storage organ in the roof of the cloaca, and eggs are fertilized

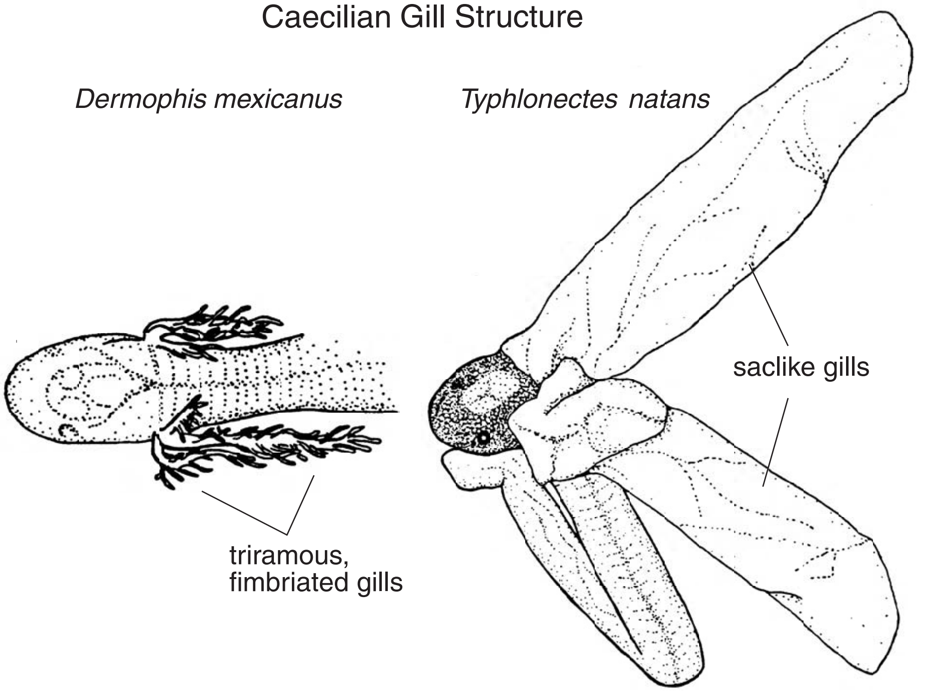


FIGURE 4.8 Gill structure in the larvae of viviparous caecilians. (Left) *Dermophis mexicanus* (Caeciliidae) with triramous, fimbriated gills. (Right) *Typhlonectes natans* (Typhlonectidae) with enlarged, saclike gills; these highly vascularized gills may absorb nutrients from the parent. Adapted from Wake (1993b).

inside the female's cloaca as they pass by the spermatheca.

Several modes of reproduction are found among the families of salamanders with internal fertilization (Table 4.2). Eggs and larvae may be aquatic, or eggs may be terrestrial and larvae may be either aquatic or terrestrial. Terrestrial eggs with direct development are common in one lineage of salamanders, the Plethodontidae.

Four species of salamanders are viviparous: two species of *Salamandra* and two species of *Mertensiella*, all members of the Salamandridae. *Salamandra atra* exhibits matrotrophy, including both histophagy and adelphophagy; in contrast, *Salamandra salamandra* is lecithotrophic (embryos are retained inside the mother's body until birth, but no nutrients are provided by the mother; Table 4.1). Gestation in *S. atra* may extend from 2 to 5 years, depending on the severity of the climate (Wake, 1993b). Only two young, one from each oviduct, are produced. Subsequent eggs produced after the fetuses begin developing are consumed (adelphophagy). The corpora lutea are functional during the entire gestation period, and the female's oviducts become secretory during the second year of gestation. In *S. salamandra*, ecological conditions play a role in determining the reproductive mode. In lowland areas, females give birth to advanced larvae, but in montane areas with colder conditions, the larvae are retained in the female's oviducts until they are fully developed. Little is known about reproduction in the two species of *Mertensiella*; both likely give birth to advanced larvae.

Anurans

Frogs have the greatest diversity in reproductive modes among vertebrates (with the possible exception of the teleost fishes). The ancestral reproductive mode in amphibians includes deposition of eggs in water, but many extant species have partial or fully terrestrial modes of reproduction. Amphibian eggs are permeable and require water to prevent desiccation. Many of the terrestrial types of reproductive modes occur in tropical regions where humidity and temperature are high.

Reproductive modes in amphibians are categorized primarily by the three major situations in which eggs are placed for development (Duellman and Trueb, 1986; Table 4.2). These are: (1) eggs deposited in aquatic habitats, such as ponds, streams, water-holding plants or tree holes, or small basins of water constructed by individuals of certain species of frogs; (2) eggs deposited in arboreal or terrestrial habitats, such as leaves above pools or streams, burrows on land, or on the body of the male or female; and (3) eggs retained in or on the body.

Within each of these three major categories, further subtypes are found; in all, 29 modes of reproduction are represented in anurans. Some examples of each of these three major categories serve to illustrate the complexity and, in some cases, the bizarre reproduction of frogs.

Deposition of aquatic eggs that hatch into free-living larvae that complete development in standing or flowing water appears to be the ancestral condition in anurans, and many extant species have this mode of reproduction (Modes 1 and 2 under "Frogs" in Table 4.2). The gladiator frogs, large hylids that occur in parts of Central and South America, are examples of frogs that construct basins in which the eggs are deposited (Mode 3; see Fig. 5.1). Basins are built commonly at the edges of streams with sand or mud substrates. The male frog constructs the basin by pivoting on his body and pushing the substrate out with his limbs. In *Hyla boans*, the males call from sites above the basin or nest (Caldwell, 1992), whereas in *Hyla rosenbergi*, males call from small platforms at the edge of the nest (Kluge, 1981). Upon arrival of the female, eggs are deposited as a surface film in the nest; subsequent rains break down the edges (ramparts) of the nest, releasing the tadpoles into the main body of the stream.

Several species of hylid frogs (e.g., *Anotheca spinosa, Osteocephalus oophagus*, *Phrynohyas resinifictrix*) deposit eggs in water in arboreal microhabitats such as bromeliads or tree holes; their larvae are either omnivorous or are fed unfertilized eggs by the female parent who periodically returns to the deposition site (Mode 4). The Mesoamerican *A. spinosa* deposits eggs in bromeliads, bamboo internodes, or tree holes. After amplexus and egg deposition, the male disappears, but the female continues to visit the developing tadpoles about every 4.85 days and deposits nonfertile (nutritive) eggs for the tadpoles to eat. Metamorphosis requires 60–136 days, after which the female approaches a calling male, and a new fertile clutch is deposited (Jungfer, 1996). Similar behavior has been observed in the South America species *O. oophagus*, but periodically the female and male return together in amplexus and deposit a new clutch of fertilized eggs (Jungfer and Schiesari, 1995). If tadpoles are present, they consume the newly deposited fertile eggs; otherwise, the new eggs hatch and begin developing. Both of these species are obligate oophages, and their tadpoles die if eggs are not available. In contrast, tadpoles of *P. resinifictrix* are omnivorous, feeding on both detritus and on conspecific eggs (Schiesari et al., 1996).

One of the most unusual reproductive modes is that of the Australian gastric brooding frog, *Rheobatrachus silus*. The female deposits aquatic eggs and then swallows them. The eggs develop in her stomach (Mode 7). It is thought that prostaglandin E2 produced by the developing young inhibits the production of gastric secretions during the gestation period. In several months, fully formed froglets emerge from the mother's mouth.

Aquatic eggs can also be placed in a foam nest that floats on the surface of small ponds or other aquatic habitats (Fig. 4.9; Mode 8). Many leptodactylid frogs construct foam nests, including *Leptodactylus* and *Physalaemus*. In *Physalaemus ephippifer*, the foam is produced from cloacal secretions of the amplexing male and female. The male rotates his legs in a circular motion, whipping the cloacal secretions into a froth. Egg expulsion and fertilization begin once a substantial foam mass has been produced (Fig. 4.10). Each pair of frogs produces a nest of 300 to 400 eggs (Hödl, 1990).

An unusual reproductive mode is found in some species of the aquatic *Pipa* (Mode 11). Eggs are embedded into the dorsum of the female during a complicated mating ritual in which the male and female undergo turnovers under water (Fig. 4.11). While upside down, eggs are extruded from the female's cloaca and are pressed against her dorsum by the male. They become embedded in the female's skin, where they develop into tadpoles (e.g., *Pipa carvalhoi*) or fully emerge as froglets in about two months (e.g., *Pipa pipa*).

The second major category of reproductive modes encompasses frogs that deposit their eggs in arboreal or terrestrial sites. Throughout tropical regions of the world many species deposit eggs on land; in the Amazonian region, for example, more than one-half of all species have terrestrial eggs.

Like all dendrobatid frogs, *Colostethus* deposits relatively small clutches of terrestrial eggs (up to 30; Mode 14). Males and females court on land, and eggs are deposited in leaf litter on the forest floor. During the initial period of development, the male (in most species, but females in some) attends the eggs. After about a week, the eggs hatch and the male wriggles down among the tadpoles and they move up onto his back. He then transports the tadpoles to water, often a small stream or pool in the forest, where the tadpoles swim free and complete their development without further parental care.

At least one species of *Colostethus*, *C. stepheni*, has nonfeeding tadpoles that complete their development in a terrestrial nest (Mode 15). These nidicolous tadpoles remain in the nest in the forest leaf litter about 30 days prior to metamorphosis. Tadpoles of *C. stepheni* are pigmented but lack an oral disc and associated mouthparts (Juncá et al., 1994; Juncá, 1998).

In the Australian *Assa darlingtoni* (Myobatrachidae), males have inguinal pouches for tadpole transport (Mode 16). After an extended amplexus lasting up to nine hours, a terrestrial clutch of eggs is produced. The clutch is guarded by the female, and after about 11 days the egg mass begins to liquefy and the tadpoles hatch.

FIGURE 4.9 Production of a foam nest by a paired male and female *Leptodactylus knudseni*. These large leptodactylids may deposit eggs in the same nest more than once. Tadpoles develop in the foam and are washed into a nearby pond if heavy rains occur. Photograph by W. Hödl.

The male returns and performs a complex series of movements to guide the larvae to his inguinal pouches; the movements can include using his feet to scoop and tuck the tadpoles under him. The larvae use their tails to move onto the male and into the pouches. After 59–80 days in the pouch, the froglets emerge fully formed, having increased their weight 2.6 times in comparison to their entry weight. The male continues to feed and call while carrying the embryos.

Other unrelated species of frogs carry tadpoles in pouches on their backs or, in one genus (*Rhinoderma*), in the vocal sacs of the male. An experiment with *Rhinoderma darwinii* from Argentina showed the possibility that the male provides nutrients for the larvae (Goicoechea et al., 1986). Radioactive material was injected into the lymphatic sacs of males carrying an average of 11 larvae in their vocal sacs. Subsequently, these tracer compounds appeared in the tissues of the larvae, suggesting patrotrophy. This is the first case of patrotrophy in amphibians but it might also occur in *Assa* and other species in which larvae are carried by males for several weeks.

Many anuran lineages have evolved direct development; in this mode, eggs are deposited terrestrially and the embryo develops entirely within the egg, emerging as a froglet (Mode 17). All species of the leptodactylid *Eleutherodactylus* have large eggs with direct development (Fig. 4.12). Male *Eleutherodactylus cooki* in Puerto Rican caves guard clutches of about 16 eggs; occasionally, a male guards a nest with double and triple clutches (Joglar et al., 1996). Froglets emerge from the nest within 22–29 days after egg deposition.

Many frogs have arboreal clutches of eggs that are attached to leaves or tree branches above water. When the tadpoles hatch, they drop into ponds or streams (Mode 18) or into water-filled cavities or tree holes (Mode 19). This mode occurs in many species of hylid frogs in the genera *Hyla*, *Phyllomedusa*, and *Agalychnis*, and in most Centrolenidae.

Two closely related species of *Agalychnis*, *A. craspedopus* and *A. calcarifer*, deposit eggs above pools formed in buttresses of large fallen trees (Hoogmoed and Cadle, 1990; Caldwell, 1994). Their courtship is long, as much as 12 hours. About midmorning, the amplexing pair deposits a small clutch of eggs on a wall or on hanging vegetation above the water. *A. calcarifer* lays 20 to 28 eggs in a clutch and *A. craspedopus* 14 to 21 eggs per clutch. Their eggs are relatively large (9–12 mm diameter) and heavily laden with yolk; ovum diameter is 4 mm. In 7–15 days, the eggs hatch and the larvae drop into the water, where they complete their development in several months.

Many New Guinea microhylids have large eggs that undergo direct development (Mode 20). The eggs are deposited in arboreal sites such as leaf axils or hollow stems, and a parent remains with the eggs. One species of *Oreophryne* deposits about 10 eggs on the upper surfaces of leaves. The egg mass is enclosed in a membrane that is

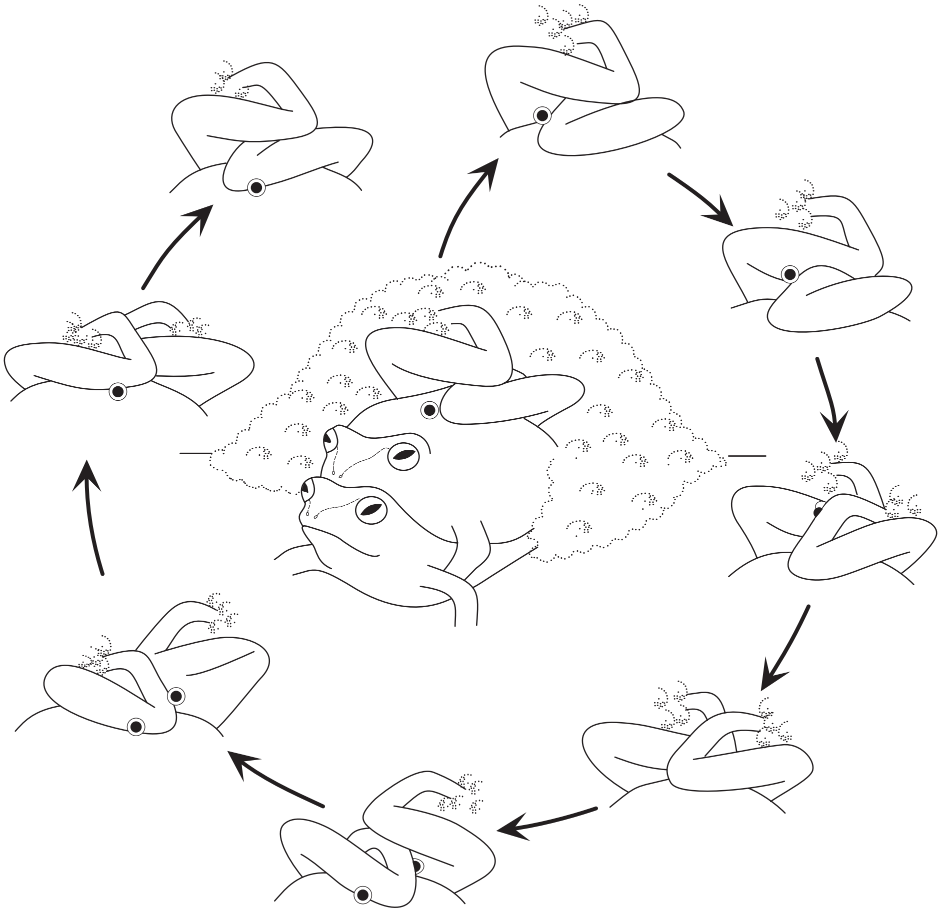


FIGURE 4.10 Secretions from a male and female are whipped by rapid leg movements into a foam nest by the Brazilian leptodactylid *Physalaemus ephippifer*. At the same time, eggs are deposited and fertilized. The black circles represent the path of an egg as it is extruded from the female and pushed into the growing mound of foam; several hundred eggs will be deposited in a single nest. Adapted from Hödl (1990) with permission of the Charles University Press, Prague.

distinct from the egg capsules. Presumably, this membrane adds an extra degree of protection. A male attends the eggs during part or all of their development (Johnston and Richards, 1993).

Many species of the tropical *Leptodactylus* produce foam nests either in burrows or in small depressions. Developing tadpoles are subsequently washed into nearby pools that form with the onset of heavy rains (Mode 21). *Leptodactylus mystaceus* males call from small depressions to attract a female. Shortly after amplexus begins, the pair constructs a foam nest in the depression (Fig. 4.13), and upon the nest's completion and egg deposition, the pair separates and both parents depart. No further parental care occurs. If rains are delayed, the original foam produced by the parents begins to dissipate. However, the tadpoles generate new foam by vigorously wriggling their bodies together. Under these conditions, tadpole development is arrested until rains begin.

The third major category of reproductive modes in frogs is retention of the eggs in the female's oviduct. Only five species, representing two lineages, possess internal development. Embryo nutrition is lecithotrophic for three species and matrotrophic via histophagy for two. The leptodactylid *Eleutherodactylus jasperi* of Puerto Rico has lecithotrophic eggs that develop inside the fused lower portions of the oviducts (Wake, 1993b). The female retains the eggs and developing froglets for about 33 days from the time of amplexus to birth of 3–5 froglets. No morphological evidence exists for transfer of nutrients to the embryos; in addition, some yolk remains in the intestines of the froglets when they are born.

The other four species of viviparous frogs are members of the African bufonid lineage *Nectophrynoides. Nectophrynoides* contains six species, two of which are oviparous—one with free-swimming larvae and the other with direct development. The four species of

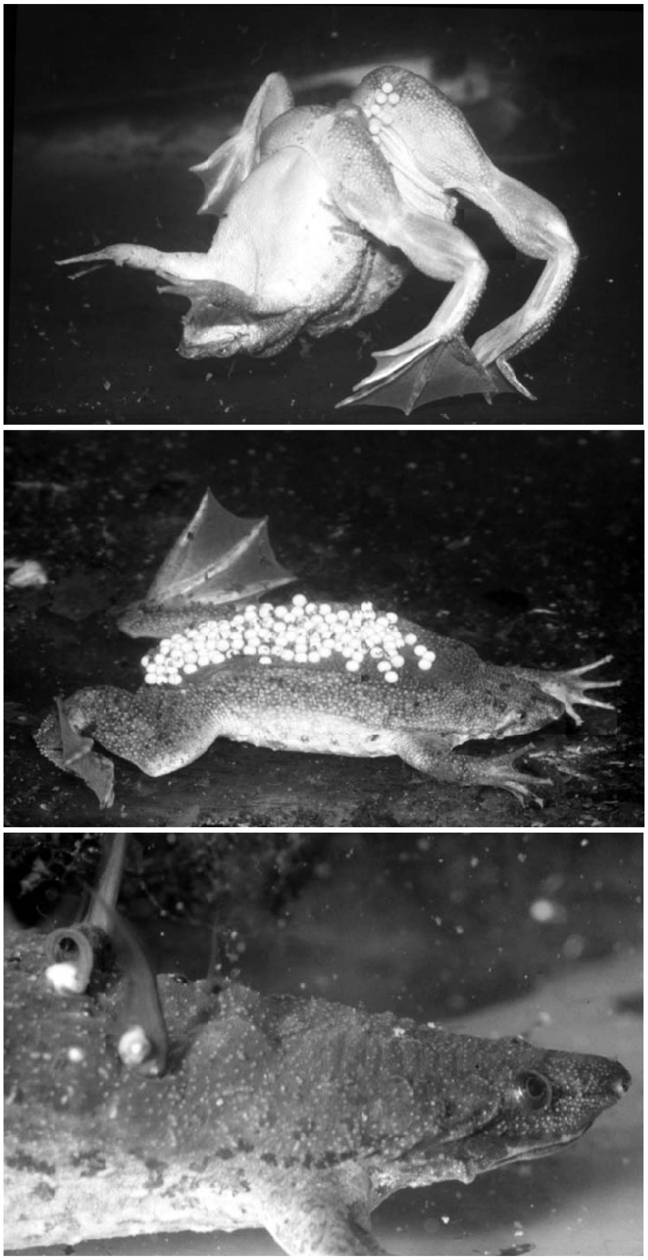


FIGURE 4.11 (Top) Mating ritual of *Pipa parva*. The pair somersaults in the water as eggs are released and fertilized; the male then presses the eggs into the female's dorsum, where they embed in her skin. (Middle) A female *P. parva* with freshly deposited eggs on her dorsum. (Bottom) Tadpoles emerging from pockets on the back of a female *Pipa carvalhoi*. Photographs by K.-H. Jungfer.

viviparous *Nectophrynoides* includes two lecithotrophic taxa (*N. tornieri* and *N. viviparus*). They produce large yolk-filled ova, ranging from 3 to 4 mm. In contrast, the two matrotrophic taxa (*N. liberiensis* and *N. occidentalis*) produce small ova of 0.5 to 0.6 mm diameter (Wake, 1993b). The gestation period for *N. occidentalis* lasts for about nine months, and during the last two months of gestation, the oviducts produce a concentrated mucopolysaccharide secretion to nourish the embryos. The embryos or larvae have a ring of large papillae around the mouth; presumably these papillae absorb the nutrients but this suggestion remains unconfirmed. Birth of 4–35 froglets occurs in the early rainy season.

Reptiles

All crocodilians, turtles, and the tuatara deposit eggs. A majority of snakes and lizards also lay eggs. In most species, hatching appears to be synchronous (Fig. 4.14). Nonetheless, more than 19% of the lizards and 20% of the snakes are live-bearers (Blackburn, 1982, 1985; Shine, 1985b). Thus, viviparity has evolved independently in at least 45 lineages of lizards and 35 lineages of snakes. In oviparous reptiles, embryo nourishment comes from the yolk (lecithotrophy). Females of some oviparous species, such as the snake *Liochlorophis vernalis* and the lizard *Lacerta agilis*, retain eggs until the embryos are within only a few days of hatching. Among those species that bear live young, maternal contribution of nutrients (matrotrophy) to development varies considerably. In some viviparous species, development of embryos is supported entirely by yolk in the egg (lecithotrophy), just as in oviparous species. Examples include the live-bearing horned lizard *Phrynosoma douglassi* and all snakes in Boinae. In others, such as *Mabuya heathi*, developmental nutrition derives entirely from the mother via a placenta (Blackburn et al., 1984).

Viviparity—Functional Aspects

Viviparity in amphibians has arisen relatively infrequently compared to reptiles. In terms of the number of species with viviparity, caecilians are most successful; among salamanders and frogs, only two lineages in each group retain embryos. No amphibians have evolved a placental type of matrotrophy; instead, fetuses most commonly ingest or absorb nutrient-rich secretions from the female's oviduct. In one salamander, the fetuses also eat subsequent eggs or embryos. Respiratory adaptations are not the same (or homologous) in viviparous reptiles and amphibians. Preexisting respiratory structures of embryonic amphibians (gills, skin) increase their vascularization and, when juxtaposed against the oviduct lining, likely enhance gas exchange during development (Guillette, 1987).

The evolutionary transition from oviparity to viviparity in reptiles involved the retention of eggs for increasing periods of time in response to environmental variables (Tinkle and Gibbons, 1977), a topic examined in the next chapter. The transition from producing eggs with shells to producing live offspring that receive

FIGURE 4.12 Direct-developing eggs of *Eleutherodactylus.* In this species, eggs are deposited in leaf litter in a tropical forest. Note the well-developed back legs of the embryos. Photograph by J. P. Caldwell.

nutrients from the mother while in the oviduct required respiratory, hormonal, and nutritive specialization. Embryonic membranes, including the yolk sac or the chorioallantois in viviparous placentotrophic squamates, became highly vascularized and interdigitated with the wall of the oviduct to accommodate gas and nutrient exchange (Blackburn, 1993a).

The timing of hormone production and release required adjustments to avoid the expulsion of embryos prior to their complete development. In oviparous vertebrates, the corpora lutea, which typically degenerate rapidly following ovulation, produce progesterone. Because progesterone inhibits oviduct contraction, a decreasing level of progesterone results in oviductal contraction and expulsion of eggs or embryos. In viviparous species and those with egg retention, the corpora lutea persist following ovulation and continue to produce progesterone (Guillette, 1987).

FIGURE 4.13 (Left) Nest construction by a male *Leptodactylus mystaceus*; a male calls from the depression to attract a female. (Right) A foam nest with eggs is produced by the male and a female. The nest is abandoned, and tadpoles are flooded from the nest when heavy rains occur. Photographs by J. P. Caldwell.

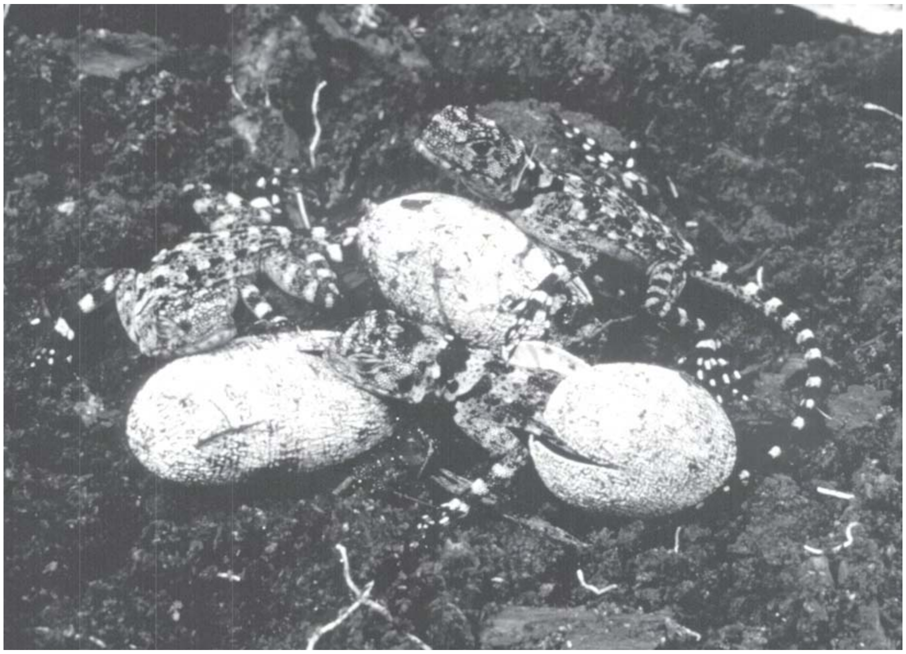


FIGURE 4.14 Synchronous hatching occurs when eggs of the Amazonian lizard *Tropidurus plica* are disturbed. Photograph by L. J. Vitt.

Recent studies on a facultative placentotroph reveal some clues on the functional transition from lecithotrophy to matrotrophy via placentotrophy. In the colubrid snake *Virginia striatula*, embryos can develop exclusively on yolk reserves as in typical lecithotrophic reptiles, or they may receive some nutrients (particularly calcium) from the female's oviducts (Stewart, 1989). Calcium passes across the oviductal lining to the embryo's yolk sac, which is pressed against the oviduct, thus establishing a functional relationship between the maternal and fetal tissues. In a sense, the mechanism is not very different from the production of eggshells in oviparous species except that female tissue transfers calcium to fetal tissue rather than to a fibrous matrix that becomes the shell. Once a transfer mechanism arises, the transfer of other nutrients can follow and a reduction in yolk can occur. Females no longer need to invest all of their energy in offspring at one time. Rather, they can spread their nutritional commitment to offspring over a more extended time period. This change can ultimately lead to obligate placentotrophy. The evolution of viviparity is discussed in more depth in the next chapter.

Our understanding of morphological aspects of squamate viviparity, in terms of placental development, dates back to Weekes' (1935) review of placentation in reptiles. More recent studies have shown that some placental development in reptiles is much more complex than that recognized in the 1930s. New World skinks in the genus *Mabuya* receive all nutrients for development through a highly specialized placenta that is functionally similar to the placenta of eutherian mammals (Fig. 4.15; Blackburn et al., 1984). Surprisingly, juvenile-sized females three months or less in age ovulate tiny ova similar to those ovulated by adult-sized females. Because there is little growth of the embryos during the first 4–7 months of gestation, the body size of these ''juvenile'' females becomes sufficiently large

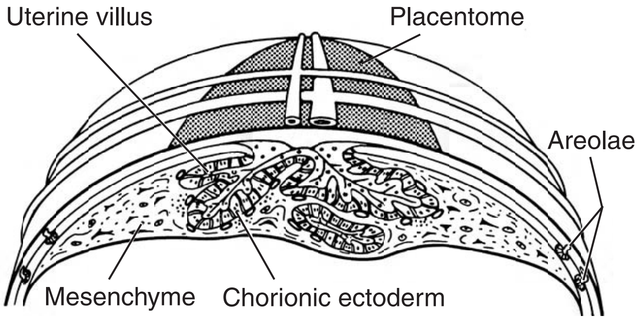


FIGURE 4.15 Diagrammatic representation of the chorioallantoic placenta in *Mabuya heathi*. The placenta lies above the embryo and consists of hypertrophied uterine (maternal) and chorionic (fetal) tissue forming the placentome, the joint structure for nutrient transfer to the embryo, waste transfer to the female, and gaseous exchange. The interdigitating structures are the chorionic areolae, the site of transfer and exchange. Adapted from Blackburn and Vitt (1992).

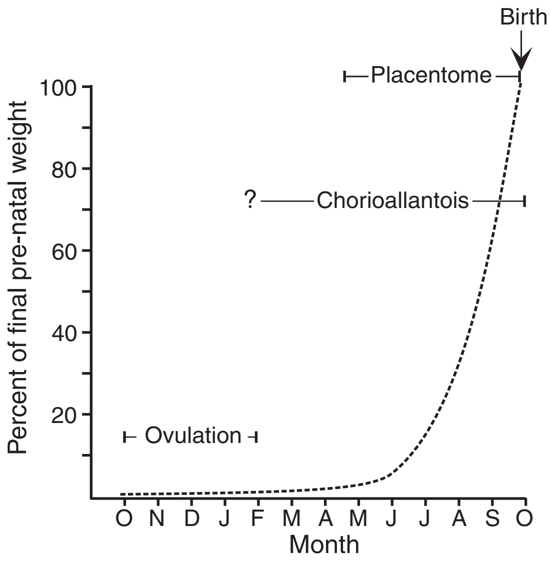


FIGURE 4.16 Generalized pattern of growth in embryos of viviparous New World *Mabuya*. Depending on species, the embryo may increase more than 74,000% of its freshly ovulated mass as the result of nutrient uptake from the female. Adapted from Blackburn and Vitt (1992).

enough to accommodate the developing embryos by the time rapid embryonic growth begins (Fig. 4.16; Blackburn and Vitt, 1992).

SEXUAL VERSUS ASEXUAL REPRODUCTION

A majority of amphibians and reptiles reproduce sexually, with males and females contributing genetic material to offspring. In a few taxa, reproduction occurs without the male's genetic contribution (Table 4.3), and in fewer yet, populations consist only of females. Such reproduction is called asexual and three types occur in reptiles and amphibians: hybridogenesis, gynogenesis, and parthenogenesis. Hybridogenesis is the production of all-hybrid populations from two parental species. Gynogenesis is the activation of development by spermatozoon penetration of an ovum without fusion of the pronuclei. In parthenogenesis, an ovum begins development in the absence of a spermatozoon and all-female populations arise.

Hybridogenesis

TABLE 4.3 Genera of Unisexual Amphibians and Reptiles

Genus	Number of species	Mode of reproduction	Representative species
Ambystomatidae			
Ambystoma	3±	G&H	*platineum*
Ranidae			
Rana	5	H&P	*esculenta*
Agamidae			
Leiolepis	1	P	*triploida*
Chamaeleonidae			
Brookesia	1	P	*affinis*
Gekkonidae			
Hemidactylus	3+	P	*garnotii*
Hemiphyllodactylus	1	P	*typus*
Heteronotia	4+	P	*binoei*
Lepidodactylus	1+	P	*lugubris*
Nactus	1	P	*pelagicus*
Gymnophthalmidae			
Gymnophthalmus	2+	P	*underwoodi*
Leposoma	1+	P	*percarinatum*
Teiidae			
Cnemidophorus	12+	P	*uniparens*
Kentropyx	1	P	*borckianas*
Lacertidae			
Lacerta	5+	P	*unisexualis*
Xantusiidae			
Lepidophyma	2	P	*reticulatum*
Typhlopidae			
Ramphotyphlops	1	P	*braminus*

Source: In part from Vrijenhoeck et al. (1989) and Darevsky (1992).
Note: G, gynogenesis; H, hybridogenesis; P, parthenogenesis.

Hybridogenesis occurs when females produced through hybridization between two closely related species produce only female offspring, all containing the genome of the mother. They accomplish this by mating with one of the parental species. During gametogenesis, the male genome is not included and the female genome is duplicated, reconstituting a diploid zygote that develops into a hybridogenetic female (Fig. 4.17).

In Europe, two closely related frogs, *Rana lessonae* and *Rana ridibunda*, hybridize over a wide geographic area, resulting in the formation of a complex of hybrids referred to collectively as *Rana esculenta* (Berger, 1977). *R. esculenta* likely arose several times by hybridization of *R. lessonae* and *R. ridibunda* in different localities, producing a diploid (RL) and two triploid (RLL, RRL) biotypes; regionally different cytogenetic structures and behaviors indicate additional origins (Table 4.4). Hybridization between *R. ridibunda* and the Spanish *Rana perezi* and an unnamed Italian species have

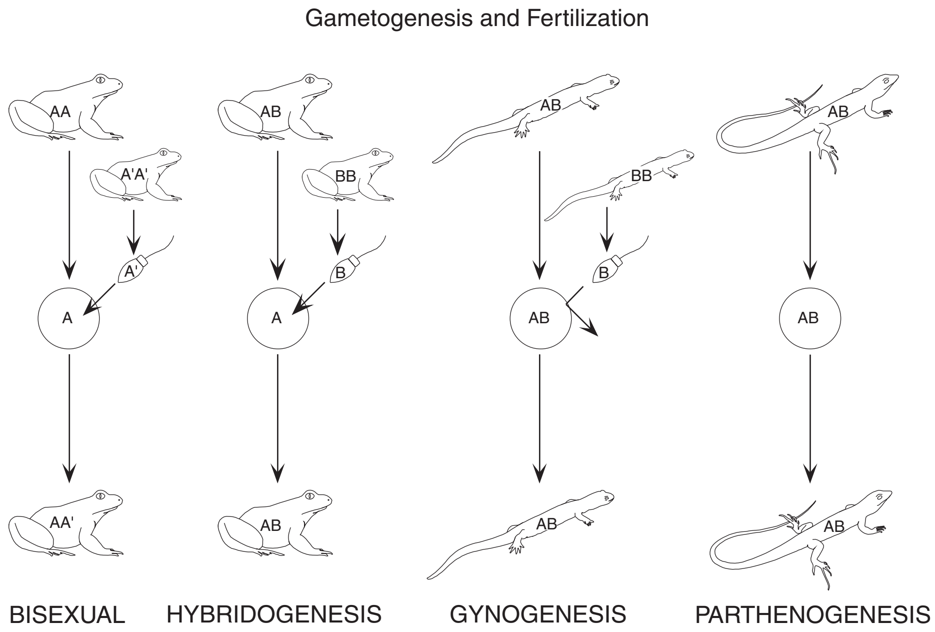


FIGURE 4.17 Schematic representation of unisexual and bisexual reproduction. Each capital letter represents a haploid complement of chromosomes. The female produced by hybridogenesis does not contain the male genome; the "B" in the offspring comes from its mother. In gynogenesis, a diversity of combinations of genomes is possible; only one combination is shown in the figure.

produced an additional two hybridogenetic lineages in this complex.

R. esculenta is widespread in Europe (from France to central Russia) and is always sympatric with *R. lessonae*. Diploid populations of *R. esculenta* are widespread and common, and some triploid populations exist. Most *R. esculenta* populations persist by female *R. esculenta* parasitizing male *R. lessonae* rather than the continual hybridization of *R. lessonae* and *R. ridibunda*. Male *R. esculenta* mate with both *R. esculenta* and *R. lessonae* females, but only the offspring of the latter pairing survive through metamorphosis. *R. esculenta* persists because *R. esculenta* produces haploid gametes with a *R. ridibunda* genome (Table 4.4). These gametes arise by a premeiotic shedding of the *R. lessonae* genome and then a duplication of the remaining *R. ridibunda* genome, followed by normal meiotic division. Males exist in these hybridogenetic populations because of XX-XY sex determination and the presence of X and Y gametes from the *R. lessonae* males.

TABLE 4.4 Genome Compositions of Offspring from Matings within the *Rana esculenta* Complex

	Females		
Males	**LL (*lessonae*)**	**RR (*ridibunda*)**	**RL (*esculenta*)**
LL	LL	RL	RL, RRL, RLL
RR	RL	RR	RE (RR)
RL	RL	RE	I

Source: In part from Graf and Polls Pelaz (1989).

Note: *Rana esculenta* is usually diploid and produces haploid gametes by a premeiotic exclusion of the *Rana lessonae* genome and reduplication of the *Rana ridibunda* genome so that normal meiosis yields haploid *ridibunda* genomes. Male *R. esculenta* are usually sterile. Abbreviations are I, inviable; LL, *R. lessonae* genome; RE, variable exclusion of *R. lessonae* genome; RR, *R. ridibunda*; RL, *R. esculenta*; and RRL, RLL, *R. esculenta* triploid genomes.

Gynogensis

In parts of northeastern North America, many breeding aggregations of mole salamanders in the *Ambystoma laterale–jeffersonianum* complex consist of diploid males and females and polyploid individuals, usually females. When the composite nature of these breeding populations was first recognized, it was assumed that both the diploid individuals (*A. laterale* [genome LL] and *A. jeffersonianum* [JJ]) and the polyploid females (*Ambystoma* klepton *tremblayi* [LLJ], *Ambystoma* kl. *platineum* [LJJ]) were genetically distinct and reproductively isolated species, and that the unisexual polyploids were maintained by gynogenesis. This explanation was accepted until the reproductive behavior and the genomic composition of numerous individuals in these breeding aggregations were examined, at which time hybridogenesis was proposed. The issue remains unresolved because the frequency and composition of the diploid, triploid, and tetraploid genomes vary greatly among breeding populations, and diploid males occur in low frequency or are absent. Multiple explanations including gynogenesis, hybridogenesis, retrogression, and introgression may be necessary to fully explain these populations.

The genomic composition of this mole salamander plexus is now known to contain the following hybrids: diploids, LJ, LT (T = *Ambystoma texanum*); triploids, LLJ, LJJ, LLT, LTT, LJT, LTTi (Ti = *Ambystoma tigrinum*); and tetraploids, LLLJ, LJJJ, LLJJ, LLLT, LTTT, LLTT, LTTTi, LJJTi, LJJT (Fig. 4.17). This diversity can only have arisen by hybridization. Some breeding aggregations have unisexual populations of the hybrids. For example, an aggregation in Illinois contained bisexual populations of *A. texanum* and *Ambystoma maculatum*, and LJJ and LJJT females; thus gynogenesis or parthenogenesis is required to maintain the hybrid populations.

Parthenogenesis

Parthenogenesis occurs when females reproduce without the involvement of males or sperm. Inheritance is clonal, and female offspring are genetically identical to their mothers (Cole and Townsend, 1990). Parthenogenesis was first discovered in the Armenian lizard *Lacerta saxicola* (Darevsky, 1958) and is now known to occur in seven lizard clades and one snake clade (Vrijenhoek et al., 1989). Of the approximately 30 species of parthenogenetic squamates currently recognized (Table 4.3), all that have been studied appear to have originated as the result of hybridization of two sexual species. Because these parthenoforms were produced by hybridization, heterozygosity is high. Genetic variation within an individual is high (Parker and Selander, 1976), but genetic variation among individuals is nearly nonexistent (Cuéllar, 1976). Low genomic variation within clones of parthenogenetic lizards has been demonstrated with studies on histocompatibility of skin transplants. Nearly 100% of skin grafts transplanted between individuals (two populations) of the parthenogenetic species *Cnemidophorus uniparens* were permanently accepted, whereas no skin grafts transplanted between individuals within a population of the sexual species *Cnemidophorus tigris* were accepted, suggesting that all *C. uniparens* can be traced back to a single individual (Fig. 4.18). Confirmation that parthenogenesis was occurring in these lizards resulted from studies in which laboratory-born individuals were raised to maturity in isolation and began producing offspring (Cole, 1984).

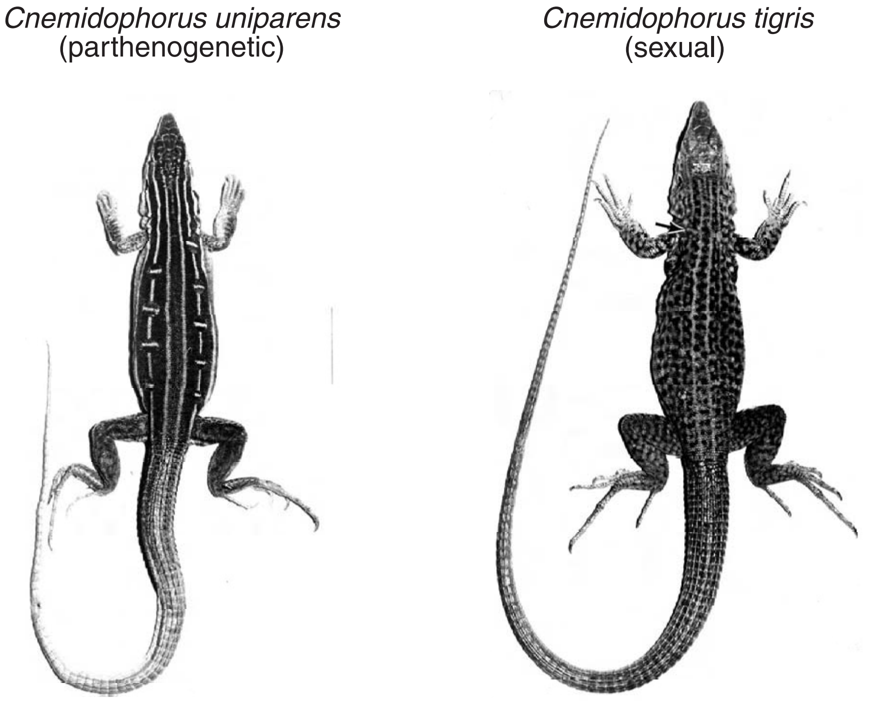


FIGURE 4.18 Skin graft test for genetic similarity in the unisexual *Cnemidophorus uniparens* (left) and the bisexual *Cnemidophorus tigris* (right). Because of the clonal nature of *C. uniparens*, all 9 grafts were accepted; in contrast, all 10 grafts were rejected in *C. tigris*. Adapted from Cuéllar (1976).

The cytogenetic events that result in production of eggs with the same ploidy as the mother have been traced only in *C. uniparens.* Premeiotic doubling of chromosomes yields a tetraploid oogonium, which is followed by normal meiosis that produces eggs with the same chromosome number as the female parent. Most parthenogenetic squamates are diploid, but some are triploid. The triploid condition results from backcrossing between a female of hybrid origin and a normal male of one of the original parental species (Fig. 4.19).

Although the cytogenetic mechanism initiating development is unknown in parthenogenetic squamates, a rather strange behavior, pseudocopulation, in which one female behaves as a male and attempts to mate with another female, occurs commonly under laboratory conditions in some parthenogens (Cole and Townsend, 1983; Crews and Moore, 1993). This behavior has been observed in the field but appears to be uncommon. Comparison of hormone levels in the courted females and the courting females of three parthenogens (*Cnemidophorus tesselatus, C. uniparens*, and *Cnemidophorus velox*) show that the courted female is preovulatory and the courting female is postovulatory or oogenetically inactive (Fig. 4.20). Courtship and pseudocopulation stimulate ovulation, indicating that the courted female is responding as though mating has occurred (Crews and Moore, 1993). Females that experience pseudocopulation appear to produce eggs at a faster rate than those that do not engage in the behavior. The evolutionary significance of pseudocopulation remains unclear because there presumably are no genomic differences between females in the clones that participate in pseudocopulation and those that do not. Nevertheless, this system provides unique opportunities to study the role of specific behaviors (courting and copulatory behavior) on female reproduction without the added variables associated with males.

Because each female of parthenogenetic squamates produces only females, the reproductive rate in terms of potential population growth is enormous compared to that of sexually reproducing squamates (Fig. 4.21). Given this apparent advantage to unisexual reproduction, why is unisexual reproduction so rare in vertebrates and indeed in most animals? This question is revisited in the discussion on sex ratios.

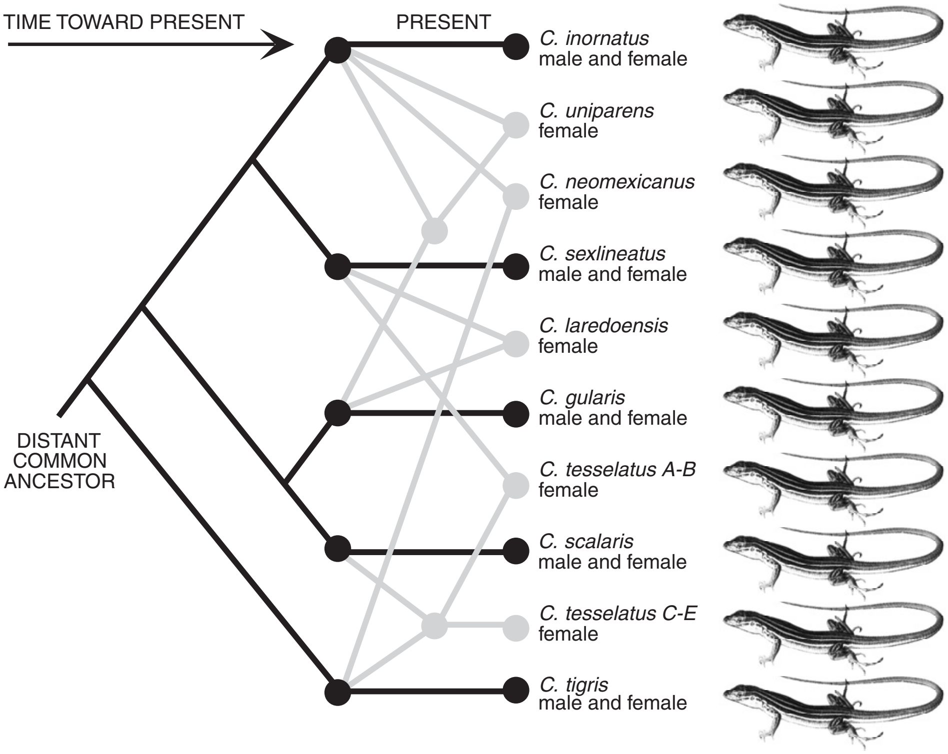


FIGURE 4.19 Genealogy of the parthenogenetic whiptailed lizards (*Cnemidophorus*) from the southwestern United States. The gray lines denote the parents that hybridized to create the parthenoforms/parthenogens. Adapted from Cole (1984).

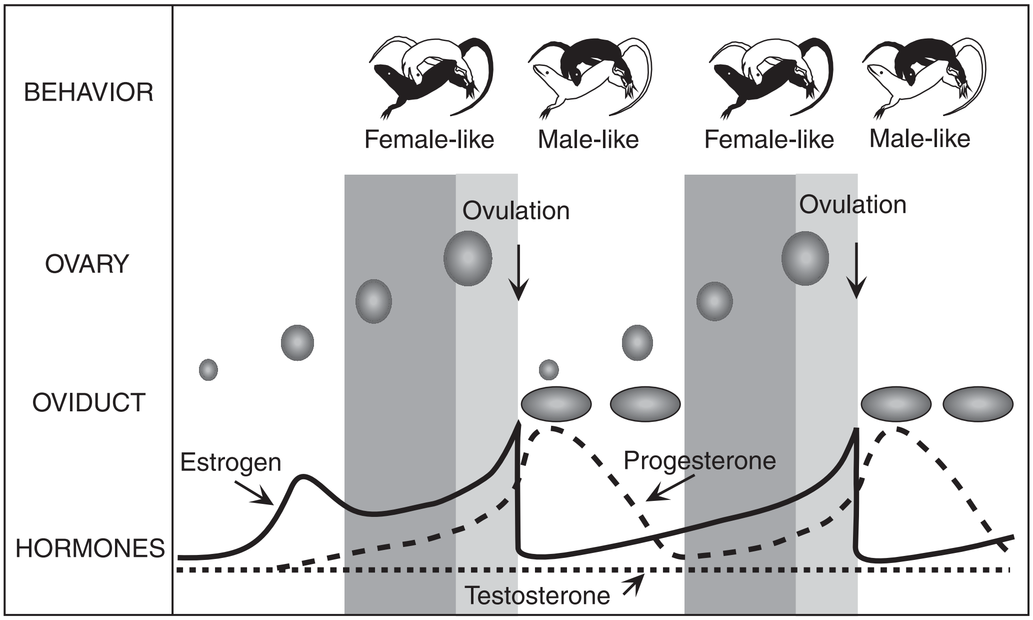


FIGURE 4.20 Relationship between hormone production, follicle development, and behavior in parthenogenetic whiptail lizards (*Cnemidophorus*) during pseudocopulation. Adapted from Crews and Moore (1993).

PARENTAL CARE

Parental care is defined for amphibians and reptiles as any form of post-ovipositional parental behavior that increases the survival of the offspring at some expense to the parent. We do not include matrotrophic provisioning of young that occurs in some viviparous species because this parental contribution to offspring survival occurs prior to birth. Parental care occurs in a diversity of taxa (Table 4.5), indicating that it has arisen independently many times within amphibians and reptiles (Duellman and Trueb, 1986; Gross and Shine, 1981). The number of evolutionary origins of parental care in amphibians is much lower than the number of species with parental care (Shine, 1988). Most amphibians and reptiles show no parental care other than nest construction for egg deposition.

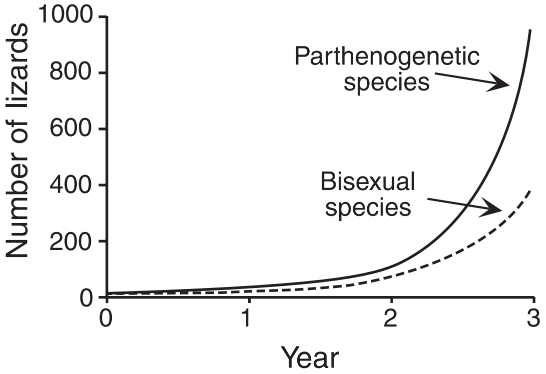


FIGURE 4.21 Hypothetical growth rates for populations of parthenogenetic and sexually reproducing *Cnemidophorus* based on laboratory data on *Cnemidophorus exsanguis* and assuming no mortality. The starting point on the graph represents hatching of one egg. Because 50% (males) of the sexually reproducing species do not produce eggs, population size of the parthenogenetic population is more than double that of the sexual species after only 3 years. Adapted from Cole (1984).

Parental care is represented in amphibians and reptiles by a variety of behaviors, and not all apply to both amphibians and reptiles. They can be summarized in general as:

1. Nest or egg attendance. A parent remains with the nest or eggs but without detectable nest defense.
2. Nest or egg guarding. A parent remains with the nest or eggs and actively defends against conspecifics or predators.
3. Egg brooding. Defined slightly differently for amphibians and reptiles. In amphibians, brooding is used for species that retain the embryos somewhere on or in the body but not in the oviducts (Crump, 1995). In reptiles, it refers only to a parent facilitating incubation by raising the temperature of the eggs (Shine, 1988).
4. Egg, larval, or hatchling transport. A parent carries offspring from one place to another.

TABLE 4.5 Known Taxonomic Distribution of Parental care in amphibians and reptiles

Group	Care provider	Families	Species	Percent
Caecilians*	Female	2/6	8/162	5
Salamanders*	M or F	8/9	72/354	20
Frogs*	M or F	15/21	206/3438	6
Turtles†	F	2/?	3/260	1
Crocodylians‡	M or F	All	All	100
Amphisbaenians[1]	—	—	—	—
Lizards§	Female	6/15	41/3000	1.3
Snakes§	Female	6/11	47/1700	2.8

Sources: *Crump (1995), †Iverson (1990), ‡Greer (1970a), and §Shine (1988).

Note: Viviparous species are not included. The numbers of families have been updated. The numbers of origins for each taxonomic group are lower than the number of species exhibiting parental care.

[1] Unknown.

5. Feeding of young. A parent brings food to offspring, for example, tadpole feeding.
6. Guarding or attending young. A parent stays with young after the eggs hatch.

Nest or Egg Attendance

Egg attendance occurs in caecilians (females), salamanders (either or both sexes), frogs (either or both sexes), crocodilians (either or both sexes), a few turtles (females), and many squamates (females). Functions of egg attendance vary. In amphibians they include aeration of aquatic eggs, hydration of terrestrial eggs, protection from pathogens or predators, or manipulation to prevent development adhesions. Attending females of the salamander *Necturus maculosus* appear to aerate their aquatic eggs by rapid gill movements (Salthe and Mecham, 1974). In glass frogs, Centrolenidae, eggs are deposited on leaves above streams and small rivers in Neotropical rain forests. In species in which males are territorial, such as *Hyalinobatrachium fleishmanni*, males attend the nests (Fig. 4.22); however, in at least one species with nonterritorial males, *Hyalinobatrachium prosoblepon*, females attend the nest (Jacobson, 1985). Males of the tropical leptodactylid frog *Eleutherodactylus coqui* provide water to eggs by direct transfer across their skin (Taigen et al., 1984). Fungus attacks eggs of the New Guinea frog *Cophixalus parkeri* and developmental abnormalities occur when attending females are removed (Simon, 1983). In reptiles, nest attendance may aid in hydration of eggs. The attending female of the skink *Eumeces septentrionalis* regulates egg water exchange by moving the eggs, coiling around the eggs, or expanding the nest cavity, thus exposing different proportions of the egg surface to substrate and air (Somma and Fawcett, 1989). Similar functions have been suggested for crocodiles (e.g., *Crocodylus porosus;* Webb et al., 1977). Nest attendance in reptiles may prevent drowning of eggs (e.g., *Opisthotropis latouchii*), deter fungal infection (e.g., *Eumeces fasciatus, Gerrhonotus liocephalus*), or aid in keeping eggs hidden (e.g., *Iguana iguana*) (Shine, 1988).

Nest or Egg Guarding

Nest or egg guarding occurs in salamanders (either sex), frogs (either sex), crocodilians (either sex), and squamates (females). Attending females of the salamander *Plethodon cinereus* (Bachmann, 1984) and males of the tropical hylid frog *Hyla rosenbergi* (Kluge, 1981) aggressively attack conspecifics that approach the nest. Nests of the frog *Cophixalus parkeri* (Simon, 1983) are attacked by arthropod predators following removal of the parent. Following oviposition, female *Iguana iguana* aggressively interact with other females that attempt to use the same nest sites (Rand and Rand, 1976). Female *Eumeces* and a number of snake species including *Naja naja* aggressively attack when disturbed while guarding eggs (Noble and Mason, 1933; Campbell and Quinn, 1975) (Fig. 4.23). Females of the Nile crocodile (*Crocodylus niloticus*) aggressively defend their nests against monitor lizards (*Varanus*) that attempt to prey on the eggs (Modha, 1967).

Egg, Larval, or Hatchling Transport

Transport of early life history stages is widespread in frogs (either sex) and crocodilians (either sex). In many frog species, eggs are carried, usually by the female, while they develop (see "Reproductive Modes" above). In some instances, transport includes brooding (see below). Transport of tadpoles is common, occurring in seven frog families (Crump, 1995). Most frequently, tadpoles are carried on the back of one parent as in most dendrobatid species (Fig. 4.23). Tadpoles are carried from a terrestrial nest site to water in the vocal sacs of male *Rhinoderma rufum*. Females of most crocodilians (e.g., *Crocodylus mindorensis* [Alcala et al., 1987]; *Crocodylus palustris* [Lang et al., 1986]; *Crocodylus niloticus* [Pooley, 1974, 1977]) carry the hatchlings in their mouth to water (Fig. 4.23).

Egg Brooding

Brooding in anurans involves retaining the eggs and/or larvae on the body of the parent for a longer period of

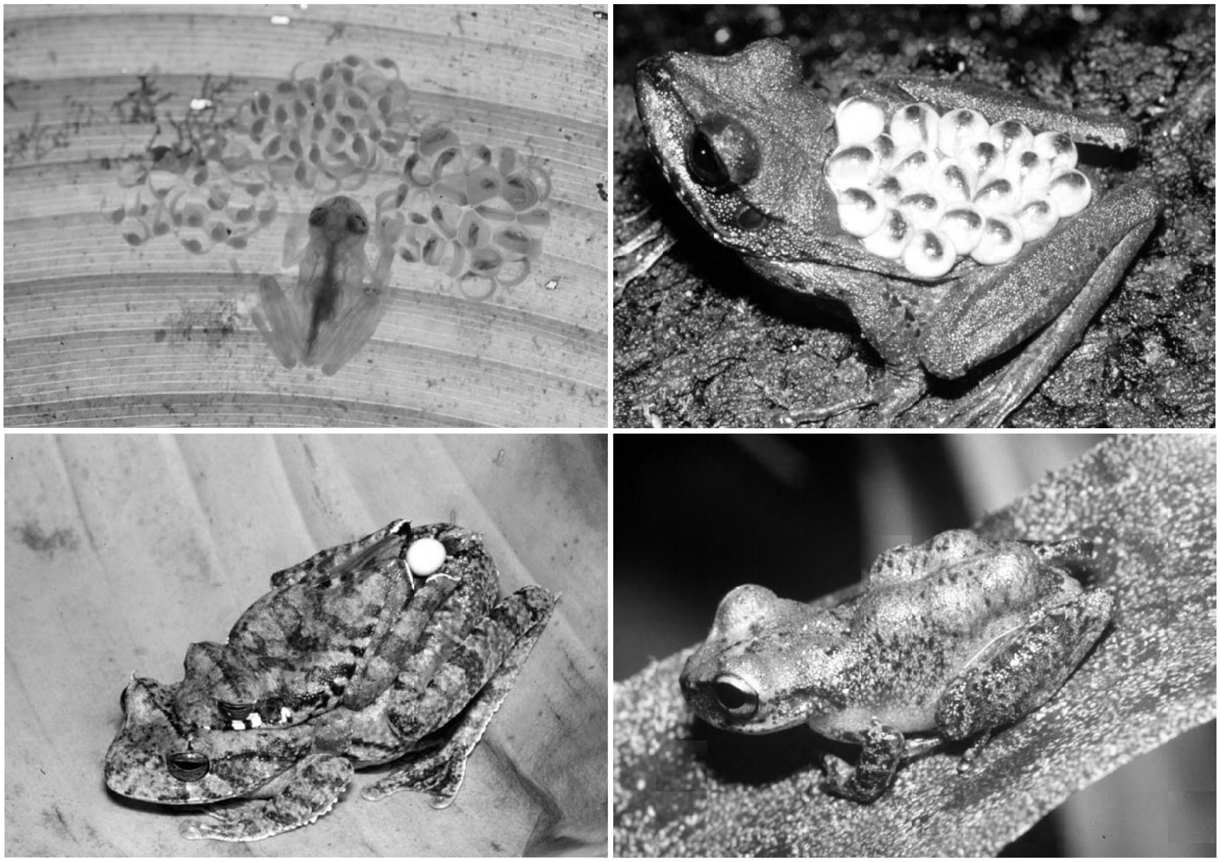


FIGURE 4.22 Clockwise from top left, male *Hyalinobatrachium valerioi* attending three clutches of eggs of different ages; female of *Stefania evansi* brooding exposed eggs on its back; female *Flectonotus fitzgeraldi* brooding five eggs in dorsal pouches; and an amplexing pair of *Gastrotheca walkeri* (large, pale yellow eggs are expelled singly from the female's cloaca, fertilized by the male, and manipulated into the brooding pouch on the female's back). Photographs of *H. valerioi* by W. Hödl; all others by K.-H. Jungfer.

time than that required to simply transport the larvae from a nest site to an aquatic site. A continuum can be seen in this behavior among the many species that exhibit brooding; eggs may be carried only until they develop into larvae, or they may be carried until they metamorphose into froglets. In dendrobatids, the eggs are not carried, but hatch in a terrestrial nest; in most species, tadpoles are quickly transported to an aquatic site, but in a few species, the tadpoles may be retained on the dorsum of the parent for a few days to a week or more, or they may be carried on the dorsum until metamorphosis. Although it is difficult to categorize all species, brooding includes sequestering the offspring on or in the body for some period of time, whereas transport involves moving the eggs or larvae from one site to another.

The male parent in *Assa darlingtoni* picks up its tadpoles from a terrestrial nest and carries them in inguinal pouches for the remainder of their development until metamorphosis (Ehmann and Swan, 1985). Eggs are placed in a dorsal pouch in the hylid lineage *Gastrotheca*; in some species, they are carried until they develop into tadpoles, whereas in others, they are carried until metamorphosis (Fig. 4.22). A few large eggs are carried in an exposed position on the back of the hylid *Stefania*, where they remain until they develop into froglets (Figs. 4.22 and 4.24). In contrast, *Flectonotus*, another hylid, broods a few large eggs in a dorsal pouch that opens by splitting down the midline (Fig. 4.22). In the gastric brooding frogs, *Rheobatrachus silus* and *Rheobatrachus vitellinus*, brooding of eggs and/or larvae occurs in the stomach of the female; in one species, froglets emerge after metamorphosis, whereas in the other species, tadpoles are released by the female. Development in these frogs is supported entirely by yolk contained in the eggs (Crump, 1995; McDonald and Tyler, 1984). In contrast to *Rhinoderma rufum*, male *Rhinoderma darwinii* brood their tadpoles in their vocal sacs until metamorphosis occurs (Crump, 1995).

FIGURE 4.23 Clockwise from top left, female of the skink *Eumeces fasciatus* attending her clutch of eggs (photograph by L. J. Vitt); female *Leptodactylus ocellatus* attending her school of tadpoles—a female will attack small birds or other predators that disturb the tadpoles (M. Vaira); a male *Epipedobates* sp. transporting its complement of tadpoles from the terrestrial nest where eggs were deposited to a small aquatic microhabitat (J. P. Caldwell); and *Crocodylus palustris* carrying newly hatched offspring to water (J. W. Lang).

Brooding in reptiles is known only in oviparous boids and it may be ubiquitous in pythons (Shine, 1988). The primary advantage of brooding is faster development of embryos by maintaining a higher temperature. The heat is provided by shivering thermogenesis (Vinegar et al., 1970). Pythons generate their own heat while brooding the eggs; this behavior raises the temperature of the clutch and increases developmental rates of the embryos (see Fig. 7.12). In at least one python species, *Liasis fuscus*, brooding of eggs is facultative and initiated by low nest temperatures (Shine et al., 1997). In another species (*Python molurus*), brooding appears obligatory because nonbrooded eggs have a high incidence of abnormal embryos.

Feeding of Young

Some frogs have evolved the ability to feed trophic eggs to their developing tadpoles. This behavior has evolved in four unrelated lineages of hylid frogs, two lineages of *Dendrobates*, and one rhacophorid. In all of these species the tadpoles develop in restricted microhabitats that have little or no food available. Typically, these developmental sites include tree holes, bamboo segments, bromeliad axils, or other types of water-holding plants. Females of several species of *Dendrobates* (e.g., *D. pumilio* [Brust, 1993]; *D. ventrimaculatus* [Summers and Amos, 1997]; *D. vanzolinii* [Caldwell and Oliveira, 1999]) deposit trophic eggs in the tadpole's aquatic microhabitat; in

FIGURE 4.24 Froglets that have nearly completed their development on the back of a brooding female *Stefania evansi*. Photograph by K.-H. Jungfer.

D. vanzolinii, both the male and female play a role in feeding the tadpoles. Trophic eggs may be fertilized or unfertilized, depending on the behavior of the species and whether courtship with the male is necessary to induce egg deposition in the female. After initially mating and depositing fertilized eggs, a female *Anotheca spinosa* returns periodically to deposit unfertilized eggs for the tadpoles (Fig. 4.25). Physical contact by the tadpoles with the female's cloaca appear to stimulate release of the eggs (Jungfer, 1996). In contrast, pairs of the Amazonian tree frog *Osteocephalus oophagus* return repeatedly to the same microhabitat to mate and deposit eggs. The first clutch deposited in an unused site develops into tadpoles, and later clutches serve as food for the tadpoles. After metamorphosis of the tadpoles occurs, the original pair continues to deposit eggs, and more tadpoles develop. Tadpoles not provided with eggs die (Jungfer and Schiesari, 1995; Junger and Weygolt, 1999).

FIGURE 4.25 (Top) A female *Anotheca spinosa* feeding trophic eggs to her tadpoles. Egg-laying may be stimulated by begging behavior of the tadpoles. (Bottom) Trophic eggs consumed by a tadpole of *A. spinosa* are visible through the transparent skin. Photographs by K.-H. Jungfer.

Guarding or Attending Young

Attending or guarding young (including tadpoles) occurs in frogs, viviparous lizards, and crocodilians. Although widespread taxonomically (i.e., Leiopelmatidae, Leptodactylidae, Microhylidae, and Ranidae), attendance and guarding of tadpoles has been verified in relatively few species (see Crump, 1995). In some instances, the parent (usually the female) remains with the tadpoles and aggressively attacks animals that disturb the tadpole aggregation (e.g., *Leptodactylus ocellatus*; Vaz-Ferreira and Gehrau, 1975) (Fig. 4.24). Parental frogs have been observed to accompany the tadpole schools as they move around in ponds (Wells and Bard, 1988), and some terrestrially breeding frogs remain with the foam nest or tadpoles (Lescure, 1979; Bell, 1985). In ranids, parental attendance includes species that dig channels that allow tadpoles to move from one body of water to another (e.g., *Pyxicephalus adspersus*; Kok et al., 1989) or dig tunnels from terrestrial nest sites to water (e.g., *Hemisus*; Crump, 1995). In a few viviparous squamates, females aid offspring emerging from placental membranes following birth (e.g., South American *Mabuya* [Rebouças-Spieker and Vanzolini, 1978]; *Xantusia* [Miller, 1954]; *Epicrates* [Groves, 1981]). Among crocodilians (observed in four genera—*Crocodylus, Alligator, Caiman*, and *Paleosuchus*), adults approach eggs in which juveniles have begun vocalizing prior to hatching and crack open the eggs with their mouths (Garrick and Lang, 1977). The parents help free the hatchlings and often pick them up in their mouths and carry them to water (Pooley, 1974). Juveniles of all studied species emit distress calls that elicit approach of adults, suggesting a protective function (Garrick and Lang, 1977; Garrick et al., 1978).

EVOLUTION OF PARENTAL CARE

Several behaviors associated with parental care appear obligatory and their evolution is readily understood. For example, if live-bearing skinks tear open the placental membranes, more neonates survive. Similarly, more neonates survive when the female eats the membranes, reducing the likelihood that chemical cues from the membranes attract chemosensory-oriented predators. If frogs with terrestrial eggs that hatch into tadpoles did not transport their tadpoles to water, there would be no descendants to pass on that particular behavior. A selective advantage accrues to frogs that move their nests farther and farther from water if intensity of predation decreases with distance from water. Simultaneous selection favors the evolution of obligatory larval transport. Clearly, the primary benefit of all forms of parental care is the increased probability of offspring survival (Shine, 1988; Crump, 1995). The diversity of parental care behaviors in amphibians and reptiles suggests that a variety of evolutionary trajectories achieve that end, and a single explanation is inadequate to explain the origin of the numerous and different types of parental care.

The majority of parental care in amphibians occurs in nonaquatic species with terrestrial modes of reproduction (Wells, 1981). In aquatic amphibians with parental care, the driving force behind the evolution of parental care appears to be physiological. For example, in *Cryptobranchus alleganiensis*, females increase oxygen availability to the developing offspring by moving the eggs around (Bishop, 1941); a similar behavior occurs in *Necturus maculosus*. Development and survival depend on oxygen, and mechanisms that favor increased oxygen availability, especially in low-oxygen situations, should be favored. Similar physiological arguments could be made for at least some terrestrial amphibians that exhibit parental care.

In amphibians, parental care is associated with increased terrestriality. Removing the egg and larval stages from water presumably confers a selective advantage because the life history stages with the highest mortality are either eliminated (as in direct-developing species) or shifted to sites with lower mortality. In many amphibians with parental care, offspring size increases with increasing terrestriality; increased size apparently increases larval survivorship. The evolutionary cost of increasing offspring size is a reduction in offspring number, but if parental care effectively reduces mortality, this cost should be offset by the increased survival of protected offspring. Among reptiles, parental care appears associated primarily with the protection of eggs from predators or fungus, but in some instances, such as in brooding pythons, parental care provides a physiological function. As in amphibians, different evolutionary scenarios explain parental care in different species.

Parental care, by definition, has costs to the parent(s). Although parental care is relatively easy to observe and document, measuring the costs of parental care is much more difficult. For many of the examples provided above, costs have not been measured. Costs to amphibians and reptiles may include a decrease in future survival, possibly because of increased predation or a reduction of time available for food gathering. Even if survival is not affected, a decrease in investment of future offspring may occur because of the time invested in the current offspring. The benefit to the parents in terms of increased survivorship of offspring must outweigh the costs, or parental care would not evolve. As an extension of this concept, biparental care, which is rare in amphibians, would not evolve unless offspring survival was higher when both parents are involved in care than if only one of them provided care.

ADDITIONAL READING

Blackburn, D. G. (1993a). Standardized criteria for the recognition of reproductive modes in squamate reptiles. *Herpetologica* **49**, 118–132.

Crump, M. L. (1995). Parental care. *In* “Amphibian Biology” (H. Heatwole and B. K. Sullivan, Eds.), pp. 518–567. Surrey Beatty & Sons Pty Ltd., Chipping Norton, NSW.

Guillette, L. J., Jr. (1987). The evolution of viviparity in fishes, amphibians and reptiles: An endocrine approach. *In* “Hormones and Reproduction in Fishes, Amphibians, and Reptiles” (D. O. Norris and R. E. Jones, (Eds.), pp. 523–569. Plenum, New York.

Shine, R. (1985b). The evolution of viviparity in reptiles: An ecological analysis. *In* "Biology of the Reptilia" (C. Gans and F. Billett, Eds.), pp. 677–680. John Wiley & Sons, Inc., New York.

Shine, R. (1988). Parental care in reptiles. *In* "Biology of the Reptilia, Vol. 16. Ecology B. Defense and Life History" (C. Gans and R. D. Huey, Eds.), pp. 275–329. Alan R. Liss, Inc., New York.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Quart. Rev. Biol.* **51,** 3–47.

REFERENCES

Gametogenesis and Fertilization: Gamete Structure and Production: Follett and Redshaw, 1974; Fouquette and Delahoussaye, 1977; Jorgensen, 1992; Newton and Trauth, 1992; Palmer et al., 1993.

Reproductive Modes: Amphibians: Caldwell, 1992, 1994; Crump, 1995; Delsol et al., 1981, 1983, 1986; Duellman and Trueb, 1986; Godley, 1983; Goicoechea et al., 1986; Hödl, 1990; Hoogmoed and Cadle, 1990; Joglar et al., 1996; Johnston and Richards, 1993; Juncá, 1998; Juncá et al., 1994; Jungfer, 1996; Jungfer and Schiesari, 1995; Kluge, 1981; Kusano, 1980; Nickerson and May, 1973; Salthe, 1969; Salthe and Duellman, 1973; Schiesari et al., 1996; Sever et al., 1996a; M. Wake, 1980, 1992a, 1993b.

Reptiles: Blackburn, 1982, 1985; Blackburn et al., 1984; Shine, 1985b.

Viviparity-Functional Aspects: Blackburn, 1993a,b; Blackburn and Vitt, 1992a; Blackburn et al., 1984; Guillette, 1987; Stewart, 1989; Tinkle and Gibbons, 1977; Weekes, 1935.

Sexual Versus Asexual Reproduction: Berger, 1977; Cole, 1984; Cole and Townsend, 1983, 1990; Crews and Moore, 1993; Cuéllar, 1976; Darevsky, 1958; Parker and Selander, 1976; Vrijenhoek et al., 1989.

Parental Care: Alcala et al., 1988; Bachmann, 1984; Bell, 1985; Brust, 1993; Caldwell and Oliveira, 1999; Campbell and Quinn, 1975; Crump, 1995; Duellman and Trueb, 1986; Ehmann and Swan, 1985; Garrick and Lang, 1977; Garrick et al., 1978; Gross and Shine, 1981; Groves, 1981; Jacobson, 1985; Jungfer, 1996; Jungfer and Schiesari, 1995; Jungfer and Weygolt, 1999; Kluge, 1981; Kok et al., 1989; Lang et al., 1986; Lescure, 1979; McDonald and Tyler, 1984; Miller, 1954; Modha, 1967; Noble and Mason, 1933; Pooley, 1974, 1977; Rand and Rand, 1976; Rebouças-Spieker and Vanzolini, 1978; Salthe and Mecham, 1974; Shine, 1988; Shine et al., 1997; Simon, 1983; Somma and Fawcett, 1989; Summers and Amos, 1997; Taigen et al., 1984; Vaz-Ferreira and Gehrau, 1975; Vinegar et al., 1970; Webb et al., 1977; Wells, 1981; Wells and Bard, 1988.

Evolution of Parental Care: Bishop, 1941; Crump, 1995; Shine, 1988; Wells, 1981.

Chapter

5

Reproductive Ecology and Life Histories

Reproductive ecology and life histories are intimately linked in amphibians and reptiles. Natural selection on reproductive variables, such as egg size or number, ultimately determines the structure of a species' life history. The linkage between reproductive ecology and life history represents trade-offs between size and number of offspring, the costs of producing offspring, seasonality in the production of offspring, and the local environment and its variability. The interaction among these factors determines when and how much energy can be invested in reproduction, both in the short term for the individual's survival by balancing reproductive energy expenditure with daily maintenance energy requirements and in the long term by determining an individual's success transferring its genes into the next generation. This broad area of reproductive ecology also encompasses the ecology of nesting, the evolution of viviparity, temperature-dependent sex determination, and the long-term impact of resource availability on the evolution of reproductive strategies and life histories. The preceding chapter showcased the diversity of reproductive modes and clutch size; the exploration of life history evolution below examines how such diversity arises and why it persists.

REPRODUCTIVE ECOLOGY

Ecology of Nesting

Amphibians

A nest is a discrete structure constructed by a reproductive adult for egg deposition. Many amphibians deposit eggs in water and consequently a nest is not commonly built. Similarly, most frogs and salamanders laying eggs on land do not construct nests but rely on preexisting sites under leaf litter (e.g., *Eleutherodactylus*), on top of leaves (e.g., *Phyllomedusa*), or on top of soil under surface objects (e.g., plethodontid salamanders). Frogs in several families (e.g., Leptodactylidae, Myobatrachidae, Rhacophoridae) construct foam nests in which the eggs reside (Duellman and Trueb, 1986). Foam nests are placed on the surface of water (e.g., *Leptodactylus ocellatus, Physalaemus*) or in shallow depressions on land (e.g., *Leptodactylus mystaceus*). The foam ultimately dissolves, and in the former case tadpoles drop into the water below and continue development. Larvae from terrestrial foam nests are washed into small, nearby streams or ponds during rain storms or can develop entirely in the nest and emerge as froglets. Interestingly, the tadpoles of some frogs with terrestrial foam nests can generate their own foam (Downie, 1984; Caldwell and Lopez, 1989). Gladiator frogs (*Hyla rosenbergi* and *Hyla boans*) construct water-filled basins that isolate the eggs from streams; the eggs are deposited as a surface film on water in the basins (Fig. 5.1; Kluge, 1981; Caldwell, 1992). A few African frogs deposit eggs underground near water (e.g., *Leptopelis*); subsequently the tadpoles emerge and enter the water. Other frogs construct underground nests, attend the eggs, and tunnel from the nest to the water (e.g., *Hemisus*; Duellman and Trueb, 1986). Salamanders with parental care (see Chapter 4, "Parental Care") coil around their egg clutches, but for most species, the nest is simply a cavity in the ground or beneath vegetation (e.g., *Hemidactylium scutatum*; Breitenbach, 1982).

Female amphibians must select a nest site in which the probability of water permanency is sufficient for those species with aquatic larvae (Rowe and Dunson, 1995). High humidity is necessary to prevent desiccation of clutches in species with terrestrial or arboreal clutches. Potentially high predation risks of different kinds are associated with different egg deposition sites. Temporary ponds typically harbor predaceous insect larvae of dragonflies, damselflies, caddisflies, and diving beetles that can feed on amphibian eggs and larvae. Tadpoles are sensitive to chemical cues emitted by some insect larvae (Petranka et al., 1987) and respond to these larvae

FIGURE 5.1 Clockwise from the top left, nest of the tropical gladiator frog *Hyla boans* (J. P. Caldwell); nest of the saltwater crocodile *Crocodylus porosus* (R. Whitaker); Indian python (*Python molurus*) brooding a clutch of eggs (M.T. O'Shea); and red-eared slider (*Trachemys scripta*) urinating on nest following egg deposition (C. K. Dodd, Jr.).

by decreasing activity (Caldwell et al., 1980; Lawler, 1989) or by remaining in hiding places for long periods of time. Clutches of *Centrolene* and *Agalychnis* deposited in arboreal microhabitats are subject to predation by grapsid crabs, cat-eyed snakes, and various insects (Hayes, 1983).

Reptiles

Most oviparous reptiles construct nests for egg deposition. Because a majority of reptile eggs require at least some water for development (Packard et al., 1977, 1981), nest sites usually occur in moist soil; inside of rotting logs or piles of humic material; inside rotted areas of standing trees; under logs, rocks, or other surface items; in social insect nests; or on the surface in relatively closed spaces, such as crevices, where humidity is high. Among crocodylians, most species construct aboveground nests that isolate the eggs from water (Fig. 5.1; e.g., *Crocodylus porosus* [Webb et al., 1977; Magnusson, 1980] and *Alligator mississippiensis* [Joanen, 1969; Goodwin and Marion, 1978; Hunt and Ogden, 1991]). *Crocodylus johnsoni*, however, places its eggs in burrows in sand (Shine, 1985a). Most species of turtles dig nests in the ground (Fig. 5.1; e.g., *Gopherus berlandieri* [Auffenberg and Weaver, 1969], *Malaclemys terrapin* [Reid, 1955], *Emydoidea blandingii* [Congdon et al., 1983], *Chelydra serpentina* [Congdon et al., 1987], *Kinosternon flavescens* [Iverson, 1990], and *Apalone muticus* [Plummer, 1976]), although at least one species, *Chelodina rugosa*, deposits its eggs in sand underwater during the wet season (Kennett et al., 1993b). Development is arrested and begins when the sand dries during the dry season. Pythons deposit eggs inside holes within vegetation and coil around the eggs. This behavior reduces water loss and provides heat by shivering thermogenesis (Fig. 5.1; Shine, 1985a; Shine and Fitzgerald, 1996; Hutchison et al., 1966). Most lizards and snakes deposit eggs in damp soil or rotting logs and humus (e.g., various species of *Eumeces* [Fitch, 1954, 1955], *Crotaphytus collaris* [Legler and Fitch, 1957], *Ameiva ameiva* [Vitt and Colli, 1994], *Farancia abacura* [Riemer, 1957], *Pituophis melanoleucus* [Burger and Zappalorti, 1986], *Tropidurus plica* [Vitt, 1991], and *Sceloporus aeneus* [Guillette and Gongora, 1986]). Many snakes and lizards and some turtles deposit eggs in ant or termite nests (Brandão and Vanzolini, 1985; Vaz-Ferreira et al., 1970; Burke et al., 1993; Riley et al., 1985), and still others deposit eggs in crevices in rocks (e.g., *Tropidurus* in the *torquatus* species group [Vitt, 1993], *Platysaurus intermedius* [Broadley, 1974], and *Phyllopezus pollicaris* [Vitt, 1986]) or under the bark of trees (e.g., *Gonatodes humeralis*; Vitt et al., 1997b).

Egg placement greatly influences the survival and growth rates of the embryos. For reptiles, mortality is greatest in the egg stage. Amphibians also suffer high egg mortality, but proportionally, mortality is greatest in the larval stage. In both amphibians and reptiles, the female's selection of a site for her clutch will influence the survivorship of her offspring. Good site selection yields high survivorship; poor site selection results in low survivorship or even a total loss of the clutch. The site selected must have the appropriate biophysical environment for the proper development of the embryos and must provide some protection from predation and the vagaries of environmental fluctuations, such as avoiding pond drying or excessive temperatures. Presumably, a female's choice, that is, her nest-site selection behavior, derives from natural selection on choices made by her ancestors. For example, in reptiles this selection reflects an interaction between the constitution of the egg (size, amount of yolk and albumin, allantoic storage of waste) and the water-transport aspects of the nest environment (Packard and Packard, 1988; Overall, 1994). Proper nest selection results in survival and the successful transfer of the parents' genes into the next generation.

The biophysical environment of the nest site influences other aspects of development and survivorship, including the duration of incubation, developmental rate, hatching success, and even the size of offspring (Fig. 5.2; Snell and Tracy, 1985; Overall, 1994). Short incubation time should be advantageous because it reduces the time that eggs are exposed to mortality factors. However, incubation times are often quite long; apparently reducing developmental time has high costs in terms of offspring quality. In the European

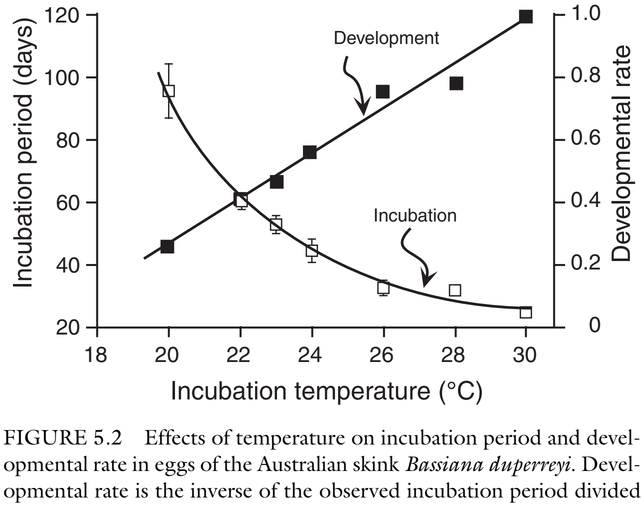


FIGURE 5.2 Effects of temperature on incubation period and developmental rate in eggs of the Australian skink *Bassiana duperreyi*. Developmental rate is the inverse of the observed incubation period divided by the shortest incubation period in the laboratory. Adapted by combining both panels of Fig. 3 in Shine and Harlow (1996).

lizard *Podarcis muralis*, hatching success is high at temperatures varying from 24 to 28°C and much lower at temperatures exceeding 32°C (Van Damme et al., 1992). Moreover, the hatchlings from the eggs incubated at lower temperatures are larger in body size (length and mass), grow faster, and perform better in sprint speed trials than hatchlings incubated at higher temperatures, even though incubation time is shorter (i.e., growth lower but development faster) at higher temperatures. The best balance between incubation time and offspring quality in *P. muralis* occurs at temperatures around 28°C, even though this temperature is lower than optimal temperatures for adult performance. These results support a suggestion by Huey (1982) that some, perhaps many, species have multiple optima; in this case, one optimum temperature exists for embryonic development and another for adult performance.

Striped mud turtles (*Kinosternon baurii*) select nest sites close to vegetation (grass tussocks and other herbaceous plants) with little open ground. Temperatures in the nests are lower than the soil in more exposed sites. Hatching success in eggs experimentally placed in nests close to vegetation compared to that in eggs in more exposed nests is substantially greater (Wilson, 1998). Mud turtles dig shallow nests; consequently, nests near vegetation avoid detrimentally high incubation temperatures. Nest depth is associated with turtle body size, specifically hindlimb length, and larger turtle species deposit their eggs deep enough in exposed areas to avoid extreme temperatures.

Most oviparous reptiles in temperate-zone environments deposit eggs in spring or early summer, and the eggs hatch in late summer or fall. These hatchlings (neonates) must immediately begin to feed in order to grow and to store energy for overwintering. In some species, however, the eggs hatch in the nest in fall, but the neonates remain in the nest through the winter (Fig. 5.3) and emerge in the spring. This phenomenon is much more widespread than commonly recognized. Among turtles worldwide, delayed emergence occurs in at least 12 genera (Gibbons and Nelson, 1978). In the painted turtle (*Chrysemys picta*), neonates emerge in fall or spring depending on locality, and in some areas either may occur (Ernst, 1971). Presumably, overwinter neonates emerge at a time (spring) when resources are most abundant and potential predation is reduced (e.g., Wilbur, 1975a,b). Warming temperatures of spring might be the cue predicting the arrival of good conditions (Gibbons and Nelson, 1978). Spending the winter in the nest has associated costs. In winters with little or no snow cover, nests freeze, killing the neonates, but in winters with snow cover, neonates do not freeze because snow insulates the nest (Breitenbach et al., 1984). A 5–year study on the nesting ecology of *C. picta* showed that winter mortality due to freezing was significant, varying from 0 to 80%.

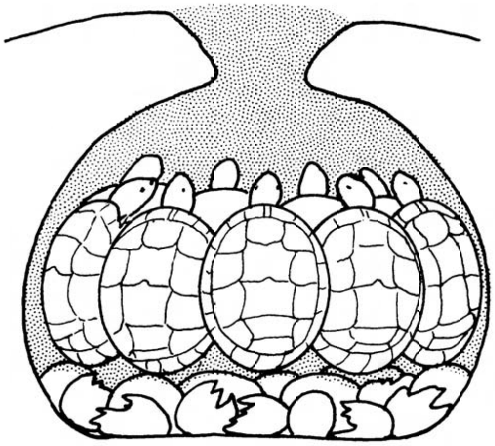


FIGURE 5.3 Spatial arrangement of hatchlings of *Chrysemys picta* in the nest during winter. From Breitenbach et al. (1984).

Temperature-Dependent Sex Determination

An amazing discovery in 1971 revealed that incubation temperatures influenced the sex of hatchling turtles (*Testudo graeca, Emys orbicularis*; Pieau, 1971). This discovery was surprising because sex was assumed to be genetically controlled in all vertebrates, even though sex reversal occurs in larval amphibians and fishes (Pieau, 1975). Subsequent studies have shown that temperature-dependent sex determination (TSD; sometimes referred to as environmental sex determination, ESD) is widespread in reptiles: for example, tuataras (*Sphenodon*; Cree et al., 1995), crocodylians (all species [Ferguson and Joanen, 1982; Lang and Andrews, 1994]), turtles (11 clades [Pough et al., 1998; Janzen and Paukstis, 1991; Vogt and Villela, 1992]), and squamates (Iguania, Gekkota, and Lacertidae [Pough et al., 1998; Janzen and Paukstis, 1991]). Because sex chromosomes are not involved and TSD occurs early during development, it is clearly sex determination and not sex reversal (Bull, 1980). TSD is usually associated with a lack of heteromorphic chromosomes but this does not necessarily cause TSD (Bull, 1980). For example, the squamate clades Teiidae and Scincidae lack heteromorphic chromosomes but there is no evidence that TSD occurs. The most common types of genetic sex determination (GSD) in reptiles and amphibians are male/female heterogamety as XY/XX (male heteromorphic), ZZ/ZW (female heteromorphic), or homomorphic sex chromosomes (sex chromosomes undifferentiated, but sex determination as in heterogametic forms). Among

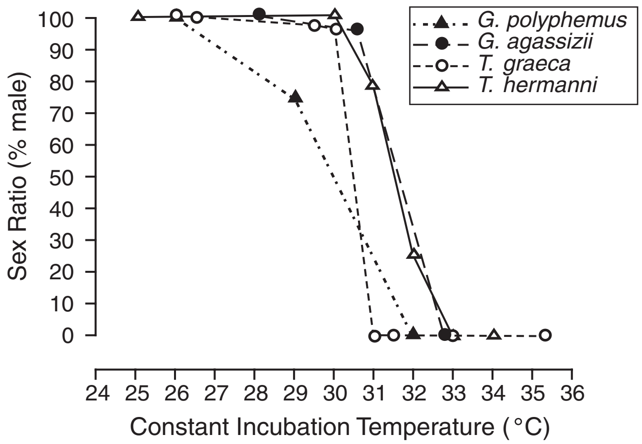


FIGURE 5.4 Sex ratios for four tortoise species (*Gopherus polyphemus, G. agassizii, Testudo graeca, T. hermanni*) raised at different incubation temperatures—males are produced at low developmental temperatures and females are produced at high developmental temperatures. Adapted from Burke et al. (1996).

species with TSD, the temperature range over which sex is determined is relatively small and varies somewhat among species (Fig. 5.4, Table 5.1).

In studied species with TSD, sex determination occurs in the second trimester of development, and the "average" temperature during that period regulates the direction of gonad differentiation (Wibbels et al., 1994). At the threshold temperature range, the gonads can become either ovaries or testes. In most crocodylians and lizards, males result from high temperatures, whereas females result from low temperatures. In turtles, females develop at high temperatures and males at low ones; in a few crocodylians, turtles, and lizards, females develop at high and low temperatures, and males at intermediate ones. The physiological mechanism of TSD is just beginning to be understood (Crews et al., 1994). At temperatures appropriate for the production of one sex over the other, the enzyme aromatase is produced in individuals that will become females and 5α-reductase for those that will become males. These enzymes induce the conversion of testosterone to estradiol to initiate ovary differentiation or dihydrotestosterone to initiate testes differentiation, respectively. Genes that code for the production of aromatase or 5α-reductase are turned on or off depending on temperature.

The ecological implications and consequences of TSD are fascinating and complex. Because developmental

TABLE 5.1 Mechanisms of Sex Determination in Amphibians and Reptiles

	Genetic sex determination			Temperature-dependent sex determination
	Heterogamety in males	**Heterogamety in females**	**Homogamety**	
Amphibians				
Salamanders	Plethodontidae, Proteidae, Salamandridae	Plethodontidae, Ambystomatidae, Sirenidae	None	None
Frogs	Bombinatoridae, Hylidae, Leptodactylidae, Pelodytidae, Ranidae	Bufonidae, Discoglossidae, Leiopelmatidae, Pipidae, Ranidae	None	None
Reptiles				
Turtles	Chelidae, Bataguridae, Staurotypinae	Bataguridae	Chelidae	Pelomedusidae, Podocnemididae, Bataguridae, Carettochelyidae, Cheloniidae, Chelydridae, Dermatemydidae, Dermochelyidae, Emydidae, Kinosternidae, Testudinidae, Trionychidae
Crocodilians	None	None	None	Alligatoridae, Crocodylidae, Gavialidae
Tuataras	None	None	None	Sphenodontidae
Squamates	Iguania, Gekkonidae, Teiidae, Scincidae	Gekkonidae, Lacertidae, Amphisbaenia, Varanidae, Boidae, Colubridae, Elapidae, Viperidae	Iguania, Gekkonidae, Lacertidae, Teiidae, Scincidae, Colubridae, Elapidae	Iguania, Gekkonidae, Lacertidae

Note: Taxa for which the mechanism remains unknown are not included. Taxa may appear more than once if different sex-determining mechanisms occur in different species (from Hillis and Green, 1990; Cree et al., 1995; Janzen and Paukstis, 1991; Lang and Andrews, 1994; Viets et al., 1994).

temperatures determine the sex ratio of offspring, the female parent has the potential to determine the sex of her offspring by selecting nest sites based on temperature. In populations where the sex ratio is highly biased toward one sex, producing offspring of the other sex would provide a fitness advantage to females who selected nests based on the sex ratio of the population. To date, there have been no studies demonstrating that this occurs or how a female would assess the sex ratio of her population. TSD may also have significant population consequences associated with nest predation. In natural nesting environments where there is a mosaic of available nest sites based on temperature, and where that mosaic is at least partially predictable on the basis of physical structure of the habitat (e.g., shaded nest sites under trees, unshaded sites in the open), differential nest predation based on nest site might cause the loss of significantly more individuals of one sex than the other, resulting in a shift in the sex ratio of hatchlings. Variation in global temperature may also influence the structure of natural populations of animals with TSD. As climates change, either due to natural cyclical events or human-induced global warming, changes in temperatures in nesting habitats alter population sex ratios and ultimately the survival of species. Major sex ratio biases have already been observed in populations of *Alligator mississippiensis* and *Caretta caretta* based on nest location (Ferguson and Joanen, 1982; Mrosovsky, 1994). In both cases, the sex ratios were highly biased toward females. Finally, any efforts to manage populations of sensitive species in which TSD occurs must consider the potential long-term effects of variation in nest temperatures, either under natural conditions or when eggs are reared in the laboratory for release into the wild (e.g., Morreale et al., 1982).

Seasonality in Reproduction

Reproduction among amphibians and reptiles varies from highly seasonal to aseasonal, and no single generalization explains the observed variation. A majority of temperate-zone species are seasonal in reproduction, but among tropical species, species reproduce in the wet season, dry season, over extended periods, or even nearly continuously. Reproduction in all species is hormonally mediated, with androgen production reaching a peak just prior to mating.

Amphibians

Temperature and rainfall no doubt are the major determinants of timing of reproduction (Duellman and Trueb, 1986), but the asynchrony of reproduction among species of amphibians occurring at single localities confirms that temperature and rainfall alone are not the sole determinants of reproductive timing. In temperate zones, some amphibians breed in late winter (e.g., *Pseudacris ornata* and *Pseudacris nigrita*, but not synchronously [Caldwell, 1987], and *Plethodon websteri* [Semlitsch and West, 1983]), in spring (e.g., *Siren intermedia* [Sever et al., 1996a] and *Hydromantes ambrosii* [Salvidio, 1993]), early to mid-summer (e.g., *Hyla arborea*; Friedl and Klump, 1997), and fall (e.g., *Ambystoma opacum*; Noble and Bradley, 1933), and some breed in spring and fall (e.g., *Rana sphenocephala*; Doody and Young, 1995). The salamander *Rhyacotriton olympicus* has an extended breeding season in western Oregon and females contain sperm in October through July (Nussbaum and Tait, 1977). The Carolina gopher frog (*Rana capito capito*) breeds only for a few days sometime between January and April (Semlitsch et al., 1995). Long-term studies on the salamander *Ambystoma talpoideum* show that breeding migrations of adults occur from September to the end of January, always during the coldest month; however, the number of breeding adults is correlated with the cumulative rainfall (Semlitsch, 1985a,b, 1987).

Although most temperate-zone amphibians appear to breed annually, some reproduce biennially (every other year). In Louisiana, approximately 35% of female *Amphiuma tridactylum* reproduce each year, suggesting that individuals reproduce every other year or even less often (Fontenot, 1999). The proximate explanation is that vitellogenesis requires nearly a full year, eggs are deposited in mid-summer (July), and females attend the eggs until November. Thus, the complete cycle requires more than a year.

Males of many salamanders have testicular cycles that coincide with ovarian cycles of sexually mature females in the population. Male *A. talpoideum* in the southeastern United States have enlarged testes from September through January, coincident with the presence of enlarged ova in females (Semlitsch, 1985b). Reproductive cycles of males and females differ within some species. In the salamander *Plethodon kentucki*, males breed annually but females breed biennially or even less frequently (Marvin, 1996). Presumably the inability of individual females to reproduce each year results from energy-accumulation limitations associated with season length. Females of species of *Plethodon* in environments with extended seasons for foraging, as in the southern United States (e.g., *Plethodon websteri*; Semlitsch and West, 1983), breed annually, whereas species like *P. kentucki* in environments with short activity seasons reproduce biennially.

In seasonal tropical environments, most amphibians breed during the wet season although there are exceptions. During the dry season in northeastern Costa Rica, none of eight species of hylid frogs reproduces even though some males of several species vocalize year around (Donnelly and Guyer, 1994). Hylid species with explosive-breeding patterns (*Smilisca baudinii* and *Scinax elaeochroa*) reproduce early in the wet season, whereas other hylids (*Hyla ebraccata* and *Agalychnis callidryas*) reproduce throughout the wet season. In Rondônia, Brazil, even though most frog species breed during the wet season, the gladiator frogs (*H. boans*) breed during the dry season, constructing nests in sand at stream edges (Fig. 5.1; Caldwell, 1992).

In relatively aseasonal tropical environments, many amphibians breed year-round, or at least appear to have extended breeding seasons. Six species of frogs in an aseasonal rain forest in Borneo breed throughout the year (Inger and Bacon, 1968). Among frog species at Santa Cecilia, Ecuador, a relatively aseasonal tropical environment, many frogs (e.g., *Scinax rubra*, *Rana palmipes*, *Hyla sarayacuensis*, *Dendrobates parvulus*) reproduce throughout most of the year, whereas others reproduce during periods varying from 3 to 5 months (e.g., *Phyllomedusa vaillanti*, *Leptodactylus wagneri*) (Duellman, 1978). The timing and intensity of rainfall appear to determine exactly when breeding occurs. It remains unknown whether individuals breed throughout the year or whether breeding at different times of the year involves different individuals.

Reptiles

A vast majority of reptiles are seasonal in reproduction (e.g., Fitch, 1970; Shine, 1985a), but when continuous reproduction occurs, it is in tropical species (Fitch, 1982). Nearly all temperate-zone reptiles worldwide reproduce seasonally. Ovulation of eggs occurs in spring, egg deposition occurs in early to midsummer, and hatching occurs in late summer. In most temperate-zone viviparous species, ovulation occurs in spring with parturition in late summer. Additional studies corroborate the preponderance of this pattern for temperate-zone reptiles in general (Table 5.2), but there are some exceptions. In the high-elevation, viviparous species of *Sceloporus*, ovulation and fertilization occur in late fall or early winter, gestation occurs during winter and spring, and offspring are born in early or midsummer (Table 5.2).

Although considerable variation in the timing of fertilization and in the yearly frequency of reproduction exists in temperate-zone species (e.g., some snakes, lizards, and turtles reproduce every other year rather than every year), the above pattern is nearly universal. Cold winter temperatures are a major constraint on reproductive seasonality of temperate reptiles. Soil temperatures and insolation are only high enough to allow rapid embryonic development in summer (Shine, 1985a).

The length of the cold season is a major constraint on the duration of the reproductive season, independent of latitude. This constraint has been neatly demonstrated for the seasonally breeding, tropical montane lizard *Sceloporus variabilis* (Benabib, 1994). At high elevations, gravid females (i.e., containing oviductal eggs) occur from December to July, whereas at low elevations gravid females are found from January to September. The elevation between the two sites differs by 955 m—enough to shorten the high-elevation reproductive season by at least a month. The few high-elevation species that produce offspring in spring or early summer are pregnant during the winter; they bask regularly, thereby elevating their body temperature and speeding embryonic development. This temperature constraint is relaxed in lowland tropical environments.

Spermatogenetic cycles often coincide with ovarian cycles in temperate reptiles. The male cycle in these species is considered prenuptial (Volsøe, 1944) because mating takes place prior to the production of eggs. The terminology has been changed recently to reflect hormonal and gonadal events in the reproductive cycle. When gonadal and hormonal events in males and females coincide, the cycle is called associated (Whittier and Crews, 1987). Associated reproduction (Fig. 5.5) does not always occur, particularly in snakes (Seigel and Ford, 1987). In some species (e.g., *Tropidoclonion lineatum*), sperm production and mating occur in fall and the fall-mated females store sperm. Fertilization occurs the following spring and offspring are produced in late summer. Sperm storage appears obligatory in some species. In these cases, the male's sperm production is out of phase with the female's ovulation and fertilization, and hence a postnuptial or dissociated cycle. In some tropical species, reproduction is nearly continuous in the population, but in most instances, whether individual males or females are continually sexually receptive is not well known. As a result, seasonal patterns are much more obscure among tropical reptiles. At one time, it was believed that tropical squamates had continuous reproduction in aseasonal tropical environments (e.g., Inger and Greenberg, 1966; Sexton et al., 1971) or reproduced during the wet season in wet–dry seasonal tropical environments (e.g., Asana, 1931; Wilhoft, 1963; Barbault, 1975). The currently known diversity of seasonal patterns of tropical squamate reproduction suggests that no single explanation is sufficient.

Among tropical Australian crocodylians, *Crocodylus johnsoni* produces eggs during the dry season, whereas *Crocodylus porosus* produces eggs at the beginning of the wet season (Webb, 1977; Webb et al., 1977). Among tropical snakes, some species reproduce nearly year round (e.g., *Styporhynchus mairii* [Shine, 1985a] and *Liophis poecilogyrus*, *L. miliarius*, and *L. viridis* [Vitt,

TABLE 5.2 Selected Examples of Temperate-Zone Reptiles with Seasonal Breeding Patterns

Species	Family	Country	Source
Spring breeding			
Alligator mississippiensis	Alligatoridae	United States	Joanen, 1969
Malaclemys terrapin	Emydidae	United States	Reid, 1955
Kinosternon flavescens	Kinosternidae	United States	Christiansen and Dunham, 1972
Chelydra serpentina	Chelydridae	United States	Congdon et al., 1987
Sternotherus odoratus	Kinosternidae	United States	McPherson and Marion, 1981
Apalone muticus	Trionychidae	United States	Plummer, 1977b
Chelodina longicollis	Chelidae	Australia	Parmenter, 1985
Cophosaurus texanus	Iguanidae	United States	Howland, 1992
Sceloporus undulatus	Iguanidae	United States	Gillis and Ballinger, 1992
Japalura brevipes	Agamidae	Taiwan	Huang, 1997b
Cordylus polyzonus	Cordylidae	South Africa	Fleming and van Wyk, 1992
Sphenomorphus taiwanensis	Scincidae	Taiwan	Huang, 1997a
Ctenotus (7 species)	Scincidae	Australia	James, 1991
Tupinambis rufescens	Teiidae	Argentina	Fitzgerald et al., 1993
Takydromus hsuehshanensis	Lacertidae	Taiwan	Huang, 1998
Mabuya capensis	Scincidae	South Africa	Fleming, 1994
Mehelya capensis	Colubridae	South Africa	Shine et al., 1996a
Mehelya nyassae	Colubridae	South Africa	Shine et al., 1996a
Coronella austriaca	Colubridae	Italy	Luiselli et al., 1996
Seminatrix pygaea	Colubridae	United States	Seigel et al., 1995
Thelotornis capensis	Colubridae	South Africa	Shine et al., 1996c
Natrix natrix	Colubridae	Italy	Luiselli et al., 1997
Aspidelaps scutatus	Elapidae	South Africa	Shine et al., 1996b
Sistrurus miliarius	Viperidae	United States	Farrell et al., 1995
Fall breeding			
Sceloporus jarrovi	Iguanidae	United States	Goldberg, 1971
Sceloporus grammicus	Iguanidae	Mexico	Guillette et al., 1980
Sceloporus torquatus	Iguanidae	Mexico	Guillette and Méndez-de la Cruz, 1993

1983, 1992a]), others reproduce mostly in the dry season (e.g., *Liophis dilepis*, *Philodryas nattereri*, *Waglerophis merremii* [Vitt, 1992a]), and still others reproduce in the wet season (e.g., *Oxybelis aeneus*, *Oxyrhopus trigeminus* [Vitt, 1992a]).

Among lizards, two studies from different continents demonstrate the diversity of reproductive patterns in seasonal tropical environments. At one highly seasonal site in caatinga of northeast Brazil where the entire lizard fauna was studied, four gekkonids, one gymnophthalmid, and two teiids reproduced nearly continuously; two tropidurines, one scincid, one teiid, and one anguid reproduced primarily during the dry season; and one polychrotine reproduced during the wet season (Vitt, 1992a). At a tropical Australian site in the Alligator Rivers Region in the Northern Territory, lizard species also varied with respect to reproductive seasonality. Among the skinks, one species (*Cryptoblepharus plagiocephalus*) reproduced year-round, five species of *Carlia* and three species of *Sphenomorphus* reproduced during the wet season, and one species of *Lerista*, two species of *Morethia*, and most *Ctenotus* reproduced during the dry season. Among the agamid lizards, *Diporiphora* and *Gemmatophora* reproduced during the wet season, and *Chelosania* reproduced during the dry season (James and Shine, 1985). Such high diversity in the reproductive timing at a single site with similar environmental variables demonstrates that seasonality in rainfall is only one of several determinants of reproductive seasonality in lizards.

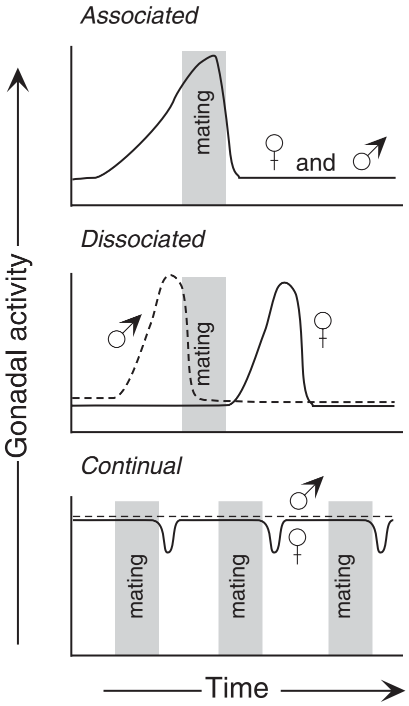


FIGURE 5.5 Schematic diagrams of sex steroid production in relation to gametogenic cycle of a spring-breeding temperate-zone reptile. Steroid levels match the peaks of gametogenesis; androgen production begins simultaneously with spermiogenesis and continues until the testes regress; and estrogen production occurs during final maturation of ovarian follicles, stopping at their maturation and ovulation. Corpora lutea produce progesterone while ova remain in the oviducts. Production declines and corpora lutea degenerate with egg-laying, but in viviparous taxa, progesterone is produced throughout pregnancy.

As in temperate reptiles, the male spermatogenetic cycle may or may not coincide with the female reproductive cycle in tropical species, and presumably sperm storage occurs in species with dissociated cycles. In some instances, spermiogenesis may occur year-round regardless of whether females are seasonal or aseasonal in reproduction (Seigel and Ford, 1987). In species with continual reproduction, individual males presumably produce sperm throughout the year and females produce successive clutches; individual females might be cyclic but the female population is continuous because there are always some females in the population that are preovulatory.

Storage of fat typically cycles with reproduction (Derickson, 1976). Fat stores are mobilized to produce eggs in females (Hahn and Tinkle, 1965; Hahn, 1967) and, because fat stores become depleted during the mating season in males, they are apparently used to supply at least part of the energy necessary for reproductive-related behaviors. In seasonally reproducing reptiles (temperate or tropical), fat stores are at their lowest in males just prior to mating and in females just as eggs are being produced.

The search for a general explanation of seasonality in reptile reproduction must center on tropical species for two reasons: (1) many reptile species are tropical, and (2) the extended period of cold temperatures associated with winter in temperate environments is not a constraint in tropical environments. Shine (1985a) has proposed possible phylogenetic conservatism for tropical Australian lizards and snakes: "The observed seasonal timing of reproduction in squamates may reflect the ancestry of the lineage: for example, many of the dry season breeders belong to genera that are characteristic of the arid zone (e.g., *Ctenotus, Lerista*), whereas the wet-season breeders tend to be species characteristic of more mesic habitats (e.g. *Carlia*)." (See also James and Shine, 1985.) Consequently, the evolutionary histories of species may determine in part seasonality of reproduction.

Evolution of Viviparity

Viviparity has evolved independently many times, particularly in squamates (Blackburn, 1982, 1985; Shine, 1985b). Indeed, the evolution of viviparity from oviparity has occurred more frequently in squamate reptiles than in any other vertebrate group (Shine, 1985a). Viviparity provides parents more control over the development of offspring than does oviparity because the female carries the offspring inside her body. Consequently, predation on eggs in the nest is no longer a threat, although the costs of carrying offspring are considerable. The female is handicapped and her performance is reduced due to the large size of developing young. Additionally, female performance is reduced over a period of time, and a gravid female might be at greater risk of predation than if she had deposited eggs.

The geographical distribution of viviparous species raises additional questions. Viviparous species might be expected to occur in temperate zones or at high elevations where temperatures are low. In these areas, the female could regulate her body temperature behaviorally and thus regulate the temperature of developing embryos. For squamate reptiles, this distribution pattern is partially matched; however, the explanation or hypothesis does not apply to all amphibians and reptiles. For example, all viviparous caecilians and most viviparous frogs are tropical so temperature is an unlikely explanation for these taxa. The same is true for viviparous lizards; some have temperate-zone distributions (e.g., *Elgaria coerulea*) or live at high elevations (e.g., *Sceloporus jarrovi, S. aeneus*), but many are tropical (e.g., *Mabuya nigropunctata, M. heathi*) or live in deserts (e.g., *Xantusia vigilis*).

Viviparity is common among caecilians, and apparently all caecilians have internal reproduction. All but a few frogs have external fertilization and reproduction, thereby predisposing them for oviparity. Seemingly this predisposition also exists for salamanders, because even though most have internal reproduction, fertilization occurs in the cloaca as the eggs pass through, and not in the oviducts. In the viviparous amphibians, nutrition for the developing embryos is either lecithotrophic or matrotrophic but without a placenta. The fetuses obtain their nourishment from oviductal secretions. In the frog *Eleutherodactylus jasperi*, small-bodied females give birth to relatively large-bodied young (Wake, 1978). This production of relatively large offspring is typical of other viviparous amphibians (e.g., caecilians; Wake, 1982, 1992a). Possibly viviparity evolved in some amphibians with internal fertilization because of the competitive advantage of large offspring. Viviparity might also arise during a transition to terrestrial breeding when coupled with internal fertilization. By retaining fertilized eggs within the oviduct until hatching occurs, females prevent their eggs from desiccation by moving to a more humid microenvironment. Nevertheless, these scenarios do not answer why viviparity is so rare in salamanders and frogs. If a primary advantage of viviparity among amphibians is the production of large offspring, then this advantage can be achieved in salamanders by other means. High mortality associated with the production of many small eggs deposited in aquatic environments can be offset by dividing the clutch into fewer, larger eggs and attending the eggs in terrestrial nests. Nest attendance combined with direct development, as occurs in most plethodontid salamanders, eliminates the costs associated with placing eggs in high-mortality environments, relaxes selection on the numbers of offspring, and increases the selective advantages of producing fewer, larger, and presumably more competitive offspring. Because amphibians do not require the higher developmental temperatures of reptiles, there is little thermal advantage to carrying offspring in the body of the female. Egg attendance and direct development obtain the same result in amphibians as viviparity does in squamates: the elimination of a high-mortality stage of the life history.

Among squamate reptiles, current consensus accepts temperature, and specifically cold climates, as the primary factor promoting the evolution of viviparity. The basic arguments are: (1) females carrying offspring can behaviorally obtain and maintain body temperatures above substrate temperatures, whereas eggs experience the vagaries of environmental temperatures; (2) development is more rapid in embryos at higher temperatures; and (3) neonate survival is higher because accelerated development allows them to enter the environment earlier and become established prior to cold weather (Shine, 1983). Evidence supporting the cold climate hypothesis comes from a variety of sources. Squamate reptiles occurring at the highest latitudes and elevations are all viviparous (Tinkle and Gibbons, 1977; Shine, 1985b). Recently evolved viviparous squamates tend to inhabit cold environments (Shine and Bull, 1979; Blackburn, 1982).

A species need not currently live in a cold environment for cold climate to have been the selective factor leading to viviparity. Once viviparity has arisen within a clade, the viviparous species could have dispersed into warmer areas, so their current distributions might be quite different from those in the past. For example, *Mabuya nigropunctata*, a tropical viviparous skink, is widespread in the Amazon Basin. Although it is an apparent exception to the cold climate hypothesis, it is a member of the New World radiation, of which all viviparous members have a unique placenta (Blackburn and Vitt, 1992). The complex type of matrotrophy that occurs in all New World *Mabuya* certainly did not arise independently in each species. Rather, an ancestor that colonized the New World already possessed viviparity and placentotrophy, probably in response to cold climates associated with a north temperate distribution in the Old World. Similar examples abound. Within the Australian snake genus *Pseudechis* (Elapidae), five species are oviparous and one is viviparous. Only the viviparous species, *Pseudechis porphyriacus,* inhabits a cold habitat. Alternative ecologically based hypotheses for the evolution of viviparity are rejected on the basis of comparative data suggesting that even in this case, the cold climate hypothesis is the only viable one (Shine, 1987).

LIFE HISTORIES

An organism's life history is a set of coevolved traits that affect an individual's survival and reproductive potential (e.g., Tinkle et al., 1970; Dunham and Miles, 1985; Dunham et al., 1988). Stearns (1976) considered the key life history traits to include "brood size, size of young at birth or hatching, distribution of reproductive effort, interaction of reproductive effort with adult mortality, and the variation in these traits among an individual's progeny." Approaching the study of life histories from the perspective of easily measurable traits, whether they are quantitative (e.g., age-specific survivorship, offspring size) or qualitative (e.g., oviparous versus viviparous, montane versus desert), allows identification of natural patterns and provides insight into factors that may influence the evolution of life histories. Such an approach is particularly useful for generating testable hypotheses. From one perspective, a life history represents a set of rules that determine energy allocation decisions based on variation in operative environments (Dunham, 1993). Operative environments include the ranges of temperatures, humidities, resources, and other variable conditions experienced by individuals throughout their lifetimes. This allocation perspective provides the potential to identify underlying evolutionary causes of observed patterns by an examination of trade-offs in energy use. Heuristically attractive, the latter approach brings all aspects of ecology, physiology, and behavior into life histories.

Approaches to the study of life histories of amphibians and reptiles have been quite different from the outset because most amphibians have complex life cycles involving a larval stage and reptiles do not. Many amphibians can only be observed during their breeding season, which places further limitations on the study of their life histories. Consequently, life history studies in amphibians and reptiles have historically emphasized different variables and/or focused on different stages of the life history.

Reproductive Effort and Costs of Reproduction

Reproductive effort was originally discussed by Fisher (1930) in terms of energy allocation. He proposed that certain conditions might cause organisms to divert more or less energy to reproduction. Reproductive effort is usually viewed in terms of the total amount of energy spent in reproduction during a defined time period, such as one reproductive episode or season. This approach is particularly useful because it provides the opportunity to examine the effects of the timing and intensity of reproductive investment on other life history traits during the animal's lifetime. Reproductive effort has two components: the energy invested by the female, and the way that energy is proportioned into individual offspring (Williams, 1966). Investing heavily in reproduction at one time has numerous costs (see below). If the total energy investment (potential expenditure) in an individual's lifetime reproductive effort is the individual's reproductive value at the beginning of adulthood, an individual's reproductive value will decline with each successive reproductive event. More explicitly, any current reproductive investment decreases an individual's reproductive value, and what remains (of the total potential investment) is called residual reproductive value. An individual of a species that only reproduces once in its lifetime expends its entire reproductive value in that single event, in contrast to declining reproductive value for species that reproduce repeatedly. In the latter case, natural selection should favor age-specific reproductive efforts that maximize reproductive value at each age (Hirschfield and Tinkle, 1975). Reproductive effort, thus, is defined in terms of costs and reflects a trade-off between energy allocated to reproduction and its effect on future fecundity and survival. Theoretically, a species investing heavily in reproduction early in life (high reproductive effort during each episode) has a relatively short life expectancy, and a species that invests little in reproduction (low reproductive effort in each episode) has a high life expectancy.

In general, these predictions are met by amphibians and reptiles. In relative terms, amphibians typically have high reproductive efforts and relatively short life expectancies compared to reptiles. Most frogs and salamanders lay clutches of eggs comprising a large portion of their body mass and thus constitute a large portion of their overall energy budget. Some reptiles, such as crocodylians and turtles, deposit relatively small clutches (in terms of total energy) during each reproductive episode but do so year after year.

A tortoise that spreads its reproductive effort over a long life and short-lived *Anolis* lizards that episodically invest in reproduction during a short life represent two extremes in the patterns of energy allocation to reproduction. Aldabra tortoises (*Geochelone gigantea*) reach sexual maturity in 13–17 years, live to 65–90 years, reach body sizes varying from 19 to 120 kg, and reproduce repeatedly. Among three isolated island populations, reproductive effort varies depending on density, which reflects per capita resource availability (Swingland, 1977). Reproductive effort is greatest in the population with the lowest density and reaches its minimum in the population with the highest density. When resources increase from one year to the next, reproductive effort increases more in the high-density population than in the low-density population, suggesting that low per capita resource availability constrains reproductive effort in the high-density population.

Anoles (*Anolis)* are early maturing, live relatively short lives, are relatively small in body size, and reproduce repeatedly (summarized by Dunham et al., 1988). Each reproductive episode results in the production of a single egg. Because all anoles produce a single-egg clutch, this reduced, fixed clutch size likely evolved in an ancestor to the anole clade. Compared with similar sized lizards with variable clutch size (Fig. 5.6), anoles have low reproductive efforts per episode (Andrews and Rand, 1974). Although the evolutionary cause of the low reproductive effort in anoles (and other lizards with low, fixed clutch size) remains unknown (but see below), it does allow frequent egg deposition and deposition of eggs at different sites, both of which likely reduce egg predation. When examined on an annual basis, which for many

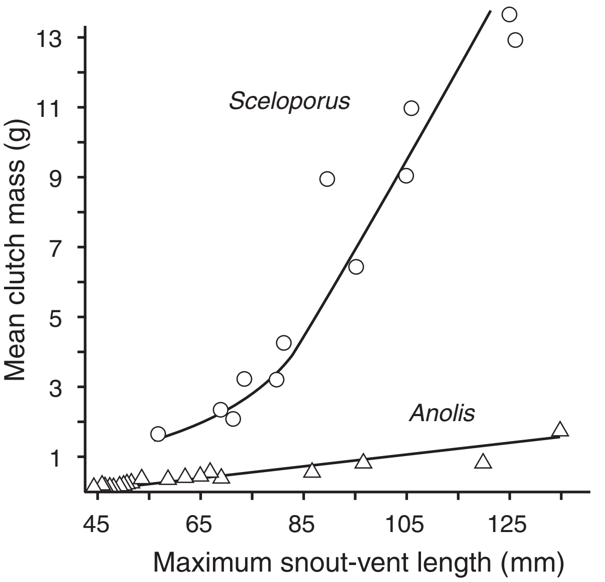


FIGURE 5.6 Species and populations of *Sceloporus* lizards with variable clutch sizes have relatively massive clutches of eggs at any given body size when compared with *Anolis* lizards that have fixed clutch sizes of a single egg. In addition, clutch mass increases linearly with body size in *Anolis*, but exponentially in *Sceloporus*. Adapted from Andrews and Rand (1974); refer to the original paper for species identifications.

anoles *is* the total natural life span, reproductive effort is actually high, constituting about 25% of the total annual lifetime energy budget (Andrews, 1979). These short-lived lizards divide their lifetime reproductive efforts into numerous episodes, each of which represents a relatively low investment in reproduction. The primary cost of repeated reproduction over short time intervals is a short life span for these lizards.

Costs of reproduction can be divided into two major categories: potential fecundity costs and survival costs (Bell, 1980; Shine and Schwarzkopf, 1992). Fecundity costs represent the energetic expenditure of reproduction. The tortoise and *Anolis* patterns described above and many others center around these costs. Energy invested in reproduction is energy that is not available for growth or maintenance (e.g., Tinkle and Hadley, 1973, 1975; Nagy, 1983b; Rocha, 1990). Survival costs are more complex but center around the increased vulnerability of females that are carrying eggs or embryos, either directly from the effect of clutch mass on mobility or indirectly due to reduced physical condition following parturition and its effect on escape behavior or overwintering. Survival costs appear to be much more important as determinants of reproductive effort in relatively short-lived organisms (Shine, 1980c; Shine et al., 1996d).

Survival costs can be indirectly estimated by comparing performance or behaviors of animals with and without eggs. The ratio of clutch weight to body weight (relative clutch mass; Vitt and Congdon, 1978) provides an operational estimate of the burden of a clutch on a female. Gravid Australian skinks exhibit reduced performance as measured by running speed, and females of some skinks bask more when gravid than when nongravid (Shine, 1980c). As relative clutch mass increases, females become progressively slower in running trials, suggesting that survival costs increase proportionately with increased reproductive effort. Oviparous North American skinks, *Eumeces*, also have reduced running speed and less endurance while gravid. These costs are balanced by reduced activity that presumably not only decreases predation risk but also allows active foraging species to invest more in reproduction than they otherwise might (Cooper et al., 1990). The same situation appears to be true for snakes (Seigel et al., 1987).

Costs can also be incurred by ecological constraints on reproductive investment. Dorsoventrally flattened lizards in South America (*Tropidurus semitaeniatus*) and Africa (*Platysaurus* species) have reduced clutch size and low relative clutch mass, presumably as part of a coevolved set of morphological and reproductive traits designed to enhance use of narrow crevices for escape (Vitt, 1981). In the small-bodied Australian skink *Lampropholis delicata*, body shape varies geographically with relative clutch volume, suggesting either that morphology constrains reproductive investment per episode below optimal levels or that life history trade-offs have resulted in the coevolution of morphology and reproductive investment. Comparison between oviparous and viviparous populations of the Australian skink *Lerista bougainvillei* reveals that body volume increases as the result of a combination of increased female size and increased relative clutch mass associated with viviparity, even though the number and size of offspring remain relatively constant (Qualls and Shine, 1995). In this example, the added clutch mass represents a survival cost of viviparity.

Although most attention has been given to females in assessing costs of reproduction, some evidence suggests that males incur high costs as well (Olsson and Madsen, 1996). In male European adders (*Vipera berus*), sperm production is a major reproductive expenditure. Total body mass decreases during spermatogenesis and prior to the initiation of reproductive behaviors associated with finding and courting females (Olsson et al., 1997).

Brood Size and Size of Young

Assuming that energy is limited, a given reproductive effort (clutch mass or energy) can be expended in the production of either a few large offspring or many small ones. The identification and measurement of the trade-offs between size and number of offspring are difficult, and generally relate to natural selection operating on eggs, larvae (amphibians), or juveniles. In most instances, offspring size within a population is relatively constant. Natural selection should favor the offspring size yielding the highest probability of survival and future reproduction success. As a result, energy expenditure theoretically favors either a clutch of numerous small offspring or one of fewer, larger offspring (Smith and Fretwell, 1974). The number and relative size of eggs vary greatly in amphibians and reptiles. Many bufonids, for example, produce thousands of tiny eggs, whereas *Eleutherodactylus* and dendrobatid frogs produce a few large eggs or offspring. The maximum number of eggs produced by any reptile is nowhere near the maximum numbers produced by some frogs and salamanders; nevertheless, great variation exists among reptile species as well. Historical constraints render most ecologically based generalizations about size and numbers of young subject to further examination.

Field data and laboratory studies show that a trade-off exists between the number and size of offspring produced in sand lizards (*Lacerta agilis*). Further, the total reproductive investment is determined by resource availability. Resource levels also influence the allocation of energy to individual offspring, which are larger when resources are most abundant. Independent of this source of variation in hatchling size, hatchling mass is greatest in small clutches and lowest in large clutches, demonstrating the trade-off between offspring numbers and size (Fig. 5.7; Olsson and Shine, 1997). In the Australian water python (*Liasis fuscus*), clutch size increases with maternal body size and is associated with the physical condition of the females. Healthier females produce larger clutches, independent of the effect of body size, and they also produce larger eggs, confirming the trade-off between offspring size and number within a population of snakes (Madsen and Shine, 1996a).

Females of the salamander *Ambystoma talpoideum* have increased clutch size and egg size as they grow larger (Semlitsch, 1985b). The increase in body size of females and potentially the greater energy available to adults as a function of their body size account for the increase in both clutch size and egg size. The number of offspring is maximized, and relatively large offspring presumably hatch earlier and metamorphose at a larger size.

Lizards with low fixed clutch size have no variation in the number of offspring produced in any single reproductive episode. Selection cannot operate on clutch size in these species and, as a result, there can be no trade-off between offspring size and number as in species with variable clutch size. This issue was considered indirectly in the comparison of clutch mass of *Sceloporus* (variable clutch size) with *Anolis* (no variation in clutch size) in Figure 5.6. Gekkonid lizards have a fixed clutch size of one or two eggs, depending upon species (Fitch, 1970; Vitt, 1986). They produce relatively larger offspring than lizards with variable clutch size (Pianka, 1986; Christian and Bedford, 1993), and egg size is relatively constant within a population even though egg quality may vary (Selcer, 1990). When clutch size is fixed at a low value, some potential energy savings of producing few offspring are transferred to the production of larger offspring. Presumably, females produce the largest offspring possible because dividing the clutch into numerous packets is not an option. A tight linear relationship between female and offspring size across species with fixed, low clutch size adds support to this hypothesis (Fig. 5.6). Moreover, this observation suggests the possibility that selection on optimal offspring size influences the evolution of female body size in species with low, fixed clutch size.

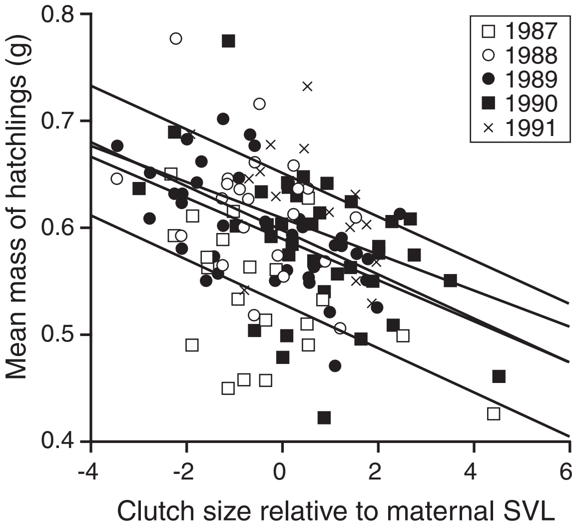


FIGURE 5.7 Annual variation in the trade-off between number of eggs and size of eggs in *Lacerta agilis*. The influence of body size on clutch size has been removed by expressing clutch size as residuals from the common regression. Adapted from Olsson and Shine (1997).

Several nonexclusive hypotheses can explain low clutch size (and clutch mass) in anoles, geckos, microteiids, and some other lizards. One hypothesis is that because anoles have adhesive toe pads for locomotion on smooth surfaces in arboreal environments, the inability to bear the extra load associated with carrying eggs selected for a low fixed clutch size (Andrews and Rand, 1974). If the ancestor of all *Anolis* lived on smooth surfaces where toe pad lamellae determined load-bearing capacity and there was a functional limit on how large adhesive toe pads could be in *Anolis*, then a single evolutionary event could explain low fixed clutch size in all anoles. This hypothesis might also be applicable to gekkonine geckos, in which at least two evolutionary events are necessary. Most gekkonines have a fixed clutch size of two eggs, but some (e.g., *Thecadactylus rapicauda*) have a clutch size of one egg. Unlike anoles, gekkonines have evolved very large adhesive toe pads and it seems unlikely that the load bearing associated with their small clutches is limited by the size of their toe pads. Both anoles and gekkonines have claws as well, so the load-bearing hypothesis is only tenable if the ancestor in each instance lived on smooth surfaces where adhesive toe pads were necessary. A large number of present-day arboreal lizards have large clutches (e.g., *Polychrus marmoratus*; Rand, 1982); they do not have adhesive toe pads and do not live on smooth surfaces. Few present-day anoles live on smooth surfaces. The load-bearing hypothesis does not apply to sphaerodactyline geckos, gymnophthalmids, or other lizards (some scincids, tropidurines, and others) that also lack adhesive toe pads.

Another hypothesis is that reduced clutch size allows more frequent clutch production, thereby providing the opportunity to distribute offspring in time and space and reduce predation. Similar to the load-bearing hypothesis, this hypothesis is difficult to test, especially in lineages with fixed clutch size, because a single evolutionary event in the ancestor of each lineage can account for the low fixed clutch size in the entire lineage. Nevertheless, this hypothesis could apply to all known cases of low fixed clutch size, if such selection produced the condition in the ancestor.

Yet another hypothesis is that low fixed clutch size allows the production of relatively larger and presumably more competitive offspring. The overall negative relationship between clutch size and offspring size in squamates lends some support for this hypothesis. Like the predation hypothesis, this selective force could account for all known instances of low fixed clutch size.

A final hypothesis is that low clutch size results from morphological constraints on females for the use of specific microhabitats. Species conforming to the load-bearing hypothesis might be included here as a special case. Low fixed clutch size in dorsoventrally flattened lizards that use narrow crevices for escape might be another example (e.g., *Platysaurus* [Broadley, 1974; Vitt, 1981]).

Even though egg size tends to be constant (i.e., optimal) in many species, this constancy is not universal. Data on three turtle species raise questions concerning the generality of the optimal offspring size theory. Turtles are potentially constrained in egg size because their pelvic girdle is less flexible than that in many other reptiles. Eggs cannot be larger in width than the diameter of the pelvic aperture. In the chicken turtle (*Deirochelys reticularia*), small females (135 mm plastron length) have narrow pelvic apertures and produce small eggs. As they grow larger, they produce bigger eggs (Fig. 5.8). In the painted turtle (*Chrysemys picta*), small females (115 mm plastron length) have narrow pelvic apertures and produce small eggs. At about 125–130 mm plastron length, even though the size of the pelvic aperture continues to enlarge with increasing female size, egg diameter levels off. In the slider (*Trachemys scripta*), all females produce eggs of about the

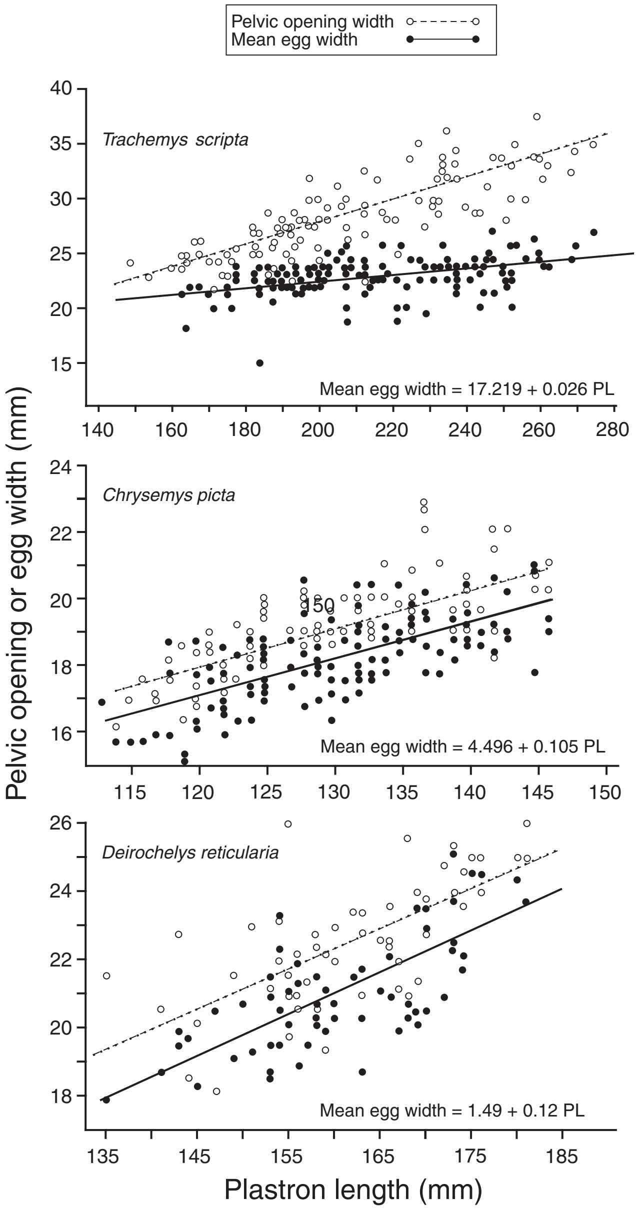


FIGURE 5.8 Variation in the size of the pelvic opening of turtles and width of eggs associated with increasing body size in three species of emydid turtles. Adapted from Congdon and Gibbons (1987).

same diameter regardless of their body size or the size of their pelvic apertures (Congdon and Gibbons, 1987). The lack of variation in egg size in sliders indicates that selection has resulted in an optimal offspring size that is smaller than could be produced relative to the pelvic aperture diameter. In painted turtles, the optimal egg size (i.e., egg size at which there is no further increase) is constrained in small females owing to their narrow pelvic apertures; however, egg production by small females is advantageous even if the eggs and resulting hatchlings are below optimal size. Apparently, there is no optimal egg size in chicken turtles because eggs size is directly associated with female body size across the entire body size range of adults.

Life History Variation

Amphibians

Life histories of most amphibians consist of egg, larval, juvenile, and adult stages. Because of the distinct morphological, physiological, and behavioral changes that occur during metamorphosis and the change in habitat between larval and juvenile stages, amphibian life cycles are complex (Wilbur, 1980). In species with direct development, the larval stage is absent. In some species, individuals with larval morphology become sexually mature and reproduce, and the "typical" adult morphology is never achieved. Other interesting variations in life histories of amphibians occur as well. Life history studies of amphibians have concentrated either on the dynamics of the larvae, which are relatively sedentary and constitute a primary growth stage, or on adults, which are relatively mobile and are the dispersal and reproductive stage. Additionally, numerous experimental studies have focused on larvae because the larval period likely regulates amphibian population size (Wilbur and Collins, 1973).

No long-term life history studies exist on caecilians. Compared with other amphibians, they produce relatively small clutches of large eggs or small broods of large offspring. It would not be surprising if most species are late-maturing and long-lived, but long-term studies are necessary to determine this, and the secretive habits of caecilians have prevented such studies. Life history characteristics vary greatly among salamander species. Among the species with aquatic larvae, salamanders differ from frogs in that the larval morphology is similar to that of the adult except gills are present and limbs may be less well developed than in the adults. Frogs exhibit the greatest diversity in life histories among tetrapod vertebrates. Among species with aquatic larvae, the larval morphology is entirely different from that of the adult. Larval morphology changes to adult morphology as a consequence of a major metamorphosis during which the tail is resorbed, larval mouthparts are replaced by adult mouthparts, fore- and hindlimbs emerge from the body, and major changes occur in the physiology and morphology of the digestive system (Duellman and Trueb, 1986). In species with direct development, hatchlings are nearly identical morphologically to adults but much smaller in body size.

The complexity of amphibian life histories is evident through the factors influencing survival at each stage. Amphibian eggs experience mortality from desiccation due to drying of egg deposition sites and predation by insects, fish, reptiles, birds, and even other amphibians (e.g., Howard, 1978a,b; Caldwell, 1993). Terrestrial breeding amphibians and those that place their eggs on vegetation above water have eliminated sources of egg mortality associated with the aquatic habitat. Survival of bullfrog (*Rana catesbeiana*) eggs, for example, varies from 10 to 100%; predation by leeches and developmental abnormalities are major sources of mortality. The quality of the male territory appears to be the primary determinant of egg survival in these frogs (Howard, 1978a). In woodfrogs (*Rana sylvatica*), survival of eggs is extremely high (96.6%; Seigel, 1983). Amphibian larvae experience some of the same sources of mortality, but, because of their mobility, rapid growth rates, and in some instances production of noxious chemicals for defense, they are able to offset some mortality. Amphibian larvae of many species are capable of rapid growth as a result of their ability to respond to rapid increases in food availability typically occurring in breeding sites (e.g., Wassersug, 1974; Slade and Wassersug, 1975). For larvae, the environment rapidly changes from one in which resources are abundant and predators are scarce just after ponds fill, to environments rich in predators (mostly aquatic insects) and relatively low in resources as larval density increases. Larger larvae are less susceptible to predation and metamorphose at a larger body size (e.g., Semlitsch and Gibbons, 1988). Survival rates of larvae vary considerably. Bullfrog (*R. catesbeiana*) tadpoles in Kentucky have a survival rate varying from 11.8 to 17.6% among ponds (Cecil and Just, 1979). In the salamander *Ambystoma talpoideum*, survival to metamorphosis varies among ponds and among years within particular ponds (Semlitsch, 1987). In one pond in South Carolina, no larvae metamorphosed over a 4-year period. In another pond, survival varied from 0.01 to 4.09% over a 6–year period. The length of time that ponds held water (hydroperiod) accounted for much of the variation in larval survival (Pechmann et al., 1989).

The juvenile stage is also a rapid growth stage, and, because recently metamorphosed amphibians are inexperienced in their new environment, mortality due to predation is likely high. Experienced adults likely face their greatest threat of mortality during breeding events. High localized densities of amphibians during breeding provides opportunities for predators that do not exist during much of the year. In some frog species, male vocalizations actually attract predators such as the frog-eating bat, *Trachops* (Tuttle and Ryan, 1981).

Reptiles

Life histories of all reptiles include egg (or embryo in viviparous species), juvenile, and adult stage. Reptile life histories are much simpler than those of amphibians because there is no larval stage.

Crocodylians and Turtles All crocodylians and turtles, when compared with squamates, are late maturing, reproduce over extended time periods (many years), and are long-lived. Most mortality occurs in early life history stages, the eggs and juveniles (e.g., Andrews, 1982b; Webb et al., 1983; Tinkle et al., 1970, 1981; Congdon et al., 1983, 1987). Clutch size varies from 6 to 60 eggs among species of crocodylians (19 species; Greer, 1975), and is largest in *Crocodylus niloticus* (60) and *Crocodylus porosus* (59). The largest clutch size for an individual was a *C. porosus* with 150 eggs. Larger species and individuals tend to produce larger clutches. A typical crocodylian life history is exemplified by the Philippine crocodile, *Crocodylus mindorensis* (Alcala et al., 1988). Females produce multiple clutches of 7–25 eggs that hatch after 77–85 days. Females guard the nest, and vocalizations of pipped young cue the females to open the nest and transport juveniles to water.

Squamates Considerable variation exists in life history traits of squamates. Many small lizards, such as *Uta stansburiana*, are early maturing (9 months), reproduce repeatedly, and have short life spans (Tinkle, 1967). Others, such as *Cyclura carinata*, are late maturing (78 months), produce a single brood per year, and are relatively long-lived (Iverson, 1979). Among snakes, similar life history variation exists. *Sibon sanniola* reaches maturity in 8 months and produces a single clutch per year (Kofron, 1983) whereas *Crotalus horridus* reaches sexual maturity in 72 months and produces a brood every other year (Gibbons, 1972). Numerous attempts have been made to determine relationships among the life history characteristics of squamates. The first, by Tinkle et al. (1970), was based on a limited set of data. Nevertheless, it was clear that lizard life histories could be grouped into species that mature at large size, produce larger broods, and reach sexual maturity at a relatively late age, and those that mature at small size, produce smaller broods, and reach sexual maturity early in life. More sophisticated analyses based on more extensive data sets and inclusion of additional variables confirm some of these generalizations and refute others. Lizard life histories can be categorized primarily on the basis of brood frequency (Fig. 5.9). Single-brood species are subdivided into three categories: (1) oviparous species with delayed maturity and large brood size; (2) oviparous species with small broods; and (3) viviparous species. Multiple-brooded species include: (1) small-bodied, early maturing species with small broods, and (2) larger bodied species, with early maturity and large broods. Snake life histories fall into three categories (Fig. 5.10). The first includes oviparous and single-brooded species (mostly colubrids) that have increased body size and clutch size, and delayed maturity. The second category comprises viviparous species that breed annually (some elapids and colubrids). The third group consists of viviparous species that reproduce biennially (all of the viperids and the garter snake, *Thamnophis sirtalis,* from the northern part of its range).

Seasonal versus Aseasonal Environments

Early theory suggested that life histories of organisms living in seasonal environments, particularly temperate zones, should be different from those living in aseasonal environments, particularly the wet tropics (Dobzhansky, 1950). Seasonal environments were considered to be less resource limited than aseasonal environments (*r*- versus *K*-selection; see Pianka, 1970). Species in aseasonal environments should spread their reproductive investment out temporally and thus produce more clutches with fewer and larger eggs in each clutch. Larger offspring would presumably have a competitive advantage in such resource-limited environments. In seasonal environments, reproductive investment is constrained to fewer, larger clutches because the season is short and competition among offspring would be relaxed due to high resource availability. Some support for these ideas is evident in the first insightful analysis of life history data for lizards (Tinkle et al., 1970), albeit the data used for analysis were limited (see Dunham et al., 1988).

Testing these ideas with squamates has been difficult partly because different evolutionary lineages are involved in most comparisons, and partly because reproductive variables used are not always comparable. For example, some lineages (anoles, geckos, gymnophthalmids, and others) have clutch sizes that do not vary, whereas other lineages (most iguanians, teiids, scincids, and varanids) have clutch sizes that vary with body size (see Fitch, 1970, 1982, 1985). Hypotheses should be tested within taxonomic groups that have species in both seasonal and aseasonal environments. A comparison of life history characteristics among Australian lizards revealed that congeneric tropical and temperate zone species do not differ in clutch size when the effects of

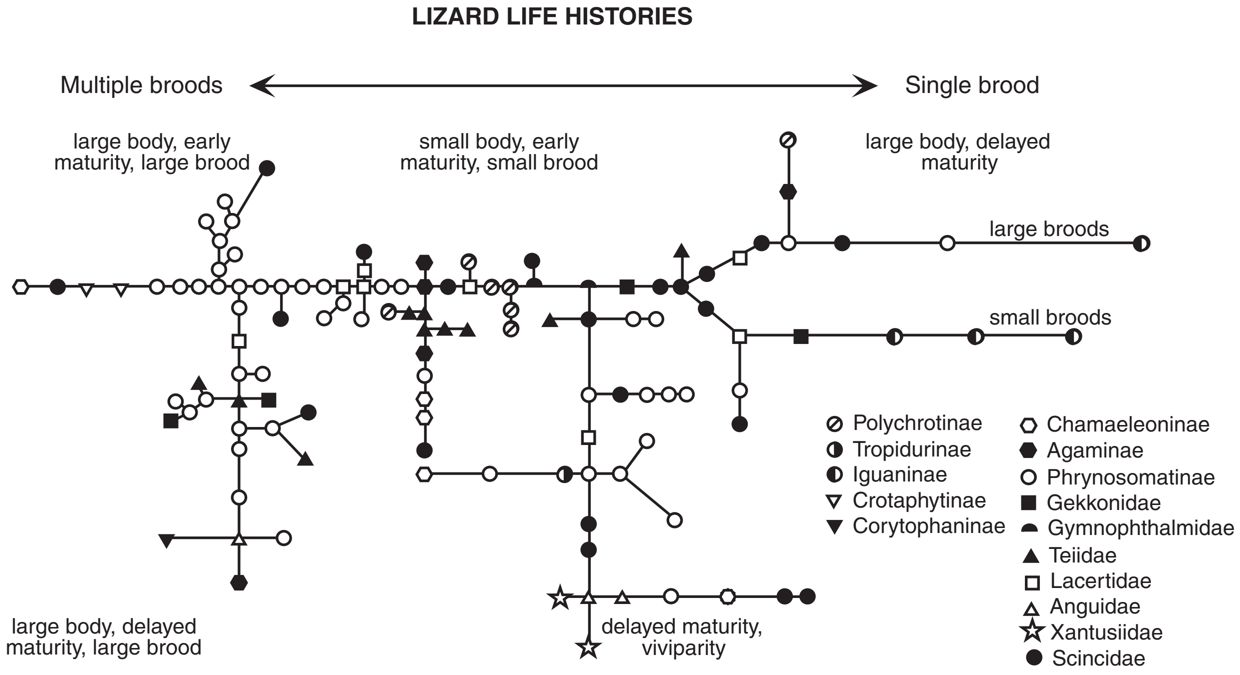


FIGURE 5.9 Prim diagram showing axes of variation in life history traits of lizards. Adapted from Dunham et al. (1988), with taxonomy for the Iguania updated.

body size are eliminated. Body size of egg-laying skinks does not differ between tropical and temperate environments (James and Shine, 1988). Tropical skinks, however, have lower clutch sizes and lower relative clutch masses than temperate zone species. Also, greater numbers of species with low, invariant clutch size occur in the tropical environment. Consistent variation in life history traits exists that is not attributable to seasonal versus aseasonal environments. Egg volume, for example, increases with female body size in *Cryptoblepharus* but not in species of *Carlia*.

Phenotypic Plasticity in Life History Traits

Variation in life history traits includes timing of reproduction, size and number of offspring, number of clutches,

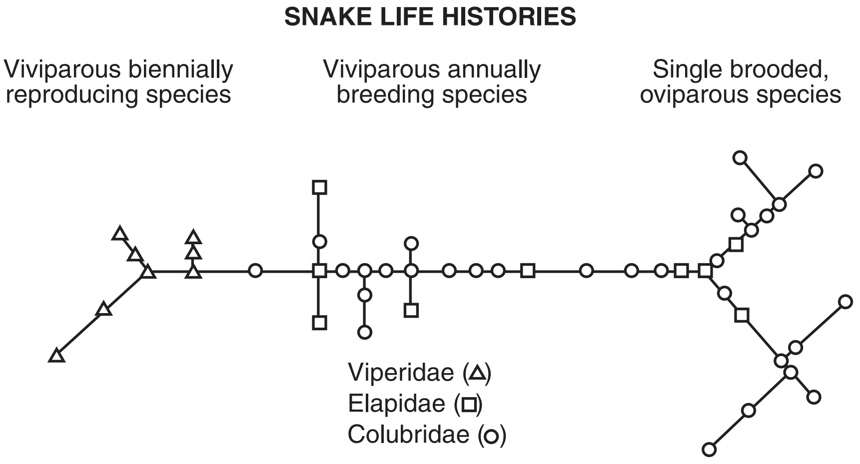


FIGURE 5.10 Prim diagram showing axes of variation in life history traits of snakes. Only three snake families are included so the analysis must be considered preliminary. Nevertheless, coadapted sets of life history traits appear evident. Adapted from Dunham et al. (1988), with errors corrected.

and individual growth rates. This variation is well known within amphibian and reptile populations, and most often appears associated with variable energy resource availability (Stearns, 1976). This within-population variation is termed ''phenotypic plasticity'' and has been examined in both field and laboratory studies (Bull, 1987).

Both the number of eggs produced and the frequency of clutch production decline in New Mexico populations of the lizard *Urosaurus ornatus* as the result of reduced resources (Ballinger, 1977). Lower rainfall during one year reduces prey populations, and this in turn limits the lizard's ability to obtain adequate energy for reproduction. Variation in prey availability associated with rainfall also accounts for variation in growth rates in the lizard *Sceloporus merriami* (Dunham, 1978).

In laboratory studies where energy intake has been precisely controlled, both garter snakes (*Thamnophis marcianus*; Ford and Seigel, 1989) and ratsnakes (*Elaphe guttata*; Seigel and Ford, 1991) respond to increased resource availability by increasing clutch mass and the number of offspring produced. *E. guttata* also increases relative clutch mass in response to increased resource availability. In both of these snakes, offspring size does not respond to resource levels, indicating that offspring size is optimized within narrow limits in these snakes.

Variation of biophysical regimes within reptile nests can influence the phenotypic variability of offspring. Female skinks (*Bassiana duperreyi*) living in a mountainous region of southeastern Australia deposit clutches under logs or rocks at different depths, resulting in nearly identical patterns of temperature fluctuation. Experiments reveal that incubation periods decrease and developmental rates increase with increasing temperature. Hatchlings from clutches incubated at 22°C are larger in snout vent length, have lower running speeds, and spend less time basking 1 month after birth than hatchlings from clutches incubated at 30°C (Shine and Harlow, 1996). High variance associated with fluctuating nest temperatures also influences hatchling phenotypes (morphology, running speed, activity levels, and basking behavior), as does identity of the mother (maternal effects). Similar phenotypic responses to nest conditions occur in pythons (*Liasis fuscus*) that facultatively brood their eggs in tropical Australia. Python nest temperatures are influenced by both nest site selection and whether the female broods the eggs (Shine et al., 1997).

Until recently, most experimental studies on the influence of temperature or moisture on reptile development, and ultimately phenotypes of offspring produced, have been performed under constant temperature conditions. Few, if any, amphibian or reptile eggs experience constant temperatures throughout development. Carefully designed field and laboratory experiments that attempt to mimic natural conditions offer the opportunity to determine the phenotypic consequences of variation in the developmental environment of amphibians and reptiles and will contribute considerably to our understanding of the evolution of life histories.

Synthesis

The ecology of amphibian and reptile reproduction is complex. The decisions females make when selecting nest sites and constructing nests can have profound effects on survival and development of eggs as well as on the morphology, performance, and, in some instances, even the sex of offspring. Amphibians and reptiles may reproduce within very short time periods or over extended time periods, or may even skip years between reproductive episodes. Viviparity has released many squamates and some amphibians from mortality associated with clutch deposition and prolonged, unprotected incubation periods, but not without associated costs. Performance of females carrying offspring is reduced and behavioral modifications are associated with carrying offspring over extended time periods.

Investment in reproduction is costly in terms of both energy and survival. The interaction between age-specific reproductive effort and its survival costs has produced an impressive diversity of life history patterns in amphibians and reptiles. Life histories vary from species with high reproductive efforts, early attainment of sexual maturity, and short life spans to low reproductive efforts, late maturity, and long life spans. Life history patterns are constrained by phylogeny, with some lineages composed of species having life histories quite different from species in other lineages. Similar constraints due to morphology and foraging behavior exist. Among species with variable clutch size, a trade-off exists between the size of offspring and the number of offspring produced. Species producing many offspring typically produce small offspring, whereas species producing few offspring usually produce relatively large offspring. The idea that offspring size is optimized is supported by the large number of species in which offspring size does not appear to vary. However, offspring size variation in some species appears related to resource availability, morphological constraints, or even the possibility that more than a single optimum exists.

ADDITIONAL READING

Bull, J. J. (1980). Sex determination in reptiles. *Q. Rev. Biol.* **55**, 3–21.

Duellman, W. E., and Trueb, L. (1986). ''Biology of Amphibians.'' McGraw-Hill Book Co., New York.

Dunham, A. E., Miles, D. B., and Reznick, D. N. (1988). Life history patterns in squamate reptiles. *In* "Biology of the Reptilia. Vol. 16. Ecology B. Defense and Life History." (C. Gans and R. B. Huey, Eds.), pp. 441–552. A. R. Liss, New York.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Quart. Rev. Biol.* **51:** 3–47.

Stearns, S. C. (1977). The evolution of life history traits: A critique on the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8:** 145–172.

Stearns, S. C. (1992). "The Evolution of Life Histories." Oxford University Press, Oxford.

Wake, M. H. (1992a). Reproduction in caecilians. *In* "Reproductive Biology of South American Vertebrates" (W. C. Hamlett, Ed.), pp. 112–120. Springer-Verlag, New York.

REFERENCES

Reproductive Ecology: Ecology of Nesting: Auffenberg and Weaver, 1969; Brandão and Vanzolini, 1985; Breitenbach, 1982; Breitenbach et al., 1984; Broadley, 1974; Burger and Zappalorti, 1986; Burke et al., 1993; Caldwell, 1992; Caldwell and Lopez, 1989; Caldwell et al., 1980; Congdon et al., 1983, 1987; Downie, 1984; Duellman and Trueb, 1986; Ernst, 1971; Fitch, 1954, 1955; Gibbons and Nelson, 1978; Goodwin and Marion, 1978; Guillette and Gongora, 1986; Hayes, 1983; Huey, 1982; Hunt and Ogden, 1991; Hutchison et al., 1966; Iverson, 1990; Joanen, 1969; Kennett et al., 1993a,b; Kluge, 1981; Lawler, 1989; Legler and Fitch, 1957; Magnusson, 1980; Overall, 1994; Packard and Packard, 1988; Packard et al., 1977, 1981; Petranka et al., 1987; Plummer, 1976; Reid, 1955; Riemer, 1957; Riley et al., 1985; Rowe and Dunson, 1995; Shine, 1985a; Shine and Fitzgerald, 1996; Snell and Tracy, 1985; Van Damme et al., 1992; Vaz-Ferreira et al., 1970; Vitt, 1986, 1991, 1993; Vitt and Colli, 1994; Vitt et al., 1997b; Webb et al., 1977; Wilbur, 1975a,b; Wilson, 1998.

Temperature-Dependent Sex Determination: Bull, 1980; Cree et al., 1995; Crews et al., 1994; Ferguson and Joanen, 1982; Janzen and Paukstis, 1991; Lang and Andrews, 1994; Morreale et al., 1982; Mrosovsky, 1994; Pieau, 1971, 1975; Pough et al., 1998; Viets et al., 1994; Vogt and Villela, 1992; Wibbels et al., 1994.

Seasonality in Reproduction: Asana, 1931; Barbault, 1975; Benabib, 1994; Caldwell, 1987, 1992; Derickson, 1976; Donnelly and Guyer, 1994; Doody and Young, 1995; Duellman, 1978; Duellman and Trueb, 1986; Fitch, 1970, 1982; Fontenot, 1999; Friedl and Klump, 1997; Hahn, 1967; Hahn and Tinkle, 1965; Inger and Greenberg, 1966; Inger and Bacon, 1968; James and Shine, 1985; Marvin, 1996; Noble and Bradley, 1933; Nussbaum and Tait, 1977; Salvidio, 1993; Seigel and Ford, 1987; Semlitsch, 1985a,b, 1987; Semlitsch and West, 1983; Semlitsch et al., 1995; Sever et al., 1996a; Sexton et al., 1971; Shine, 1985a; Vitt, 1983, 1992a; Volsoe, 1944; Webb, 1977; Webb et al., 1977; Whittier and Crews, 1987; Wilhoft, 1963.

Evolution of Viviparity: Blackburn, 1982, 1985; Blackburn and Vitt, 1992; Shine, 1983; Shine, 1985a,b; Shine, 1987; Shine and Bull, 1979; Tinkle and Gibbons, 1977; Wake, 1978, 1982, 1992a.

Life Histories: General: Dunham, 1993; Dunham and Miles, 1985; Dunham et al., 1988; Stearns, 1976; Tinkle et al., 1970.

Reproductive Effort and Costs of Reproduction: Andrews, 1979; Andrews and Rand, 1974; Bell, 1980; Cooper et al., 1990; Dunham et al., 1988; Fisher, 1930; Hirschfield and Tinkle, 1975; Nagy, 1983b; Olsson and Madsen, 1996; Olsson et al., 1997; Qualls and Shine, 1995; Rocha, 1990; Seigel et al., 1987; Shine, 1980c; Shine and Schwarzkopf, 1992; Shine et al., 1996d; Swingland, 1977; Tinkle and Hadley, 1973, 1975; Vitt, 1981; Vitt and Congdon, 1978; Williams, 1966.

Brood Size and Size of Young: Andrews and Rand, 1974; Broadley, 1974; Christian and Bedford, 1993; Congdon and Gibbons, 1987; Fitch, 1970; Madsen and Shine, 1996b; Olsson and Shine, 1997; Pianka, 1986; Rand, 1982; Selcer, 1990; Semlitsch, 1985b; Smith and Fretwell, 1974; Vitt, 1981, 1986.

Life History Variation: Alcala et al., 1988; Andrews, 1982b; Caldwell, 1993; Cecil and Just, 1979; Congdon et al., 1983, 1987; Duellman and Trueb, 1986; Gibbons, 1972; Greer, 1975; Howard, 1978a,b; Iverson, 1979; Kofron, 1983; Pechmann et al., 1989; Seigel, 1983; Semlitsch, 1987; Semlitsch and Gibbons, 1988; Slade and Wassersug, 1975; Tinkle, 1967; Tinkle et al., 1970, 1981; Tuttle and Ryan, 1981; Wassersug, 1974; Webb et al., 1983; Wilbur, 1980; Wilbur and Collins, 1973.

Seasonal versus Aseasonal Environments: Dobzhansky, 1950; Dunham et al., 1988; Fitch, 1970, 1982, 1985; James and Shine, 1988; Pianka, 1970; Tinkle et al., 1970.

Phenotypic Plasticity in Life History Traits: Ballinger, 1977; Bull, 1987; Dunham, 1978; Ford and Seigel, 1989; Seigel and Ford, 1991; Shine and Harlow, 1996; Shine et al., 1997; Stearns, 1976.

Part III

PHYSIOLOGICAL ECOLOGY

The basis of life is ultimately the chemical reactions that occur within cells of individual organisms. Physiological processes operate within a narrow environmental range and function best in an even narrower range. The environment must be neither too hot nor too cold, be neither too wet nor too dry, and have the proper proportions of gases, especially oxygen. Cellular chemistry and function are closely integrated with osmotic balance, the maintenance of specific ionic concentrations within cells and tissues. Chemical reactions in turn require fuels that are converted by oxidation into energy to power the life processes, and the efficiency of these reactions depends upon temperature. Osmoregulation, respiration, thermoregulation, and energetics compose the most important physiological processes.

Amphibians and reptiles live in diverse environments, varying greatly in solute concentrations, temperature, oxygen availability, and fuel and nutrient resources. An individual's behavior and physiological homeostatic mechanisms interact to maintain its internal environment within tolerance limits, thereby ensuring the animal's survival and ultimately its ability to reproduce. For ectotherms, temperature may be the single most important physiological variable because all cellular processes are temperature dependent. Nonetheless, all the preceding environmental variables affect life and how it is lived. Physiological ecology examines the complex interplay between physiological processes and the organism's physical and chemical environments. It integrates behavioral and ecological phenomena in seeking explanations for the evolution of physiological traits.

This Page Intentionally Left Blank

Chapter 6

Water Balance and Gas Exchange

In an active amphibian or reptile, thousands of cellular reactions occur every second. These reactions require an aqueous medium, and further, water and oxygen are required to convert fuel to usable energy. These metabolic reactions power the chemistry of digestion, absorption, waste removal, cell repair and division, reproduction, and a multitude of other functions. To survive, amphibians and reptiles must maintain internal body fluids that provide a stable environment for the cells. The concentration of body fluids typically differs greatly from concentrations of solutes in the external environment and continually challenges their internal balance. Water loss and ion gain are the primary osmoregulatory challenges to amphibians and reptiles in salt water; water loss and the resultant increased concentrations of ions are the major challenges for terrestrial species; and water gain and ion loss or decreasing concentrations of ions are the primary challenges faced by freshwater species (Fig. 6.1).

WATER AND SALT BALANCE

Gaining and Losing Water

The body of an amphibian or reptile is composed of about 70–80% water, in which various ions necessary for proper physiological function are dissolved. Sodium, magnesium, calcium, potassium, and chloride are critical ions for normal physiological functions. The aqueous environment of amphibians and reptiles contains a complement of dissolved ions similar to their bodies, but in different proportions. Because amphibians and reptiles live in environments varying from xeric deserts to montane cloud forests and from fresh to saline water, a number of mechanisms are necessary to maintain osmotic balance. For an organism to function normally, the ionic concentration of intra- and extracellular fluids must remain within certain specific limits, and the nitrogenous byproducts of metabolism must be removed from the body to avoid poisoning the organism. Most amphibians and reptiles maintain homeostasis, but a few species can tolerate high plasma solute concentrations for extended time periods (anhomeostasis).

Water enters and exits the body in a variety of ways (Table 6.1). Although many similarities exist, some aspects of water gain and loss differ in amphibians and reptiles, primarily because of the structure and permeability of the skin. Amphibian skin is unique among vertebrates. It is highly permeable and lacks any kind of structures—scales, feathers, or fur—to make it less so. In

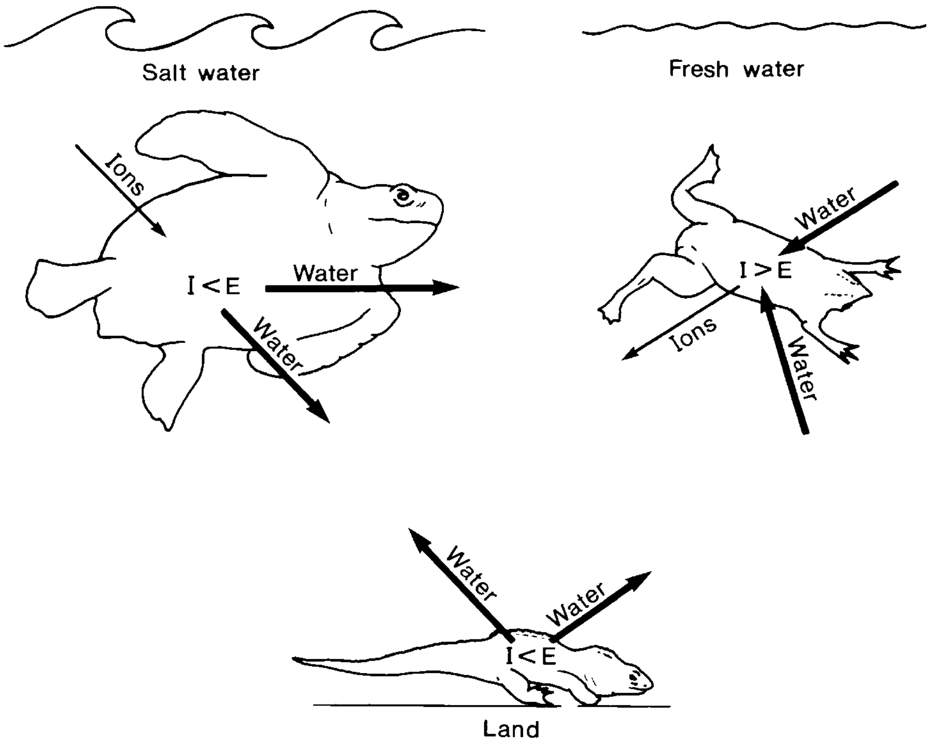


FIGURE 6.1 Osmotic challenges of amphibians and reptiles on land, in freshwater, and in salt water. In salt water and on land, the animal is hypoosmotic compared to its environment, and because its internal (I) ion concentration is less than the surrounding environment's (E) concentration (I < E), water moves outward. In freshwater, the animal is hyperosmotic to its environment, and the greater internal ion concentration (I > E) causes water to move inward.

contrast, the epidermis of the skin of most reptiles is covered with scales, which reduces water gain and loss.

Water is acquired by amphibians and reptiles through drinking (reptiles only), food (preformed water), uptake across skin, metabolism (usually very little), and in some species through the lining of the cloaca or esophagus (Shoemaker and Nagy, 1977). By far, the greatest source of water for amphibians is movement across the permeable skin. Water crosses the skin primarily through osmosis and less so by diffusion. Osmotic water gain occurs in species of amphibians that live in freshwater habitats. The ambient water has a lower ionic concentration than the body fluids, and water enters the body, increasing the volume of body fluids and thereby decreasing the concentration of solutes. When water deficits occur, terrestrial amphibians can obtain water by pressing their ventral surfaces against damp substrates or by entering crevices or burrows where ventral and lateral skin surfaces can absorb water. Breakdown of food may supply a small amount of metabolic water.

TABLE 6.1 Routes of Water Gain and Loss in Amphibians and Reptiles

Gain	Loss
Food (preformed water)	Excretion
Drinking	Feces
Integument	Urine
Metabolism	Salt glands
	Respiration
	Integument

Source: Adapted from Minnich (1982).
Note: Some routes are specific to only one group; see text.

Morphological modifications of the skin in amphibians aid in water uptake. Amphibian skin differs in permeability on various surfaces of the body. Skin varies from smooth to granular. In general, aquatic amphibians have smooth ventral skin, whereas terrestrial species have granular ventral skin. Terrestrial species that live near water, such as *Rana*, or rain forest species such as *Leptodactylus* and dendrobatids have smooth venters. Granular skin is more highly vascularized and enhances water absorption. A specialized area of the skin, the "pelvic patch," on the ventral surface of anuran thighs is more highly vascularized than any other skin surface (Czopek, 1965). By appressing this surface to moist soil, a frog can absorb water, which accounts for as much as 70–80% of total water uptake in some species of toads (McClanahan and Baldwin, 1969). The granular skin surface of frogs, especially toads, also creates narrow grooves that serve as water channels to keep the dorsal surface moist. Evaporation from the back pulls water onto the back via molecular adhesion, and capillary action pulls water from the venter, which is in contact with the soil. Salamanders have numerous vertical body grooves, the largest of which are the costal grooves, and these grooves also channel water from the salamander's underside to its back (Lopez and Brodie, 1977).

In reptiles, drinking freshwater is an important source of water gain, although this behavior varies considerably among species. Unlike amphibians, most reptiles gain almost no water through their skin. Some desert lizards (e.g., *Coleonyx variegatus* and *Xantusia vigilis*) drink water that condenses on their skin when they enter cool burrows (Lasiewski and Bartholomew, 1969). Some species of South African tortoises collect water in their shells during rainfall. By posturing with the posterior portion of the carapace elevated higher than the anterior portion, an individual can cause the water to run along the edges of the ridged carapace toward its head.

Some desert lizards living in xeric environments are capable of acquiring water from their skin by assuming stereotyped behaviors that result in capillary transport of water toward the mouth through channels between scales. This behavior has been observed in the laboratory for *Moloch horridus* and *Phrynocephalus helioscopus* and in the field for *Phrynosoma cornutum* (Bentley and Blumer, 1962; Schwenk and Greene, 1987; Sherbrooke, 1990). Typically, the body is arched during rainstorms in *P. cornutum*, and water moves from the back to the mouth.

Production of metabolic water contributes to osmoregulation in some species of reptiles. For example, metabolic water contributes 12% to total water gain in *Dipsosaurus dorsalis*. However, reptiles cannot produce metabolic water at a rate that exceeds their evaporative water loss (Minnich, 1979). The temperature at which a reptile digests its food affects how much metabolic water is produced.

Variable amounts of water are obtained from food, but the impact of this water depends on the electrolyte concentration of the food. Diet choice or feeding rates can be influenced to some degree by the concentration of electrolytes in a particular food item. Free or preformed water in the insect prey of many desert lizard species exposed to extreme heat and prolonged periods of low humidity may be the sole source of water over extended dry periods. *Urosaurus graciosus*, a small lizard in the Sonoran Desert, forages in the canopy of relatively small trees and shrubs during morning and late afternoon and remains inactive in shady sites on tree trunks during the hottest part of the day. Due to a lack of cool retreats, body temperature increases from 35°C while foraging to more than 38°C while inactive in the afternoon. Water loss is high, 38.5 ml kg^{-1} day^{-1} (Congdon et al., 1982b). In the same habitat, a closely related and similar sized species, *Urosaurus ornatus*, lives in larger trees adjacent to rivers where afternoon temperatures are lower as a result of the shading effect of the canopy, and it maintains body temperatures at 36°C or lower throughout the day. Water loss in *U. ornatus* is less, 27.7 ml kg^{-1} day^{-1}. Differences in thermal ecology account for differences in water loss between the two species. Both species gain water primarily from the insects they eat; infrequent rainfall is the only other water source. *U. graciosus* eats an average of 11.5 prey items per day and has stomach volumes averaging 0.129 cm^2, whereas *U. ornatus* eats an average of 7.7 prey items per day and has stomach volumes of only 0.066 cm^2. *U. graciosus* offsets its high rate of water loss by ingesting substantially more insect prey.

The tropical lizard *Sceloporus variabilis* has higher levels of water and metabolic flux than most similar-sized temperate *sceloporus* lizards (Benabib and Congdon, 1992). Physical, biotic, and behavioral differences between *S. variabilis* and its temperate-zone relatives account for increased rates of water and energy exchange. These lizards move more and are active longer; both water and food are more readily available to them than to most temperate-zone *sceloporus*.

Behavioral adjustments are the overriding mechanisms for water retention in terrestrial amphibians and reptiles. Most species adjust daily and seasonal activity to minimize water loss, and they seek humid or enclosed retreats such as crevices or borrows while inactive. Most terrestrial amphibians have moist skin and are unable to tolerate arid conditions, although a few unusual exceptions are known. Evaporative water loss is not deterred by the skin of amphibians. Skinned and normal frogs lose water at the same rate (Adolph, 1932), and both lose water at the same rate as freely evaporating models of the same size and shape. Under arid conditions with no ability to regulate their water loss, most amphibians would not survive longer than 1 day (Shoemaker, 1992).

Water is lost through evaporation, respiration, and excretion. Evaporation can be a significant source of water loss in terrestrial and even in semiaquatic species of amphibians. In aquatic amphibians, the excretion of dilute urine is the major source of water loss. In reptiles, water is lost in feces and relatively concentrated urine. In most species of reptiles, the skin has low permeability, but in marine species, most water loss is through the skin. Respiration can be a source of water loss for both amphibians and reptiles, particularly in arid areas. Loss from this route is small compared to water loss from other routes.

Freshwater crocodiles often experience prolonged periods of drought in which there is no surface water available. Estivating crocodiles (*Crocodylus johnsoni*) in Australia spend 3 to 4 months inactive underground with no access to water (Christian et al., 1996). Body temperatures increase with time as a result of increasing environmental temperatures, but water loss rate is only about 23% of the rate prior to estivation. The crocodiles do not dehydrate and appear to have no physiological mechanisms specifically associated with estivation. Refuges used for estivation appear to adequately accommodate homeostasis.

Reptiles have a variety of water-storage sites. The bladder is a common site of water storage. For example, the bladders of desert tortoises may occupy more than one-half of the peritoneal cavity. Other sites of water storage include the stomach in the lizard *Meroles anchietae* (Louw and Holm, 1972). The accessory lymph sac in the lateral abdominal folds of chuckwallas and the baggy folds of skin around the legs in diamondback terrapins also hold water (Norris and Dawson, 1964; Dunson, 1970).

In some frogs, modifications of skin or use of glands in skin reduce water loss (Withers et al., 1982). Several groups of arboreal frogs, collectively called waterproofed frogs, have independently evolved specialized mechanisms for withstanding arid conditions by decreasing the permeability of the skin. Frogs in unrelated clades use different mechanisms to avoid dehydration. The mechanism for water loss reduction in certain species of *Phyllomedusa*, a genus of South American hylids, is secretion of lipids from the skin glands. In *Phyllomedusa sauvagei*, the glands secrete a variety of lipids, with wax esters most abundant (McClanahan et al., 1978). The frogs have an associated stereotypic behavior, in which they systematically use their arms and legs to wipe the lipids evenly over their body (Fig. 6.2). The skin becomes shiny and impermeable to water. In waxed frogs, the rate of water loss is low at low temperatures, but above 35°C, the rate of water loss increases

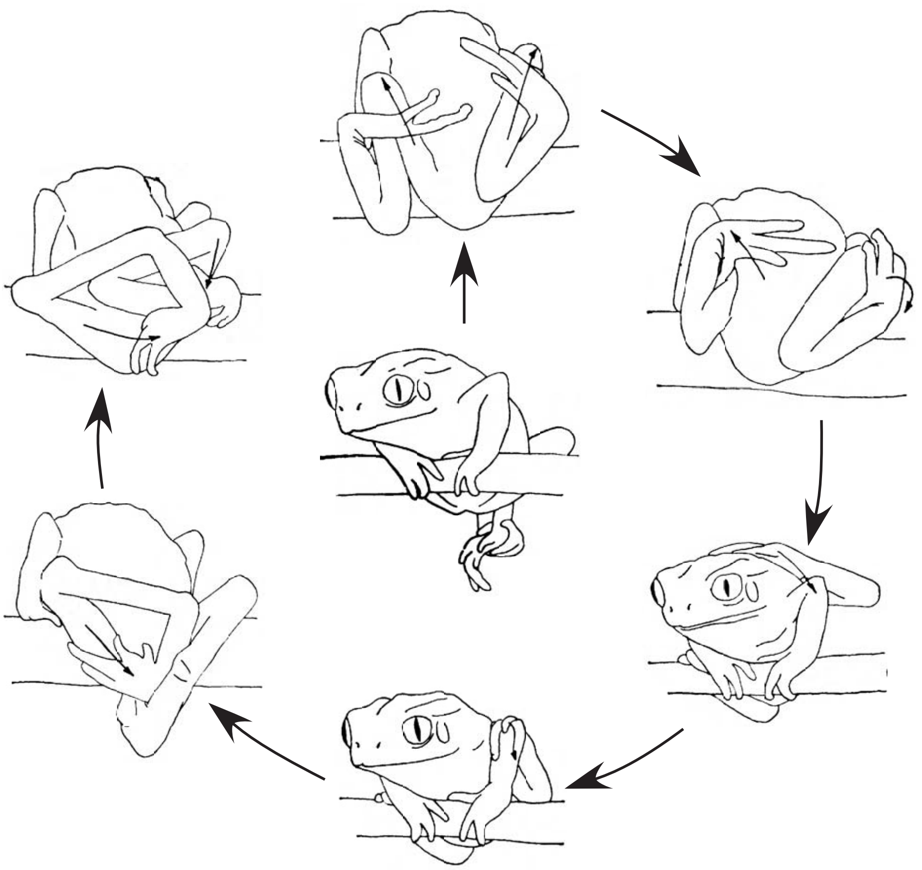


FIGURE 6.2 *Phyllomedusa sauvagei* spreads lipids from lipid glands in the skin by a series of stereotyped movements using the feet. Small arrows indicate direction of foot movement. Adapted from Blaylock et al. (1976).

significantly, indicating that the waxed skin no longer prevents water loss. Experiments with isolated wax esters from these frogs indicate that when the wax is exposed to temperatures above 35°C, it melts and no longer forms an evaporation barrier. *P. sauvagei* live in arid areas of Bolivia and adjacent countries; the highest environmental temperatures occur during the rainy season, and thus desiccation is not a problem.

South African waterproofed frogs in the genera *Chiromantis* (Rhacophoridae) and *Hyperolius* (Hyperoliidae) lose water at the same rate as expected for reptiles when exposed to arid conditions. Their mechanism for prevention of cutaneous water loss differs from *Phyllomedusa*, and their skin does not contain wax glands. These frogs live in semiarid areas in Africa where temperature can exceed 40°C; thus, heat gain is a challenge for these frogs, in contrast to *P. sauvagei*. The waterproofing mechanism lies in the structure of the dermal layer of the skin. In all frogs, the dermis contains various types of chromatophores arranged in layers. The iridophores usually are present in a single layer and reflect light through overlying xanthophores to produce bright coloration (Fig. 6.3). However, in *Chiromantis petersi* and *Chiromantis xerampelina*, the iridophores are several layers thick. In the dry season, the iridophores increase in number, filling the stratum spongiosum. The iridophores function in part to lower internal temperature by lowering radiation absorption (Schmuck and Linsemair, 1988), thereby reducing the rate of water loss. In *Hyperolius viridiflavus*, an African species that estivates in exposed areas with high temperature and low relative humidity, the number of iridophores present exceeds that necessary for radiation reflectance. Instead, accumulation of additional iridophores aids in elimination of nitrogen. Iridophores contain mainly the purines guanine and hypoxanthine, which contain nitrogen. In addition to the skin, the liver epithelium and other internal connective tissues fill with iridophores, supporting the interpretation that the iridophores function in a capacity other than radiation reflectance.

Some South African species of *Hyperolius* also are able to withstand arid conditions. These *Hyperolius* have impermeable skin in the dry season but permeable skin in the wet season. Differences in the permeability are 30–fold between the two seasons in *H. viridiflavus* (Geise and Linsenmair, 1986). Similar responses occur in Australian frogs as well. *Litoria caerulea* and *Cyclorana australis* live in dry savannas, and the outer surface of their skin bears a thin proteinaceous layer whose resistance to water is further enhanced by a lipid coating (Christian and Parry, 1997). Arboreal species of North American *Hyla* lose water at a slower rate than nonarboreal frogs; the skin mechanics of these species have not been examined.

Inactivity and the formation of an impermeable encasement are common mechanisms to survive droughts in amphibians. The development of an epidermal cocoon has evolved independently in several taxa of frogs,

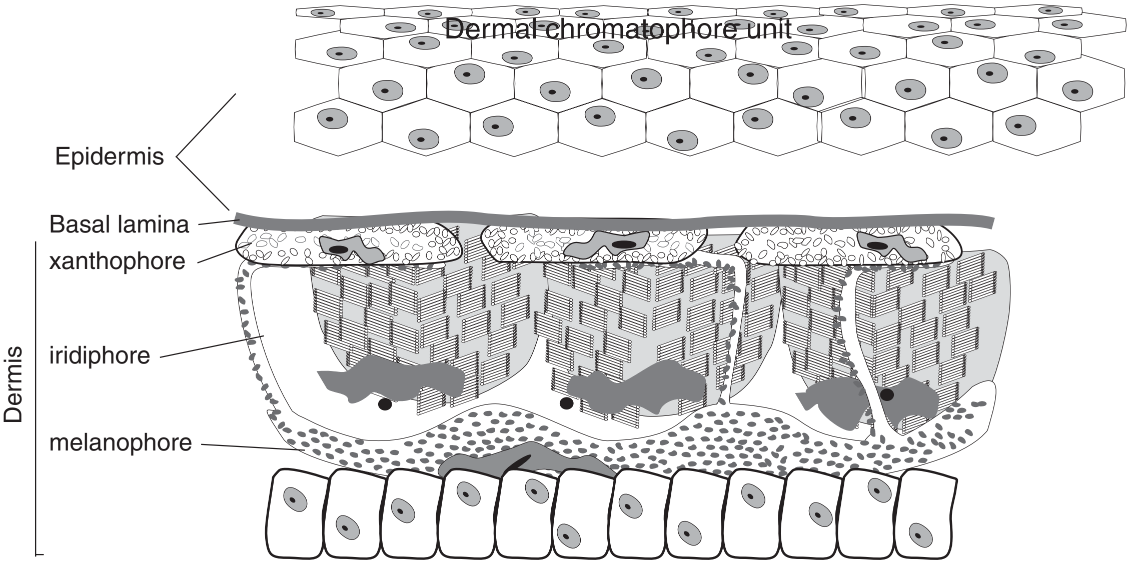


FIGURE 6.3 The arrangement of chromatophores in amphibian skin, called the dermal chromatophore unit. The unit consists of xanthophores, which give yellow, orange, or red coloration; the iridophores, which reflect light and cause bright colors; and the basal melanophores, which have dendritic processes that extend between the xanthophores and the iridophores.

FIGURE 6.4 The hylid frog *Cyclorana novaehollandiae*, encased in its cocoon, emerges after a rainstorm and begins to eat the cocoon. The cocoon consists of retained layers of shed skin. Photograph by S. J. Richards.

including *Cyclorana* (Fig. 6.4), *Limnodynastes, Neobatrachus, Pyxicephalus, Ceratophrys, Smilisca, Pternohyla*, and *Leptopelis*, and in a few salamanders, including *Siren*. Cocoons form from multiple skin shedding events, except that the layers of skin are not truly shed but remain attached to the frog. With each ecdysis event, the externalmost epidermal layer lifts off the new skin and fuses to the previous shed skin (Fig. 6.5). The multiple-layered skin cocoon creates an impermeable sac around the frog that opens only at the nares, allowing the frog to breath. In the Argentine *Lepidobatrachus llanensis* (McClanahan et al., 1976, 1983), the cocoon accumulates at the rate of 1 layer a day, and in the Australian hylid *Litoria alboguttata*, a 24-layer cocoon formed in 21 days after water was withheld in a laboratory experiment (Withers and Richards, 1995). Cocoons form in dry periods during underground estivation. In this protected situation, air movement is low, and as the soil gradually dries, ecdysis proceeds and the layers of skin accumulate to form a cocoon.

Similarly, the salamanders *Siren intermedia* and *Siren lacertina* form cocoons when their pools of water dry and they estivate in the bottom mud to avoid dehydration. Initially, the cocoons were reported to form from dried mucous gland secretions, but subsequent studies revealed that salamander cocoons consist of epidermal layers, just as in frogs (Reno et al., 1972; Etheridge, 1990).

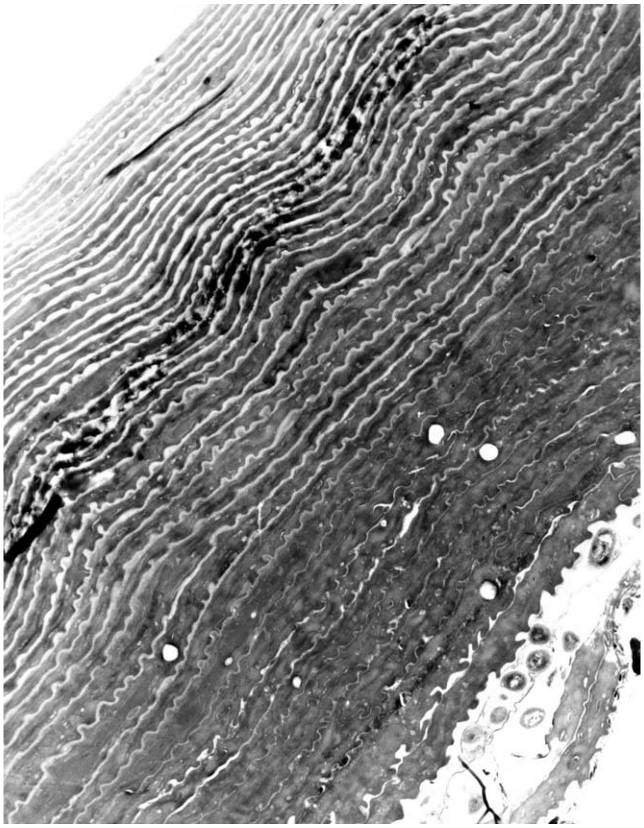


FIGURE 6.5 Photomicrograph showing 39 layers of stratum corneum forming the cocoon of the South American frog *Lepidobatrachus llanensis*. Photomicrograph by R. Ruibal.

Dehydrated or resting amphibians typically adopt water-conserving postures. These postures include folding the arms and legs tightly beneath the body and flattening the ventral surface close to the substrate. When emerging (at night, for example), many species seek damp substrates from which they absorb water. In the water-absorbing posture, frogs and toads hold the back limbs away from the body and press the ventral surfaces onto the substrate (Fig. 6.6). If the substrate contains renewable water (a pond edge, for example), the frog remains in the same position; however, if the substrate is nonporous, the frog continually readjusts its position to take up additional water. Hormonal control of cutaneous water uptake appears to be similar to that which regulates the drinking response in other tetrapods (Hoff and Hillyard, 1991).

The tropical rain frog *Eleutherodactylus coqui* uses adjustments in posture and activity to regulate water flux (Pough et al., 1983). By resting the chin on the substrate and drawing the limbs up underneath the body during periods of inactivity, a minimum amount of surface is exposed, and cutaneous water loss is reduced (Fig. 6.7). While calling, males expose a maximum amount of surface area, which results in increased water loss, and, in addition, expansion and contraction of the body and vocal sac during calling causes the boundary air surrounding the frog to mix with environmental air, increasing the rate of water loss even more. A threefold difference can occur between frogs in water-conserving postures versus non-water-conserving postures. Because of water loss during calling, males experience increased solute concentrations that negatively impact metabolism

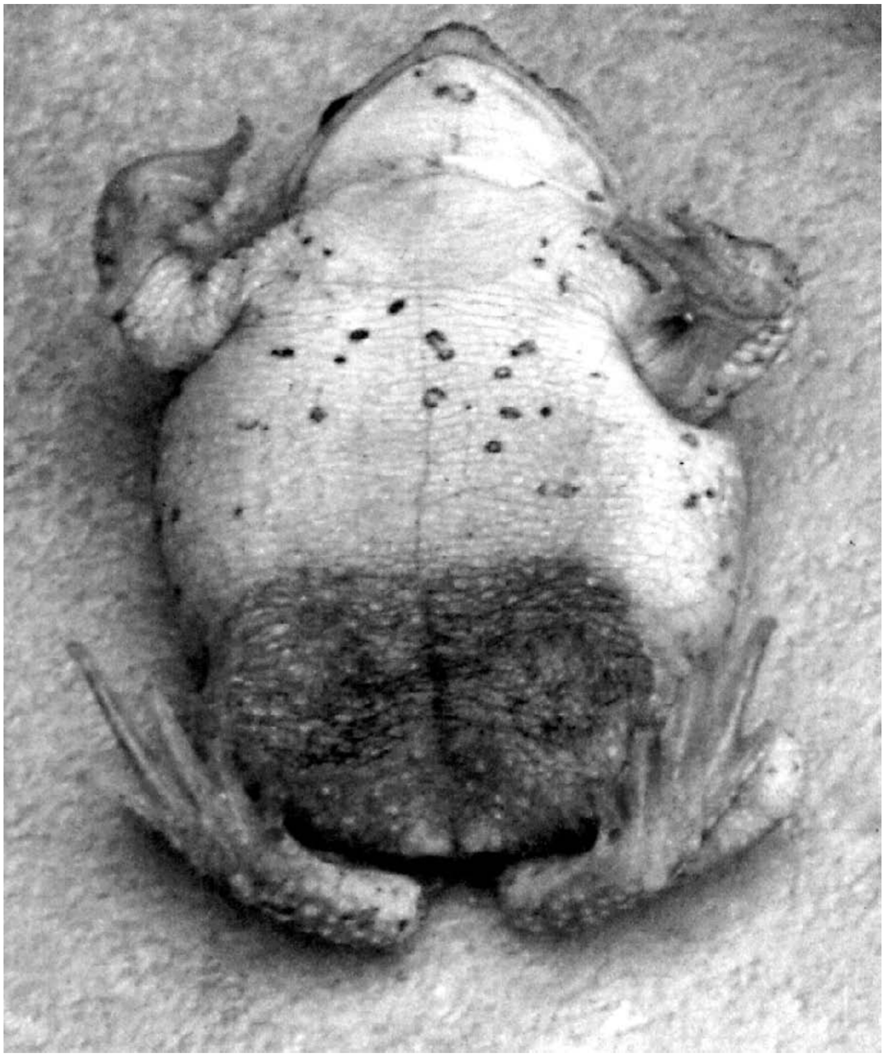


FIGURE 6.6 Photo of *Bufo punctatus* on glass showing the ventral water absorption patch. Photograph by L. J. Vitt and J. P. Caldwell.

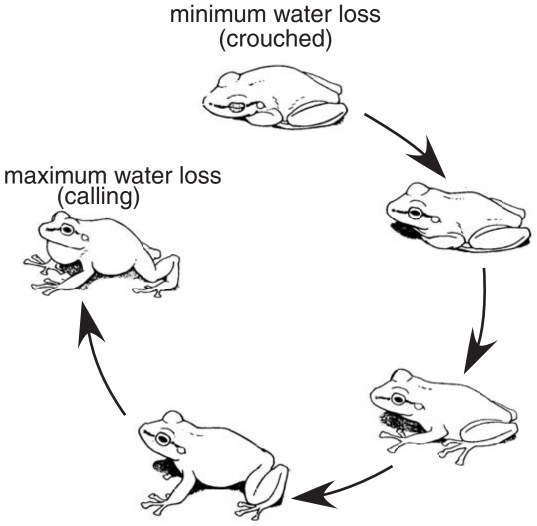


FIGURE 6.7 *Eleutherodactylus coqui* uses different postures to regulate water loss. The chin-down posture with legs underneath the body minimizes water loss. Water loss is greatest during bouts of calling by males when the greatest amount of skin surface area is exposed. Adapted from Pough et al. (1983).

and potentially result in reduced calling performance, at least as measured by jumping experiments. The ability of these frogs to absorb water from damp surfaces partially offsets the osmoregulatory costs of calling activity, and the payoff for calling is an increase in reproductive success.

Osmoregulation—Maintaining Homeostasis

Osmoregulation, the control of water and salt balance, presents different challenges to organisms living in freshwater, salt water, and aerial or terrestrial environments (Fig. 6.1). Many structures and organs are involved in osmoregulation, including the skin, gills, digestive tract, kidneys, and bladder. In freshwater, an amphibian or reptile is hyperosmotic—the ionic concentration of the body is greater than that of the environment, and if not regulated, water moves in, cells swell and possibly burst, and ions become too dilute. Excessive hydration can be avoided in several ways. Permeability of the skin can be decreased or urinary output can be increased, although salts must be conserved. Marine species face the opposite challenge. They are hypoosmotic in relation to their environment—the ionic concentration of the body is less than the environment, and if unregulated, water moves out, causing dehydration and a concentration of salts in the body fluid. Dehydration can be circumvented by decreasing permeability of the skin and reducing the amount of water in urine, although nitrogenous waste must still be removed before reaching toxic levels. Terrestrial species are also at risk of dehydration, but from evaporation rather than osmotic loss of water. They counteract this problem physiologically in a manner similar to marine species.

Kidney Function

In a general way, kidneys of amphibians and reptiles have similar morphology and function in a similar manner (Fig. 6.8). Metabolic byproducts and water diffuse into the kidney tubules from the circulatory system via the glomeruli, where capillaries interdigitate with the kidney tubules. In the proximal tubules, glucose, amino acids, Na^+, Cl^-, and water are resorbed. Nitrogenous waste products and other ions are retained in the urine, and additional water and Na^+ are removed in the distal tubules. In amphibians, due to a high filtration rate, about one-half of the primary filtrate enters the bladder even though more than 99% of filtered ions have been resorbed. As a consequence, urine produced by most amphibians is dilute. Some striking exceptions include African reedfrogs (*Hyperolius*), which exhibit increased levels of urea in plasma during dry periods, and the frogs *Phyllomedusa* and *Chiromantis*, which are uricotelic (Shoemaker and Bickler, 1979). In reptiles, the filtration rate is lower than that of amphibians, and resorption of solutes and water is greater. Between 30 and 50% of water that enters the glomeruli of reptiles is resorbed in the proximal tubule alone. Urine generally empties into the large intestine in reptiles, but some have urinary bladders. In all cases, whether amphibian or reptile, the urine flows from the urinary ducts into the cloaca and then into the bladder or the large intestine. Additional absorption of Na^+ by active transport can occur in some freshwater reptiles from water in the bladder. Most reptiles produce relatively concentrated urine, which minimizes water loss. In some species, salt glands and other structures are involved in the control of Na+ excretion, typically in marine species to remove excess salts.

Kidney structure differs somewhat between amphibians and reptiles, partially as a result of different embryonic origins. The opisthonephros of amphibians develops from posterior extensions of the pronephric kidney, whereas the metanephros of reptiles develops from the posterior lumbar mass of nephrogenic tissue (Withers, 1992; Kardong, 1995). The opisthonephric kidneys of adult amphibians have two types of nephrons. In addition to fluids that are filtered from plasma in the glomeruli in the ventral nephrons, dorsally located nephrons collect fluid directly from the coelomic cavity. All filtration in reptiles occurs through glomeruli in the metanephric kidneys. Functionally, kidneys of amphibians and reptiles are similar (Fig. 6.8).

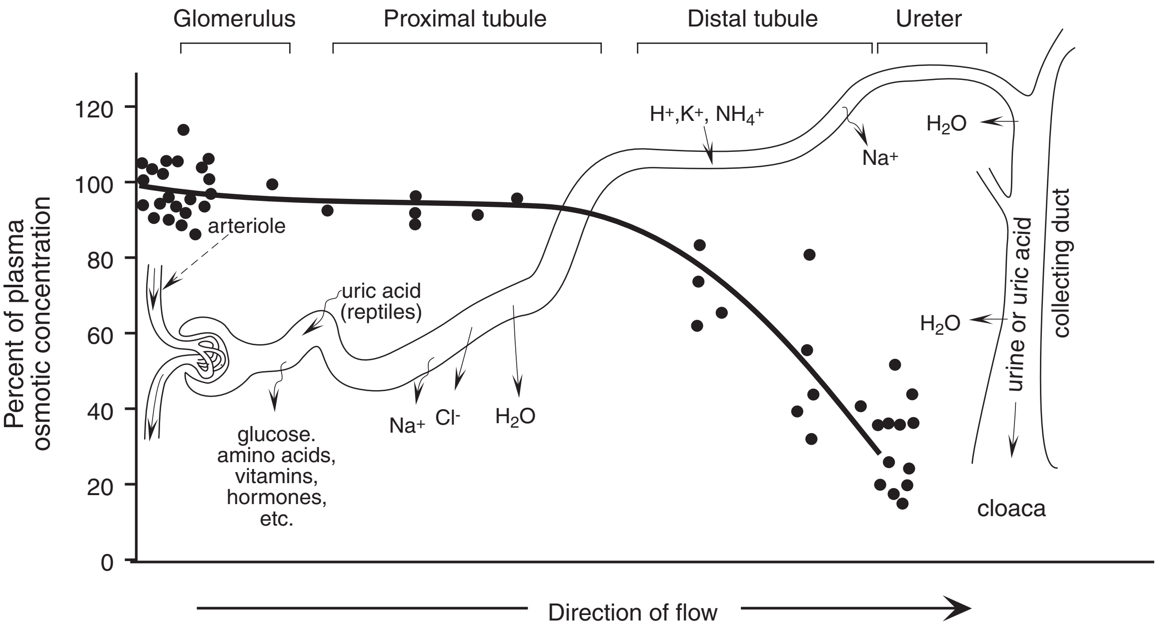


FIGURE 6.8 Diagrammatic representation of the functional kidney in amphibians and reptiles (see text for differences). Solid circles and the heavy line represent the reduction in osmotic concentration of urine for an amphibian; for a reptile, the line would be lower. Adapted in part from Withers (1992).

Aquatic and semiaquatic amphibians are capable of producing urine at high rates to offset the high water influx through their permeable skin. Very dilute urine is produced to conserve salts. When amphibians begin to dehydrate, urine production declines rapidly in order to conserve water. Glomerular filtration rate decreases within 30 minutes to 1 hour after a frog or toad begins to dehydrate. Toads may have cutaneous osmotic sensors that detect changes in extracellular fluid volume (Petriella et al., 1989).

The highly distensible amphibian bladder also functions as a water storage organ, in addition to osmoregulation. Terrestrial species of frogs and salamanders may hold as much as 20–50% of their body mass as bladder water, whereas aquatic species such as *Xenopus* have small bladders capable of holding only 1–5% of their mass (Bentley, 1966). One Australian desert frog, *Cyclorana platycephala*, can hold as much as 130% of its normal body mass in bladder water, and, not surprisingly, this species is called the "water-holding" frog (van Beurden, 1984). Many species of frogs are capable of reabsorbing their bladder water to maintain suitable levels of plasma solutes. Bladder water extends the survival time of amphibians in environments in which they are losing water.

Chuckwallas (*Sauromalus obesus*) in the Mojave Desert maintain relatively constant solute concentrations even though they live in environments in which water is highly seasonal and unpredictable (Nagy, 1972). When the vegetation that composes their diet is abundant, they obtain sufficient water from their plant food, and the excess water is excreted. When vegetation is dry, the lizards do not eat and remain inactive inside crevices where temperatures are relatively low. Their water loss rates are low in this situation. Although the plants that they eat are always hyperosmotic, primarily because of high K^+ concentrations, excretion of potassium urate by nasal salt glands removes electrolytes with little associated water loss. Effectively, these lizards separate electrolyte excretion from water excretion, thereby maintaining homeostasis.

Nitrogen Excretion

Digestion of food and catabolism of protein result in the production of wastes, including various nitrogen-containing products, and particularly ammonia, urea, and uric acid. Prolonged dehydration leads to accumulation of nitrogen waste, which causes death if not removed or diluted. Organisms that primarily excrete ammonia are called ammonotelic; those that excrete urea, ureotelic; and those that excrete uric acid, uricotelic. Among amphibians, reptiles, and other vertebrates, patterns of nitrogen excretion are generally related more to habitat than to phylogeny.

In general aquatic animals excrete ammonia. Ammonia is a small molecule that readily diffuses across skin and gills if sufficient water is available, but ammonia is inefficiently excreted by the kidneys. Ammonia is highly toxic, and animals cannot survive even moderate ammonia concentrations in their body fluids. For this reason during the evolution of terrestriality, selection favored the excretion of a less toxic form of nitrogen, such as urea or uric acid; the latter is the least toxic nitrogenous byproduct. For example, three species of *Rana* are obligatory ammonotelics, and individuals of these species die when deprived of water (Shoemaker and McClanahan, 1980). Other ranids are ureotelic and can tolerate moderate dehydration without dying. Totally aquatic amphibians, such as *Xenopus* and nearly all larvae, excrete ammonia. At metamorphosis, the larvae of most species switch from excreting ammonia to excreting urea (see below). Under normal conditions, *Xenopus* continues to excrete ammonia throughout its life, but it is physiologically adaptable. When its aquatic habitats dry, *Xenopus* estivates in the mud and physiologically shifts to urea excretion, thereby avoiding the toxic effects of ammonia accumulation.

Urea is soluble in water and has relatively low toxicity compared to ammonia. In many amphibians, urea is the primary excretory product. All terrestrial species produce urea. Certain liver enzymes that function in urea production are widespread in aquatic and terrestrial amphibians, suggesting that this method of excretion appeared early in the evolutionary history of tetrapods.

Uric acid has a low solubility and requires very little water for excretion. Most snakes and lizards excrete uric acid, which serves to conserve water in species living in arid areas. Uricotelism appears to have evolved independently in a few lineages of the waterproofed frogs. *Phyllomedusa sauvagei* and some species of *Chiromantis* produce urates, salts of uric acid, even when ample water is available. Ninety percent of the water filtered by the kidney is reabsorbed in *P. sauvagei.*

The saltwater crocodile *Crocodylus porosus* takes in substantial amounts of seawater during feeding and has no freshwater available. As a result, while they are in seawater, a net loss in body water occurs. Most sodium (55%) is excreted through lingual salt glands, but a considerable amount (42%) is excreted across the cephalic epithelium (Mazzoti and Dunson, 1989). Loss of water occurs primarily across the skin (55%) and epithelia of the head (36%).

Reptiles have little difficulty with osmoregulation in freshwater. Because of their relatively impermeable skin, water influx and solute efflux across the skin are relatively low. Aquatic species that take in significant amounts of water produce dilute urine and reabsorb solutes in the kidney, urinary bladder, and colon.

The Terrestrial Transition

Most amphibian larvae are aquatic and must undergo a transition to terrestrial life. Because larvae are hyperosmotic in relation to their aquatic environment and adults are hypoosmotic in relation to their terrestrial environment, the osmoregulatory challenges are reversed and require different behavioral, morphological, and physiological solutions (see Fig. 6.1). This change in lifestyle sets amphibians apart from all other vertebrates and reflects part of the transition from water to land that led to the diversification of terrestrial tetrapods.

With few exceptions, anuran larvae live in aquatic habitats; thus, behavioral adjustments to water gain or loss are not possible. Because excess water influx is a problem, amphibian larvae would be predicted not to take in water through the mouth. However, studies have shown that larvae ingest large quantities of water when feeding. Water turnover decreases during metamorphosis, but whether this change results from a decrease in ingestion of water during feeding is unknown.

At metamorphosis, the organs responsible for osmoregulation undergo extreme morphological and physiological changes. Larval skin has a simpler structure than adult skin, for example, and gills are replaced by lungs in many species. Whereas adults can regulate ion exchange across the skin by active transport of solutes, anuran larvae are incapable of this type of regulation, apparently because they lack the proper enzymes to carry out the reactions. Instead, active transport of solutes occurs in the gills of anuran larvae. Active transport of solutes does occur across the skin in salamander larvae in contrast to tadpoles.

Special Problems in Extremely Xeric and Marine Environments

No amphibian is truly marine. Nevertheless, 61 species of frogs and 13 species of salamanders are tolerant of hypersaline environments to some degree (Table 6.2). Three species of frogs (*Rana cancrivora*, *Bufo viridis*, and *Xenopus laevis*) live in habitats with unusually high salinity (Katz, 1989), and a few species of the salamander *Batrachoseps* live near salt water in tidal areas. *R. cancrivora* inhabits estuaries in Southeast Asia, where it feeds predominately on marine crabs and crustaceans. This frog, in addition to other brackish species, remains in osmotic balance with seawater by maintaining a high level of urea in the blood. To create these high levels, urea is retained and, in addition, urea synthesis is increased. The enzymes responsible for these reactions are found at higher levels in frogs that inhabit the most saline environments.

Seaturtles, sea snakes, diamondback terrapins (*Malaclemys*), and some species of *Crocodylus* are found in water of varying degrees of salinity. The ionic concentration of body fluids in these species is maintained at higher levels than in freshwater species. Much of the

TABLE 6.2 Amphibians Known to Live or Tolerate Brackish Water

Ambystomatidae
  Ambystoma velasci
Dicamptodentidae
  Dicamptodon ensatus
Plethodontidae
  Batrachoseps major
  Plethodon dunni
Salamandridae
  Taricha granulosa
  Triturus vulgaris
Sirenidae
  Siren lacertina
Bufonidae
  Bufo boreas
  Bufo viridis
Discoglossidae
  Bombina variegata
  Discoglossus sardus
Hylidae
  Acris gryllus
  Pseudacris regilla
Leptodactylidae
  Eleutherodactylus martinicensis
  Pleuroderma tucumana
Microhylidae
  Gastrophyrne carolinensis
Pelodytidae
  Pelodytes punctatus
Pelobatidae
  Pelobates cultripes
  Spea hammondii
Pipidae
  Xenopus laevis
Ranidae
  Rana cancrivora
  Rana clamitans
  Rana cyanophlyctis

Source: Adapted from Balinsky (1981).
Note: List includes only selected species.

TABLE 6.3 Occurrence of Salt Glands in Reptiles

Lineage	Salt secreting gland	Homologies
Turtles		
Cheloniids, dermochelyids, and *Malaclemys terrapin*	Lacrimal gland	Lacrimal salt gland of birds
Lizards		
Agamids, iguanids, lacertids, scincids, teiids, varanids, and xantusiids	Nasal gland	None
Snakes		
Hydrophiines, *Acrochordus granulatus*	Posterior sublingual gland	None
Cerberus rynchops	Premaxillary gland	None
Crocodylians		
Crocodylus porosus	Lingual glands	None

increase in solutes is due to higher levels of sodium, chloride, and urea. This response also typically occurs when freshwater species are experimentally placed in seawater.

Reptiles in saline habitats tend to accumulate solutes as the salinity level increases. Numerous species have independently evolved salt glands that aid in the removal of salt (Table 6.3). Other species survive in salt water because of behavioral adjustments. The mud turtle *Kinosternon baurii* inhabits freshwater sites that are often flooded by seawater, but when salinities reach 50% of seawater, the turtle leaves water and remains on land (Dunson, 1979). One important key to the survival of reptiles in marine environments is that they do not drink seawater. Experiments with freshwater and estuarine species of *Nerodia* revealed that drinking is triggered in freshwater species experimentally placed in seawater, presumably because of dehydration and sodium influx. These snakes continue to drink seawater, which leads to their eventual death. In contrast, estuarine species in the same genus are not triggered to drink seawater, presumably because their skin is not permeable to seawater and they do not become dehydrated (Dunson, 1978, 1980).

Anhomeostasis

Some reptiles living in extreme environments can withstand extreme fluctuations in body water and solute concentrations. Desert tortoises (*Gopherus agassizii*) inhabit a range of environments in deserts of southwestern North America. By storing wastes in their large urinary bladder and reabsorbing water, they minimize water loss during droughts. Nevertheless, during extended droughts, they can lose as much as 40% of their initial body mass, and the mean volume of total body water can decrease to less than 60% of body mass (Peterson, 1996). Rather than maintaining homeostasis in the normal sense, concentrations of solutes in the body increase with increasing dehydration (anhomeostasis), often to the highest levels known in vertebrates, but the most dramatic increase occurs in plasma urea concentrations. When rainfall occurs, increases in solute concentrations are reversed when tortoises drink water from depressions that serve as water basins (Fig. 6.9). Following the ingestion of water, they void the bladder contents, and plasma levels of solutes and urea return to levels normally seen in reptiles in general. They then store large amounts of water in the bladder, and as conditions dry out, the dilute urine remains hypoosmotic to plasma for long periods, during which homeostasis is maintained. When the urine

FIGURE 6.9 The desert tortoise *Gopherus agassizii* either drinks from natural depressions or constructs shallow water catchment basins in the desert floor following periodic rainstorms (Medica et al., 1980). Photograph by P. A. Medica (not included in published paper).

reaches an isosmotic state, solute concentrations in both plasma and urine increase (Fig. 6.10).

RESPIRATORY GAS EXCHANGE

Respiration is the process by which animals acquire oxygen. Oxygen is essential for cellular metabolism, during which food is converted to energy by oxidation. Byproducts of this process are carbon dioxide and water, which must be eliminated. External respiration refers to the transfer of oxygen from the environment across the surface of the respiratory organ to the blood and to the reverse flow of carbon dioxide from the blood to the environment. Internal respiration refers to gas exchange between the blood and the cells of the body tissues. At the cellular level, this transfer of oxygen and carbon dioxide occurs by passive diffusion, and, like water, gases flow from areas of high concentration to areas of low concentration.

Differences in the physical properties of water and air determine the available oxygen supply for all animals, including amphibians and reptiles. Water is denser than air and holds much less oxygen, and the solubility of both oxygen and carbon dioxide decreases as temperature increases. Both water and air contain very little carbon dioxide; thus, the diffusion gradient for carbon dioxide out of an animal is high. The high viscosity of water relative to air encourages concentration-gradient stagnation at the boundary layer of the respiratory surfaces. This problem is overcome by mixing the boundary

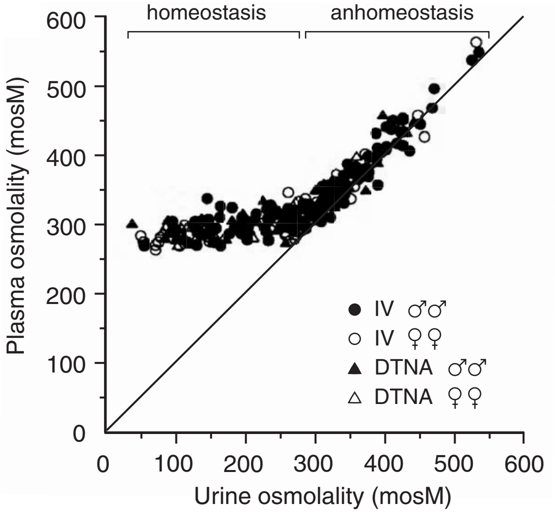


FIGURE 6.10 The concentration of plasma solutes remains stable (homeostasis) in desert tortoises as long as urine stored in the bladder is hypoosmotic to plasma. When solute concentration of the plasma reaches that of the urine (isosmotic), solute concentrations increase in both (anhomeostasis). Data from two populations are included (IV, Ivanpah Valley; DTNA, Desert Tortoise Natural Area, both in the Mojave Desert). Adapted from Peterson (1996).

layer through increased ventilation, stirring and moving the boundary layer by ciliary action, or similar mechanisms that prevent the stagnation effect. Ventilation that involves moving water is energetically expensive because the density of water provides resistance to movement and water generally has a low oxygen concentration. In air, the flow of oxygen into and out of the lungs is less energetically expensive because air has a high concentration (21%) of oxygen, and the low density of air offers little resistance to ventilation movements. The major disadvantage of air breathing is the loss of water from the respiratory surfaces, which must be kept moist to function properly. Aside from the skin of amphibians, gas exchange surfaces are not exposed to air; instead, they are found in protected cavities inside the body, where they can be kept moist, and yet water loss can be minimized.

Respiratory structures in amphibians include the skin, gills, lungs, and the buccopharyngeal cavity. No reptiles have gills, and cutaneous respiration is rare because of their impermeable skin. A few species of reptiles (e.g., *Apalone*) respire with the cloaca in addition to using the lungs. Gills are used only for aqueous respiration, lungs are used primarily for aerial respiration with some exceptions, and the skin and buccopharynx are used for aquatic and aerial respiration in different species. Most amphibians and many reptiles rely on more than one respiratory surface, using them simultaneously in some situations and alternately in others. Although the respiratory surfaces are derived from different anatomical systems, they share several traits because efficient gas exchange requires a steep concentration gradient and thin membranes between the two exchange media. Thus, respiratory surfaces are heavily vascularized and have one or only a few cell layers between the capillaries and the exchange medium. A variety of mechanisms are used to increase movement of water or air across the exchange surfaces to prevent gradient stagnation at the interface.

Respiratory Surfaces

Gills

Gills are evaginated respiratory surfaces used for breathing in water. Gills are present in all amphibian larvae and in some aquatic salamanders. They are typically highly branched structures. The numerous branches increase the available surface area for gas exchange, but owing to this branchiate structure and the absence of skeletal support, gills are strictly aquatic respiratory organs. Water is necessary to support the gills and to spread open all surfaces for gas exchange. During the early developmental stages of anuran larvae, transient, external gills develop but soon atrophy. Internal gills remain and are enclosed by a fold of skin called the operculum (Fig. 6.11). In egg-brooding hylids that retain embryos in cavities or pouches on their backs (i.e., *Gastrotheca, Flectonotus*), large, thin, bell-shaped gills encase all or part of the embryo, providing a surface for gas exchange (Fig. 6.12).

Larval salamanders have gills that vary in size and structure depending on the nature of the aquatic environment (Fig. 6.13). Salamanders (larvae or adults)

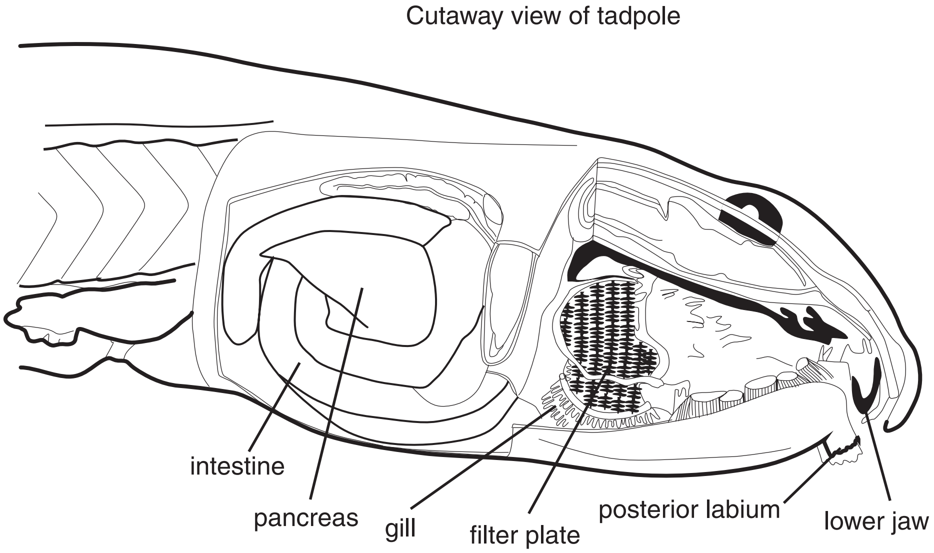


FIGURE 6.11 Longitudinal section through a tadpole, showing the placement of the internal gills beneath the operculum. Adapted from Viertel and Richter (1999).

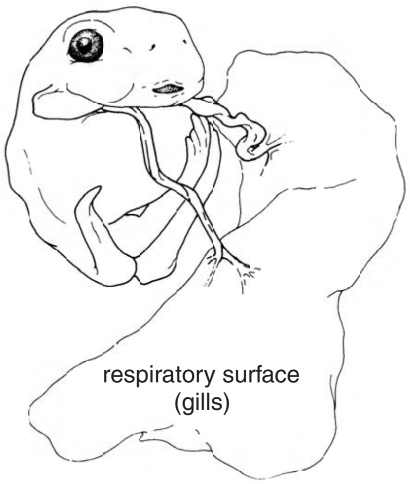


FIGURE 6.12 Direct-developing young of the hylid frog *Gastrotheca cornuta*. Offspring develop in the dorsal pouch of the female, and oxygen diffuses from the female across the thin, bell-shaped gills of the froglet. Adapted from Duellman and Trueb (1986).

that live in ponds have large, feathery gills, whereas those that live in streams or other habitats with moving water have smaller, less filamentous gills. Nonmoving water has a lower amount of dissolved oxygen, and larger gills with an increased surface area permit salamanders to survive in these habitats. Salamanders that retain gills as adults include proteids, such as *Necturus*, cryptobranchids, and paedomorphic plethodontids and ambystomatids. Gills are extensively vascularized and account for up to 60% of the oxygen intake in *Necturus* (Guimond and Hutchison, 1972, 1976).

In still water, a boundary layer forms around the gills and must be disrupted so that oxygenated water will be available to the animal. Some salamanders gently move the gills back and forth to raise the diffusive conductance for oxygen. The internal gills in anuran larvae are perfused by a buccal-pump mechanism, during which water enters the mouth, passes over the gills, and exits through a single spiracle or a pair spiracles. The relative size of gills and other respiratory surfaces varies in response to the availability of oxygen in aquatic environments.

Buccal Cavity and Pharynx

The buccopharyngeal membranes serve as a respiratory surface in a wide variety of amphibians and reptiles. In this type of respiration, the membranes in the mouth and throat are permeable to oxygen and carbon dioxide. In some species that remain submerged in water for long periods, gas exchange by this route can be significant. Respiration across the buccopharyngeal cavity provides a small percentage of gas exchange in lungless plethodontid salamanders (Czopek, 1961; Foxon, 1964). Some turtles (*Apalone*, *Sternotherus*) can extract sufficient oxygen by buccopharyngeal and cutaneous exchange for

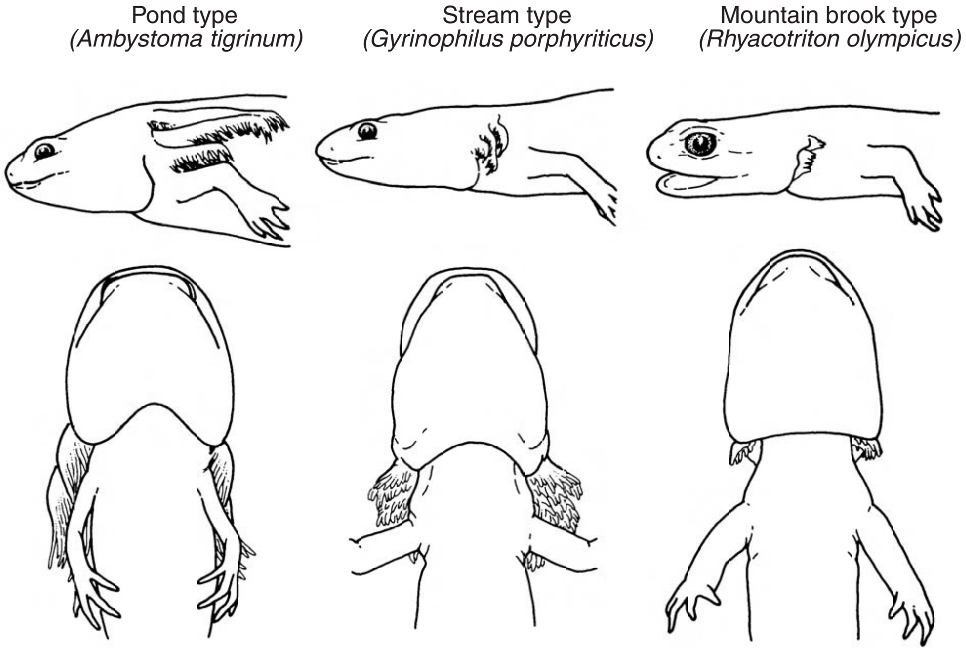


FIGURE 6.13 Adaptive types of salamander larvae, or in some cases, paedotypic adults. Adapted from Duellman and Trueb (1986).

survival during long-term submergences, such as during hibernation. Because of low temperatures during hibernation, oxygen requirements for metabolism are reduced.

Skin

The highly permeable skin of amphibians is a major site of gas exchange in terrestrial, semiaquatic, and aquatic species. Cutaneous respiration accounts for some gas exchange in certain species of reptiles (Fig. 6.14). Exchange of respiratory gases occurs by diffusion and is facilitated by a relatively thin layer of keratin and a rich supply of capillaries in the skin. Exchange of gases across the skin in water is limited by the same physical factors as exchange across other respiratory surfaces.

Ventilation of skin, as with gills and other respiratory surfaces, is required to disrupt the boundary layer that can develop. *Xenopus* has been observed to remain submerged longer and to move less frequently in moving compared to still water (West and Van Vliet, 1983). Most plethodontid salamanders have neither lungs nor gills and are largely terrestrial. The majority of their gas exchange occurs through the skin. In these salamanders, in contrast to others, there is no partial separation of the oxygenated and venous blood in the heart. Many species of this diverse group, because of their mode of respiration, are limited to cool, oxygenated habitats and to

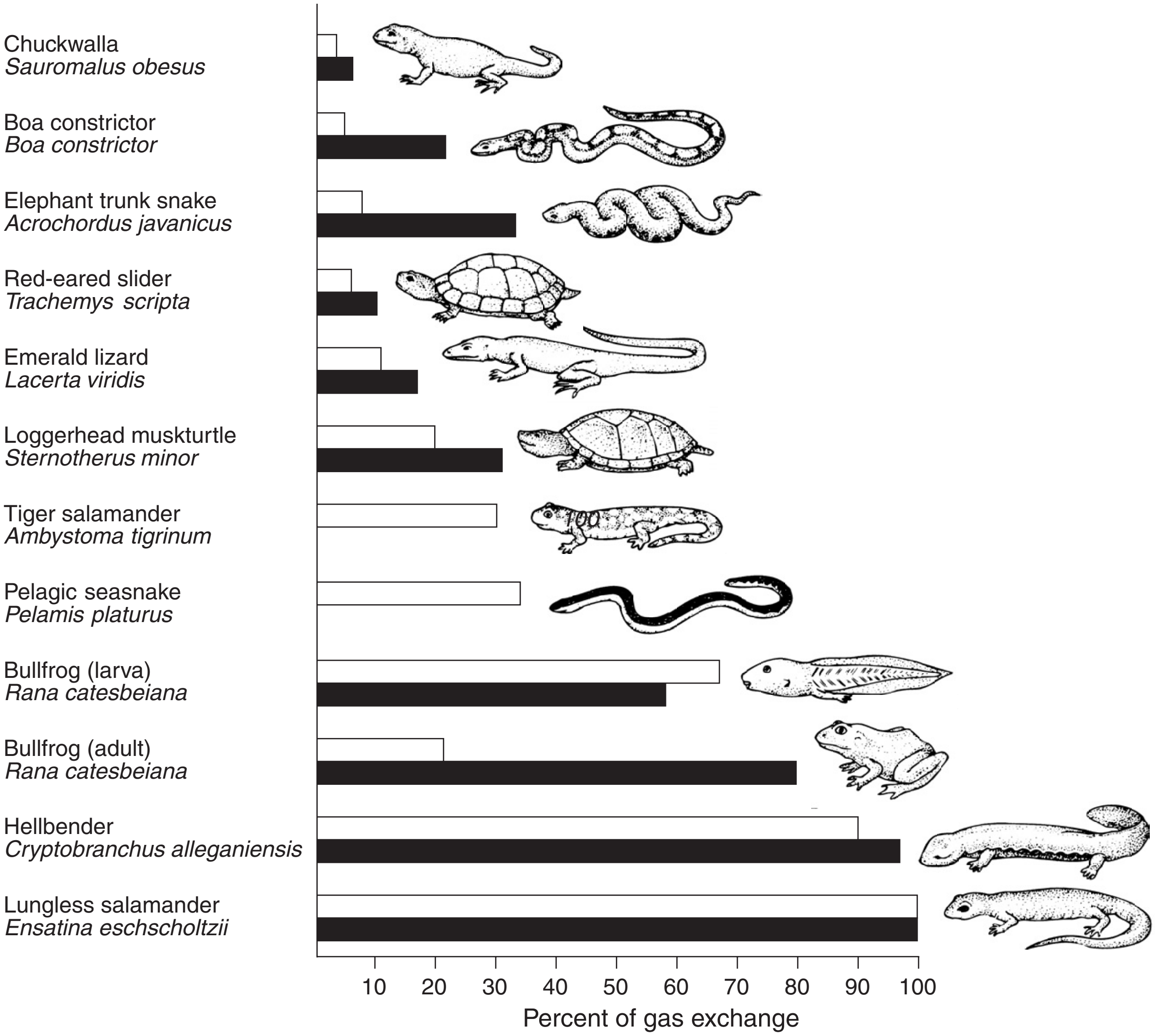


FIGURE 6.14 Cutaneous exchange of gases in amphibians and reptiles. Open bars indicate uptake of oxygen; shaded bars indicate excretion of carbon dioxide. Values represent the percent of total gas exchange occurring through the skin. Adapted from Kardong (1995).

nonvigorous activity. Their oxygen uptake is only one-third that of frogs under similar conditions (Full, 1986). Plethodontids that inhabit tropical habitats where temperatures can be high, such as *Bolitoglossa* in tropical rain forests, are active primarily on rainy nights. Waterproofed frogs sacrifice their ability to undergo cutaneous respiration in exchange for the skin resistance to water loss.

Some amphibians increase their capacity for cutaneous respiration by having capillaries that penetrate into the epidermal layer of skin. This modification is carried to an extreme in *Trichobatrachus robustus*, the "hairy frog," which has dense epidermal projections on its thighs and flanks. These projections increase the surface area for gaseous exchange. Hellbenders, *Cryptobranchus alleganiensis*, live in mountain streams in the eastern United States. These large salamanders have extensive highly vascularized folds of skin on the sides of the body, through which 90% of oxygen uptake and 97% of carbon dioxide release occur (Spotila et al., 1992). Lungs are used for buoyancy rather than gas exchange. The Titicaca frog, *Telmatobius culeus*, which inhabits deep waters in the high-elevation Lake Titicaca in the southern Andes, has reduced lungs and does not surface from the depths of the lake to breathe. The highly vascularized skin hangs in great folds from its body and legs (Fig. 6.15). If the oxygen content is very low, the frog ventilates its skin by bobbing (Hutchison et al., 1976). Other genera of frogs, salamanders, and caecilians (typhlonectids) have epidermal capillaries that facilitate gas exchange.

Gas exchange in tadpoles occurs across the skin to some degree in all species. Tadpole skin is highly permeable, similar to that of adults. Gas exchange across the skin is prevalent in bufonids and some torrent-dwelling species that do not develop lungs until metamorphosis (Ultsch et al., 1999). Microhylids, some leptodactylids, and some pipids have reduced gills, thus increasing their reliance on cutaneous respiration.

Recent studies show that some reptiles, once thought not to exchange gases through the skin, actually may use cutaneous respiration for as much as 20–30% of total gas exchange. In some aquatic species, such as *Acrochordus* and *Sternotherus*, gas exchange across the skin is especially significant for carbon dioxide (Fig. 6.14). Even in terrestrial taxa such as *Lacerta* and *Boa*, measurable amounts of gas exchange occur cutaneously. A sea snake, *Pelamis platurus*, frequently dives and remains submerged. During these dives, cutaneous oxygen uptake equals 33% of the total, and 94% of the carbon dioxide loss is through the skin. Exchange does not

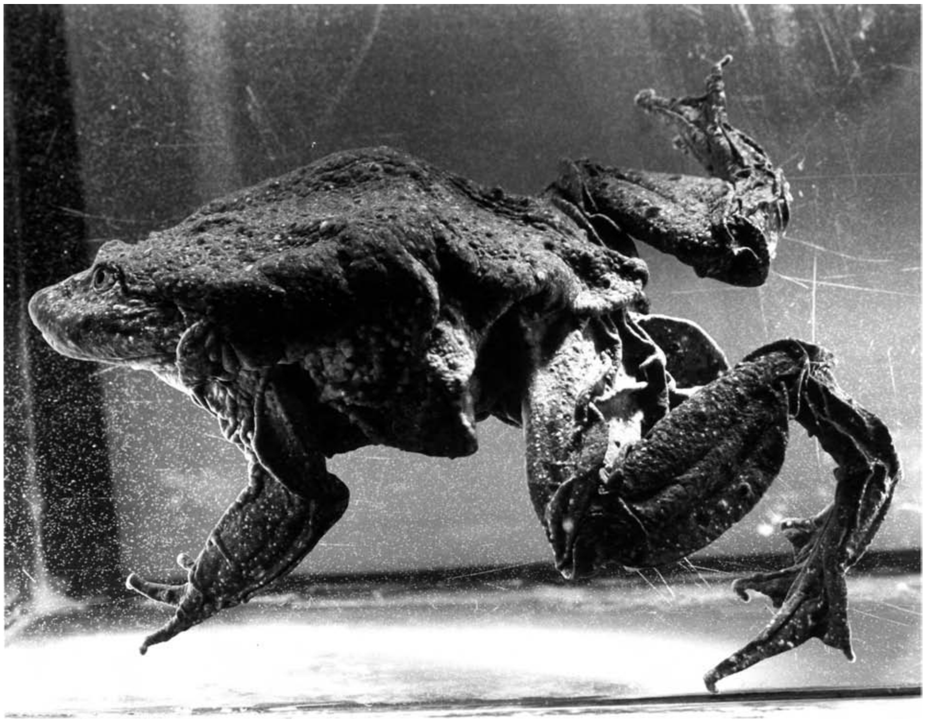


FIGURE 6.15 The Titicaca frog, *Telmatobius culeus*, lives at great depths in Lake Titicaca and does not surface to breathe. The large folds of skin greatly increase the surface area of the skin, facilitating cutaneous respiration. Photograph by V. H. Hutchison.

occur through scales but rather through the skin at the interscalar spaces.

Lungs

Lungs are the principal respiratory surface in many terrestrial amphibians and all reptiles. All extant amphibians with lungs utilize a positive-pressure buccal pump mechanism (Fig. 6.16); in contrast, reptiles (and mammals) use thoracic aspiration. In amphibians, the floor of the mouth is alternately raised and depressed. When depressed, the nostrils are open and air is taken into the buccal cavity, where it is temporarily stored. When the floor of the mouth is elevated, the nostrils close. Buccal pumping is a continual process and is a separate function from lung ventilation. At periodic intervals, the glottis is opened and deoxygenated air in the lungs is quickly expelled. The air stream passes rapidly over the oxygenated air in the buccal cavity, and the two air masses mix very little if any. The oxygenated air is then forced into the lungs.

Thoracic aspiration is used to ventilate the lungs in reptiles. The walls of the lungs can change shape, forcing air in or out of them. In lizards, intercostal muscles between the ribs contract and force the ribs forward and outward (Kardong, 1995). In turn, this movement enlarges the pleural cavity around the lungs, causing them to enlarge and fill with air. Other intercostal muscles then contract, bringing the ribs backward and inward, decreasing the size of the pleural cavity and forcing air out of the lungs.

The left lung of advanced snakes is greatly reduced. The faveoli, compartments that open into the central portion of the lung and contain the actual respiratory surfaces, are abundant in the anterior portion of the lung, but gradually decrease and are absent in the posterior portion. Respiration, therefore, occurs only in the anterior part of the lung. Ribs and their associated intercostal muscles extend the entire length of the snake's body and control inflation and deflation of the lungs as in lizards; however, different regions of the body can move independently. The posterior part of the lung serves in a special capacity when the anterior part of the body cannot be used for ventilation. Because of the long, narrow body form of snakes and because they engulf prey much larger than their body, the ribs in the forward

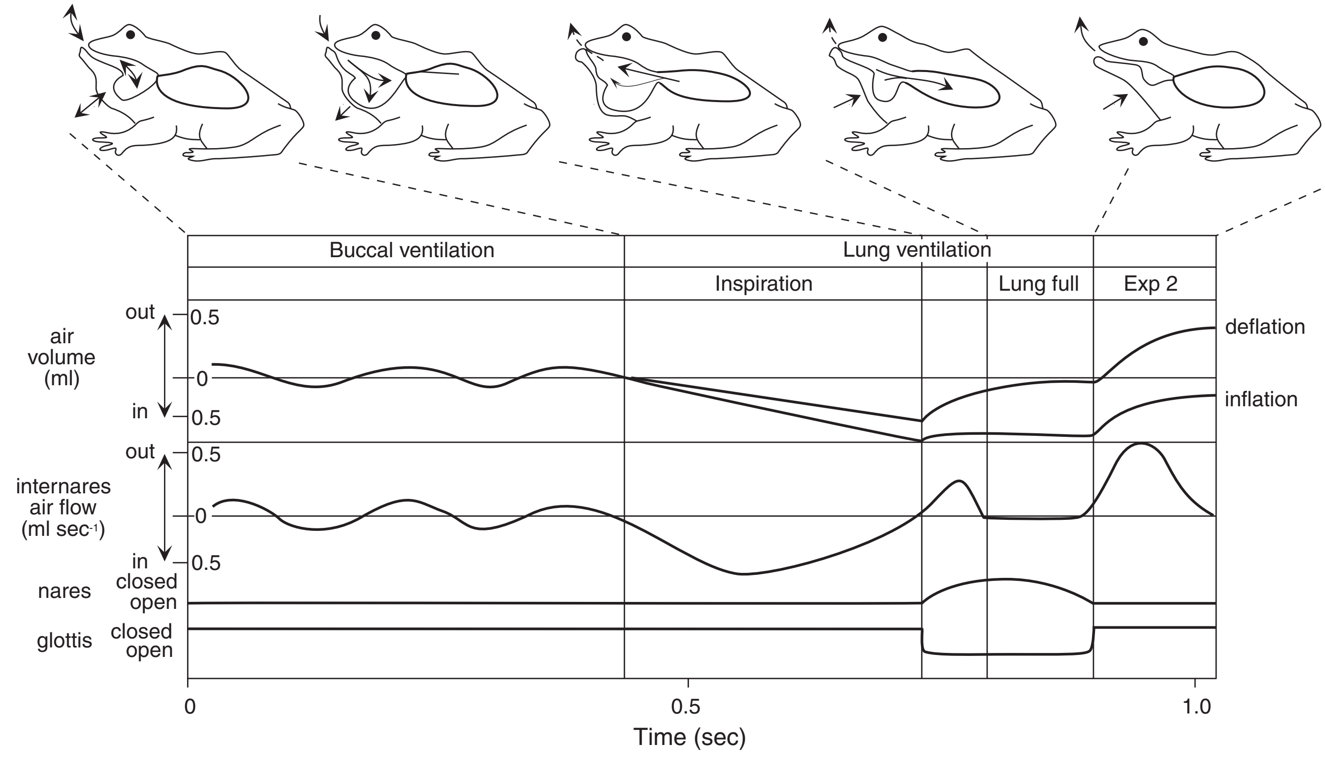


FIGURE 6.16 Respiration in a frog. Oxygenated air is taken into the buccal cavity through the nares. Deoxygenated air in the lungs is rapidly expelled and does not mix with the air in the buccal cavity. Elevation of the buccal cavity (the buccal pump) forces the new air into the lungs. The glottis is closed to hold the oxygenated air in the lungs, and the remaining air in the buccal cavity is expired by further elevation of the buccal cavity. Adapted from Withers (1992).

part of the body cannot move as prey is being swallowed. Instead, the posterior ribs move in and out, causing the sac-like posterior part of the lung to inflate and deflate and function as a bellows. Cartilaginous rings hold the trachea open, and air is thus forced in and out of the respiratory part of the lung by the action of the posterior lung.

Crocodiles and caimans use the liver to press against the lungs and force air in and out. Certain muscles cause the liver, which is located posterior to the lungs, to move. Turtles and tortoises have a special problem in that their lungs are contained inside immobile shells. The lungs and other viscera are located in a single cavity, so pressure on any part of the cavity will affect the lungs. In many species, breathing is facilitated by moving the legs in and out of the shell, which decreases or increases the body cavity, causing the lungs to fill and empty.

Some anurans have aquatic larvae that develop lungs and breathe air as tadpoles. This mechanism may account for a significant amount of oxygen uptake, but it is not the only source in any species. As much as 30% of oxygen uptake may be via the lungs in some species. Tadpoles do not appear to be dependent on air breathing. Development and survivorship is not affected in bullfrog tadpoles if they are forcibly submerged (Crowder et al., 1998).

Lungs also play a role in buoyancy regulation in tadpoles and adults of some aquatic species (Tu et al., 1999). Tadpoles occupy different positions in the water column; some are benthic, spending most of their time grazing on bottom substrate, whereas others float and feed in midwater or hang at the water surface. Specific gravity is controlled by the amount of air in the lungs; tadpoles that are prevented from gulping air sink to the bottom of experimental chambers and are unable to maintain their position in the water column.

RESPIRATION AND METABOLISM

Gas exchange is a direct function of metabolism. Metabolic activities, whether anabolic or catabolic, require the energy derived from oxidation, so oxygen is required even in a resting or hibernating state. Metabolism can occur in the temporary absence of oxygen, but an oxygen debt develops that must be repaid. Metabolic rate is measured by oxygen consumption or carbon dioxide production; metabolism and gas exchange are inseparable.

Body size and temperature influence gas exchange. As mass increases, oxygen consumption and carbon dioxide production increase, although the consumption rate declines with increasing mass. This mass-specific relationship reflects the general physical principal that mass increases as a cube of length whereas surface area increases as a square of length. The respiratory surface area may be unable to meet metabolic needs without modifications. Modifications include increasing surface by additional folds (skin) or partitions (lungs), increasing vascularization and/or placing blood vessels closer to surface, and increasing gas transport capacity of blood and increasing flow rate. Such changes may occur ontogenetically but they can also be seen by comparing taxa of different sizes.

Aerobic metabolism is strongly temperature dependent, and oxygen consumption increases two to three times for every 10°C increase in body temperature. Metabolic activity is similar in amphibians and reptiles, but different groups have different basal metabolic rates. For example, anurans typically have higher and more temperature-sensitive rates than salamanders. The temperature—metabolism relationship is linear in the majority of ectotherms, but a few snakes and lizards have decoupled metabolism from temperature over narrow temperature ranges, usually within their preferred activity temperatures, and metabolism remains constant for a 3–5°C range. Gas exchange and metabolism are influenced in varying amounts by a host of other factors. Some species show daily and/or seasonal fluctuations of the basal rate, indicating an endogenous rhythm. Metabolism in temperate species of amphibians can be acclimated and adjusted to seasonal temperature changes. Health and physiological state can modify basal metabolic rates. In alligators, for example, metabolic rate is two times higher in an animal that has fasted 1 day compared to one that has fasted 3 to 4 days.

Aerobic and Anaerobic Metabolism

An animal's normal activities are fueled by energy from aerobic metabolism, a process also called cellular respiration, that requires oxygen. Cellular respiration, the chemical transformation of food substrate in biochemical pathways, should not be confused with respiration in the sense of exchange of gases across membranes. Although aerobic metabolism generates most of the energy used by an organism, energy can also be obtained by anaerobic metabolism when oxygen is not available. Anaerobiosis is a vital process for animals because it allows rapid conversion of muscle glycogen to glucose, thus releasing energy quickly for a rapid burst of activity, such as escaping from a predator, or for surviving an anoxic event, such as prolonged submergence under water by an animal that normally breathes air. Although vital for survival, anaerobiosis is energetically costly, and prolonged use of anaerobiosis is debilitating. However, some activities, such as movement of lizard tails after autotomy, are sustained anaerobically and the oxygen debt is not repaid (see Chapter 11). During burst activity, anaerobiosis provides energy at 5 to 10 times the aerobic level, but the process rapidly depletes energy stores. Also, lactic acid accumulates in the muscle within a few minutes, causing the animal to become visibly fatigued. Recovery may require hours or even days, although the oxygen debt and lactic acid removal can proceed rapidly if anaerobiosis is not excessive. Anaerobic metabolism is highly inefficient, requiring as much as 10 times the food input for an equivalent amount of aerobic work, and total nutrient and energy replacement requires much longer. Anaerobiosis is temperature independent within much of a species' temperature activity range, thus permitting an escape response equally as rapid at a low temperature as at a high one. We examine whole-organism energetics in the next chapter.

ADDITIONAL READING

Duellman, W. E., and Trueb, L. (1986). "Biology of Amphibia." McGraw-Hill, New York.

Dunson, W. A. (1979). Control mechanisms in reptiles. *In* "Mechanisms of Osmoregulation in Animals: Regulation of Cell Volume" (R. Gilles, Ed.), pp. 273–322. Wiley Interscience, New York.

Minnich, J. E. (1982). The use of water. *In* "Biology of the Reptilia: Physiology" (C. Gans and F. H. Pough, Eds.), pp. 325–395. Academic Press, London.

Shoemaker, V. H. (1992). Exchange of water, ions, and respiratory gases in terrestrial amphibians. *In* "Environmental Physiology of the Amphibians" (M. E. Feder and W. W. Burggren, Eds.), pp. 125–150. University of Chicago Press, Chicago.

Shoemaker, V. H., and Nagy, K. A. (1977). Osmoregulation in amphibians and reptiles. *Ann. Rev. Physiol.* **39:** 449–471.

Spotila, J. R., O'Connor, M. P., and G. S. Bakken. (1992). Biophysics of heat and mass transfer. *In* "Environmental Physiology of the Amphibians" (M. E. Feder and W. W. Burggren, Eds.), pp. 59–80. University of Chicago Press, Chicago.

Ultsch, G. R., Bradford, D. F., and Freda, J. (1999). Physiology: Coping with the environment. *In* "Tadpoles: The Biology of Anuran Larvae" (R. W. McDiarmid and R. Altig, Eds.), pp. 189–214. University of Chicago Press, Chicago.

REFERENCES

Water and Salt Balance: Gaining and Losing Water: Adolph, 1932; Benabib and Congdon, 1992; Bentley and Blumer, 1962; Christian and Parry, 1997; Christian et al., 1996; Congdon et al., 1982; Czopek, 1965; Dunson, 1970; Etheridge, 1990; Geise and Linsenmair, 1986; Hoff and Hillyard, 1991; Lasiewski and Bartholomew, 1969; Lopez and Brodie, 1977; Louw and Holm, 1972; McClanahan and Baldwin, 1969; McClanahan et. al, 1976, 1978, 1983; Minnich, 1979; Norris and Dawson, 1964; Pough et al., 1983; Reno et al., 1972; Schmuck and Linsemair, 1988; Schwenk and Greene, 1987; Sherbrooke, 1990; Shoemaker, 1992; Shoemaker and Nagy, 1977; Withers and Richards, 1995; Withers et al., 1982.

Osmoregulation-Maintaining Homeostasis: Kidney Function: Bentley, 1966; Kardong, 1995; Nagy, 1972; Petriella et al., 1989; Shoemaker and Bickler, 1979; van Beurden, 1984; Withers, 1992.

Nitrogen Excretion: Mazzoti and Dunson, 1989; Shoemaker and McClanahan, 1980.

The Terrestrial Transition. Special Problems in Extremely Xeric and Marine Environments: Dunson, 1978, 1979, 1980; Katz, 1989.

Anhomeostasis: Peterson, 1996.

Respiratory Gas Exchange: Respiratory Surfaces: Crowder et al., 1998; Czopek, 1961; Foxon, 1964; Full, 1986; Guimond and Hutchison, 1972, 1976; Hutchison et al., 1976; Kardong, 1995; Spotila et al., 1992; Tu et al., 1999; Ultsch et al., 1999; West and Van Vliet, 1983.

Chapter

7

Thermoregulation, Performance, and Energetics

Globally, temperature appears as the master limiting factor in the distributional and diversity patterns of amphibians and reptiles. No amphibian or reptile can survive in the frigid environment of Antarctica and only a few occur marginally within the limits of the Arctic. Their greatest diversity lies within the tropics and warm temperate areas. Even at a regional scale or, smaller yet, in a single habitat, the spatial occurrence and temporal activity pattern of each amphibian or reptilian species show the importance of temperature on microhabitat selection and use. Because they are ectothermic and rely on environmental sources for heat gain, their options for activity are more limited than those for endothermic tetrapods, which maintain elevated body temperature from metabolic heat. This heat arises from cellular or mitochondrial metabolism. All amphibians and reptiles produce metabolic heat but at a level far below mammals and birds, and few have the necessary insulation to prevent its rapid loss. Nonetheless, many reptiles and some amphibians regulate their body temperatures within relatively narrow ranges by taking advantage of the sun and warm surfaces in the environment for heat gain, and shade, retreats, water, and cool surfaces for heat loss (Cowles and Bogert, 1944; Bartholomew, 1982).

The sun is the ultimate heat source for all amphibians and reptiles, but many gain heat indirectly by conduction and convection. Amphibians in general operate at lower body temperatures than reptiles, are more often nocturnal, and may limit activity to periods when humidity is high or rainfall occurs because they have permeable skin and experience water loss at high temperatures or low humidities. The highly impermeable integument of reptiles permits direct exposure to sunlight without excessive water loss. Basking is the most observable heat-gain behavior in reptiles (Fig. 7.1), even though most amphibians and many reptiles gain heat indirectly from surfaces they come in contact with. For amphibian and reptile species living in arid habitats or open tropical habitats, environmental temperatures may be too high during much of the day for sustained activity. As a result, activity is shifted to cooler microhabitats or cooler times of day. Patches in the environment or physical structures serve as heat sinks for such species. Exactly how an individual species responds to the thermal complexity

FIGURE 7.1 Like many lizards, *Sceloporus poinsetti* basks on boulders in direct sunlight to gain heat. Photograph by L. J. Vitt.

of its environment is influenced by a diversity of abiotic and biotic factors, some of which are extremely difficult to measure directly. A phylogenetic component to thermoregulation is just beginning to be explored in detail (e.g., Garland, 1994; Bauwens et al., 1995).

All physiological processes in ectotherms are temperature dependent in one way or another (Bennett, 1980; Bartholomew, 1982; Dawson, 1975; Rome et al., 1992). The most obvious among these for anyone who has observed or maintained amphibians is water balance; as temperature increases, rates of water loss increase. For reptiles, the most apparent process affected by temperature is behavior; a cold reptile is not as active as a warm one. Of course, the ability to perform reflects the effect of temperature on a multitude of physiological processes. Behavior of amphibians is also strongly influenced by temperature. The differences in response to temperature and moisture between amphibians and reptiles is nicely illustrated by comparing behavioral and thermal responses to the daily progression of environmental temperatures at a high-elevation site in Peru by an amphibian and a reptile (Fig. 7.2). Both the lizard *Liolaemus multiformis* and the toad *Bufo spinulosus* emerge in morning and bask in sun to gain heat (Pearson and Bradford, 1976). The lizard basks and feeds at a body temperature of about 30°C until rain occurs. The lizard then retreats for the remainder of the day. The toad ceases activity and enters a retreat at midmorning when its body temperature exceeds 20°C. When its body temperature falls to about 12°C, it emerges again to bask and gain heat. Once warm, it enters the retreat again. When rain occurs, the toad emerges and remains active the remainder of the day at a relatively low body temperature (±12°C.).

Rates of oxygen consumption and consequently metabolic processes are temperature dependent; hence, all life processes including development, growth, and reproduction are temperature dependent. Most aspects of behavior and an individual's resistance and reaction to disease vary with temperature as well. The challenge for an individual amphibian or reptile is to center its activity within a range of temperatures that optimizes behavioral and physiological function while concurrently minimizing the risk of mortality (Huey and Slatkin, 1976). In general, all of these processes are components of performance, and how an individual performs on an instantaneous, daily, and seasonal basis determines its survival and, consequently, its fitness, that is, the number of offspring contributed to the next generation.

Because the study of thermoregulation in ectothermic vertebrates has received so much attention during the past 50 years, a complex and often controversial terminology has developed (e.g., Cowles and Bogert, 1944; Bartholomew, 1982; Hutchison and Dupré, 1992). We restrict our discussion to terms that are currently widely accepted (Table 7.1). Under conditions of normal activity, amphibians and reptiles cease activity when they cannot maintain body temperatures within a specific range. The activity range is bounded by the voluntary minimum and voluntary maximum temperatures

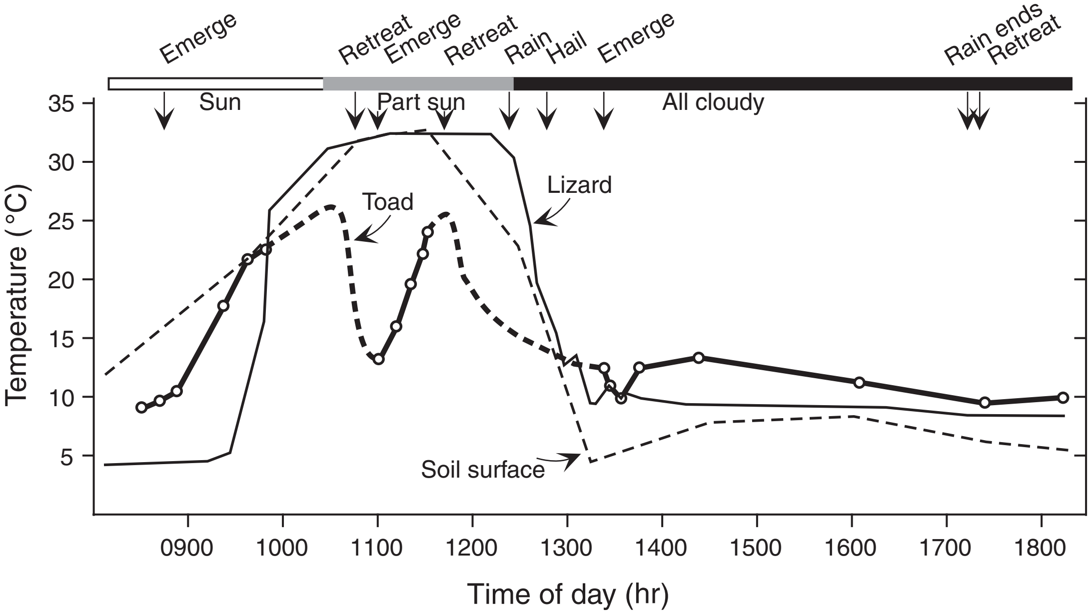


FIGURE 7.2 Lizards and frogs occurring at high elevations in Peru maintain different body temperatures and behave differently in response to temperature at the same locality. The lizard *Liolaemus multiformis* maintains a relatively high and constant body temperature throughout the day by basking. The toad *Bufo spinulosus* reaches about 23°C in the morning by basking in sun, and then retreats under a boulder at about 1050 hr. By repeated emergences and retreats, the toad maintains body temperatures below surface soil temperatures during midday. Adapted from Pearson and Bradford (1976).

(Fig. 7.3). If body temperature is allowed to rise or fall outside of these bounds, the possibility exists that the critical thermal maximum or critical thermal minimum will be reached. At these temperatures, the individual cannot escape conditions if they worsen and will ultimately reach the lethal maximum or minimum and die.

All animals have a set point temperature or a set point temperature range regulated by the hypothalamus, a region of the brain that controls temperature regulation. The set point temperature is essentially the thermostat setting that signals when an animal should initiate body temperature regulation. For mammals and birds (endotherms), the response is primarily physiological and involves the initiation or curtailment of metabolic heat production. In ectotherms, the response is usually behavioral and, to a lesser degree, physiological. As an ectotherm's body temperature shifts away from the set point temperature, the animal moves, changes orientation, or changes posture to effect heat gain or loss. In amphibians, water loss reduces heat gain via evaporative cooling. Evaporative cooling is an effective temperature control mechanism only if the amphibian has ready access to water in order to avoid desiccation stress. When ectotherms are brought into the laboratory and placed in thermal gradients, they tend to select a rather narrow range of temperatures as long as all external cues that might influence thermoregulatory behavior have been eliminated (e.g., see Hutchison and Dupré, 1992). The mean of these selected temperatures is the preferred temperature. Assuming that the animals are under no physiological stress, the preferred body temperature approximates the set point temperature.

THERMOREGULATION

Heat Exchange with the Environment

Heat exchange with the environment occurs via radiation, convection, and conduction (Fig. 7.4). A terrestrial or arboreal ectotherm receives radiant energy from the sun directly or indirectly from reflected solar radiation and the heat of substrate and air. Sunlight striking a surface is variously absorbed and reflected; the absorbed solar radiation converts to heat and raises the temperature of the object. No natural object totally absorbs or reflects solar radiation, and most organisms have a mixture of absorptive and reflective surfaces. Many can change the absorptive-reflective nature of their surfaces by color change (e.g., Atsatt, 1939; Hutchison and

TABLE 7.1 Terminology in Studies of Amphibian and Reptile Thermoregulation

Term	Definition
Activity temperature range	Normal range of temperatures in which activity occurs
Mean activity temperature (T_b)	The mean of all temperatures of active animals (T_b, body temperature)
Preferred temperature	The temperature selected by individuals in a thermal gradient when all external influences have been removed
Set point	The range of temperatures or temperature at which animals attempt to regulate T_b
Operative temperatures (T_e)	Equilibrium temperature for an animal in a particular environment
Voluntary minimum	The lowest temperature tolerated voluntarily in the lab
Voluntary maximum	The highest temperature tolerated voluntarily in the lab
Critical thermal minimum	The low temperature that produces cold narcosis, thus preventing locomotion and escape
Critical thermal maximum	The high temperature at which locomotion becomes uncoordinated and the animal loses its ability to escape conditions that will lead to its death
Poikilothermy	Wide variation in T_b in response to environmental temperature
Homeothermy	Constant T_b (within ±2°C) even with greater environmental temperature fluctuations
Ectothermy	Condition under which the external environment is the source of heat
Endothermy	Condition under which heat is produced metabolically (internally)
Heliothermy	Gaining heat by basking in sun
Thigmothermy	Gaining heat by conduction (e.g., lying on a warm rock not exposed to sun)
Acclimation	Functional compensation (relatively short time periods) to experimentally induced environmental change
Thermoregulation[a]	Maintenance of a relatively constant T_b even though environmental temperatures vary
Thermal conformity[a]	T_b varies directly with environmental temperature; there is no attempt to thermoregulate

Sources: Cowles and Bogert (1944), Hutchison and Dupré (1992), and Pough and Gans (1982).

[a] Effective use of these terms requires context. For example, to simply say that a lizard is a thermoregulator is meaningless without a time component—it may thermoregulate behaviorally while active in the daytime but actually be a thermal conformer at night while in a refuge.

Larimer, 1960; Pearson, 1977; Christian, 1996). Dark surfaces are strongly absorptive and light ones reflective; an animal's colors and pattern, and the ability to change color, reflect a balance between thermal requirements, social advertisement, and crypsis. Subterranean ectotherms gain heat by conduction from their microhabitat or by coming into contact with the undersides of warm surfaces (e.g., rocks) that are exposed to direct sunlight (Huey et al., 1989a). For amphibians, smaller body size not only translates into potentially higher rates of heat exchange, but for the same reason (high surface to volume ratio), translates into high rates of water loss. For both small amphibians and reptiles, physiological control of heat exchange (other than by evaporative cooling) is, at best, minimal.

Temperature and Performance

Most amphibians and reptiles control body temperatures when possible because most life processes vary with temperature. These processes have been fine-tuned by natural selection to be optimal within the activity range of individual species (Fig. 7.5). The activity range itself is influenced by a myriad of physical and biological factors and differs among species as well as within species (Fig. 7.6).

In frogs, the ability to jump is critical for escape from terrestrial predators. Effective escape involves both a trajectory and an escape distance. Escape distance is a function of the distance moved with each jump and the number of consecutive jumps. Green frogs, *Rana clamitans*, can move more than 100 cm in a single jump. The distance moved, however, is temperature dependent (Huey and Stevenson, 1979). At body temperatures below 10°C and above 25°C, jumps are shorter than those between 10 and 25°C (Fig. 7.7). Presumably, cold frogs are less able to escape than frogs within their activity temperature range.

Because of the thermal sensitivity of active escape behaviors, the lizard *Trapelus savignii* alters its escape behavior to offset the effects of temperature on specific escape behaviors (Hertz et al., 1982). At higher temperatures, lizards are more likely to run than at lower temperatures. In addition, a shift from flight behavior to threat behavior not involving flight occurs with decreasing temperatures (Fig. 7.8.). The levels of threat also vary from lunging to bite at relatively high temperatures to attacking, lashing with the tail, and leaping off the substrate to bite at lower temperatures.

Field studies confirm that temperature influences performance in natural situations. The South American lizard *Tropidurus oreadicus* flees greater distances when body temperatures are low than when body temperatures are high (Rocha and Bergallo, 1990). This result

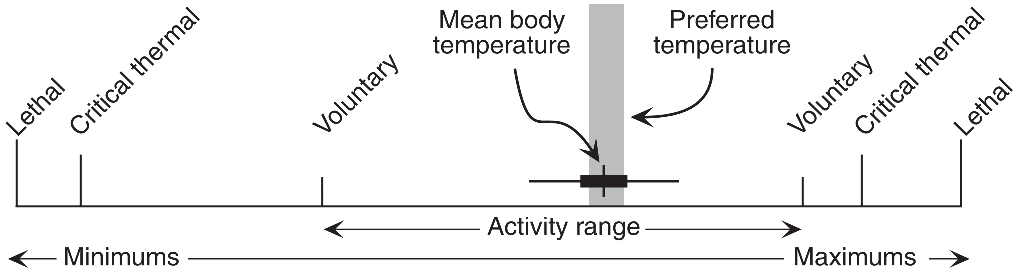


FIGURE 7.3 Profile of body temperature characteristics of an ectotherm. Mean body temperature is based on field data taken on active animals. Set temperature is based on temperatures selected by individuals with external influences eliminated. See Table 7.1 for definitions.

suggests that the lizards behaviorally respond to reductions in physiological performance associated with low body temperatures by running farther and presumably minimizing risk.

Nocturnal ectotherms are active at lower temperatures than most diurnal ectotherms, and their body temperatures tend to be more variable. Based on the hypothesis that physiological performance should be optimized at the normal activity temperatures of ectotherms, performance in nocturnal ectotherms should be greatest at the low temperatures at which activity occurs. However, nocturnal geckos perform better at temperatures above their normal activity temperatures (Huey et al., 1989b; Autumn et al., 1994). Their best peformance temperatures are similar to temperatures associated with maximal performance in diurnal

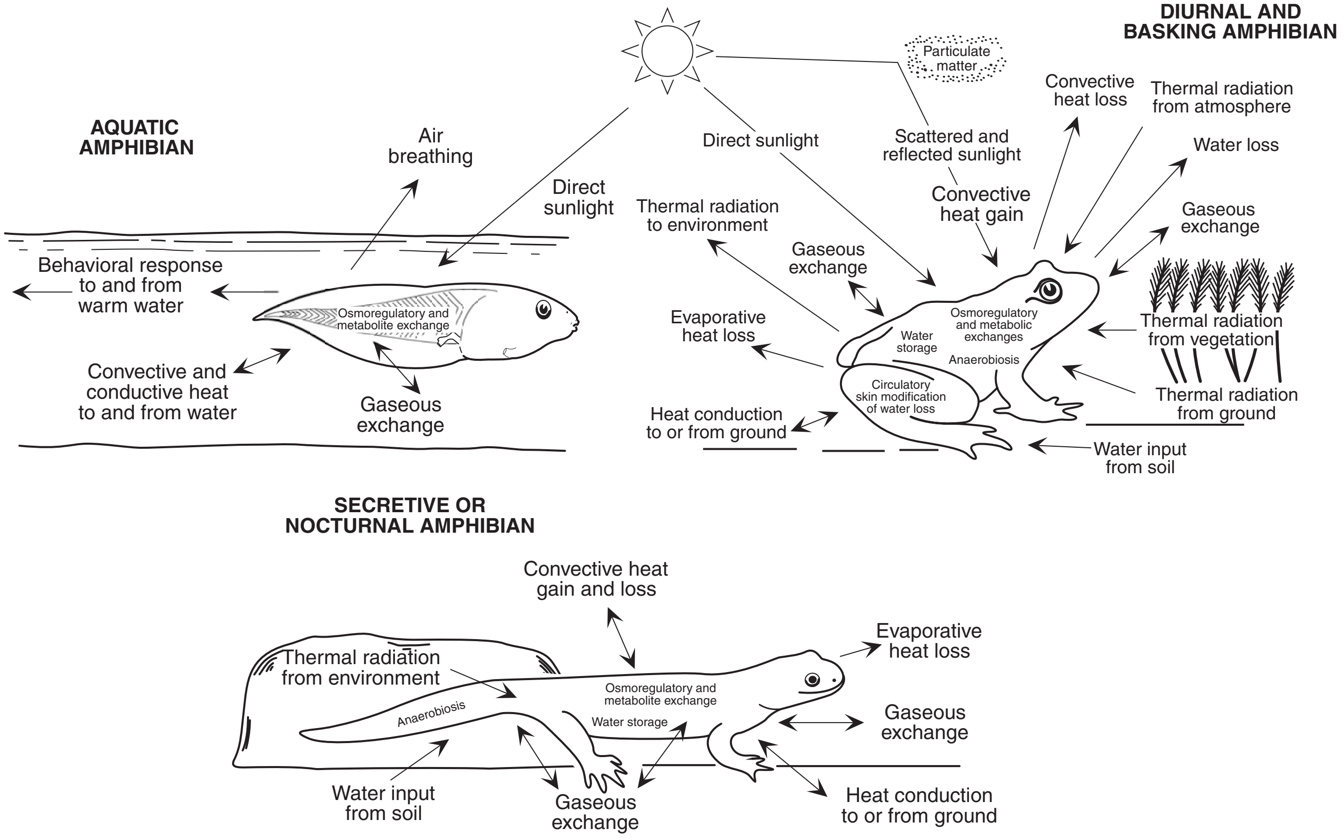


FIGURE 7.4 The environments in which individual amphibians and reptiles live provide different opportunities for heat exchange based on the medium and the physical structure of the habitat. A reptile differs from the amphibians shown because water loss is much less and influences body temperature much less. The reptile also is limited in its ability to absorb water directly from the environment. Adapted from Brattstrom (1979).

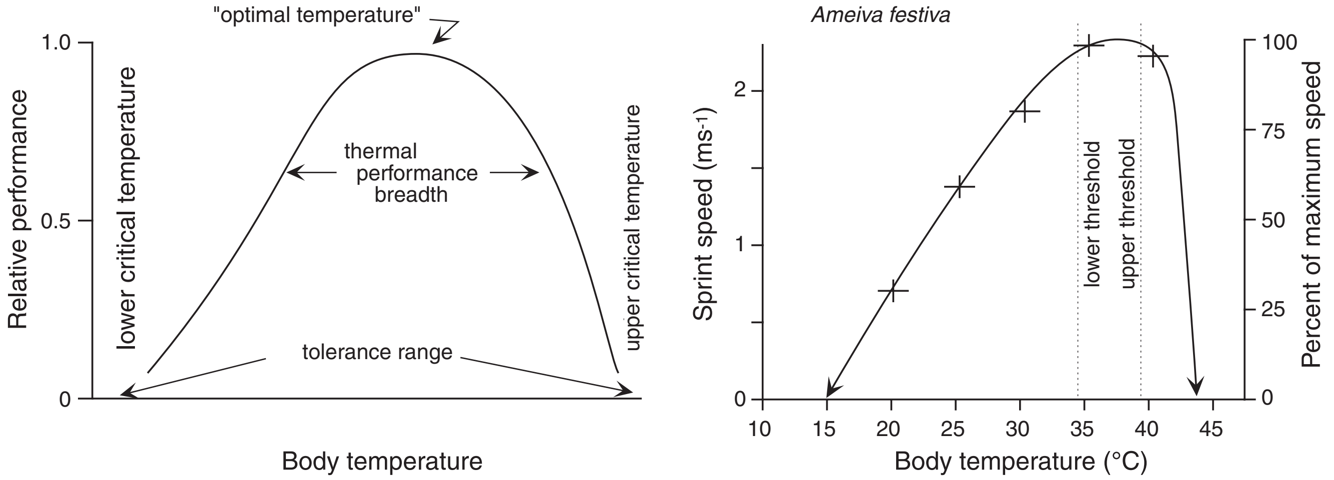


FIGURE 7.5 Theoretically, physiological and behavioral performance are maximized across a relatively narrow range of body temperatures in ectothermic vertebrates (left). Empirical data on *Ameiva festiva* demonstrate that performance is constrained by temperature. Adapted from Huey and Stevenson (1979) and Van Berkum et al. (1986).

lizards. Low body temperatures of nocturnal geckos are a consequence of nocturnal activity. Nocturnal activity results in suboptimal performance, at least as measured in the laboratory, and potentially affects escape from predators, limits feeding success, and has other consequences. Thermal physiology may reflect evolutionary conservatism, and consequently, no physiological adjustments have been made to enhance nocturnal activity.

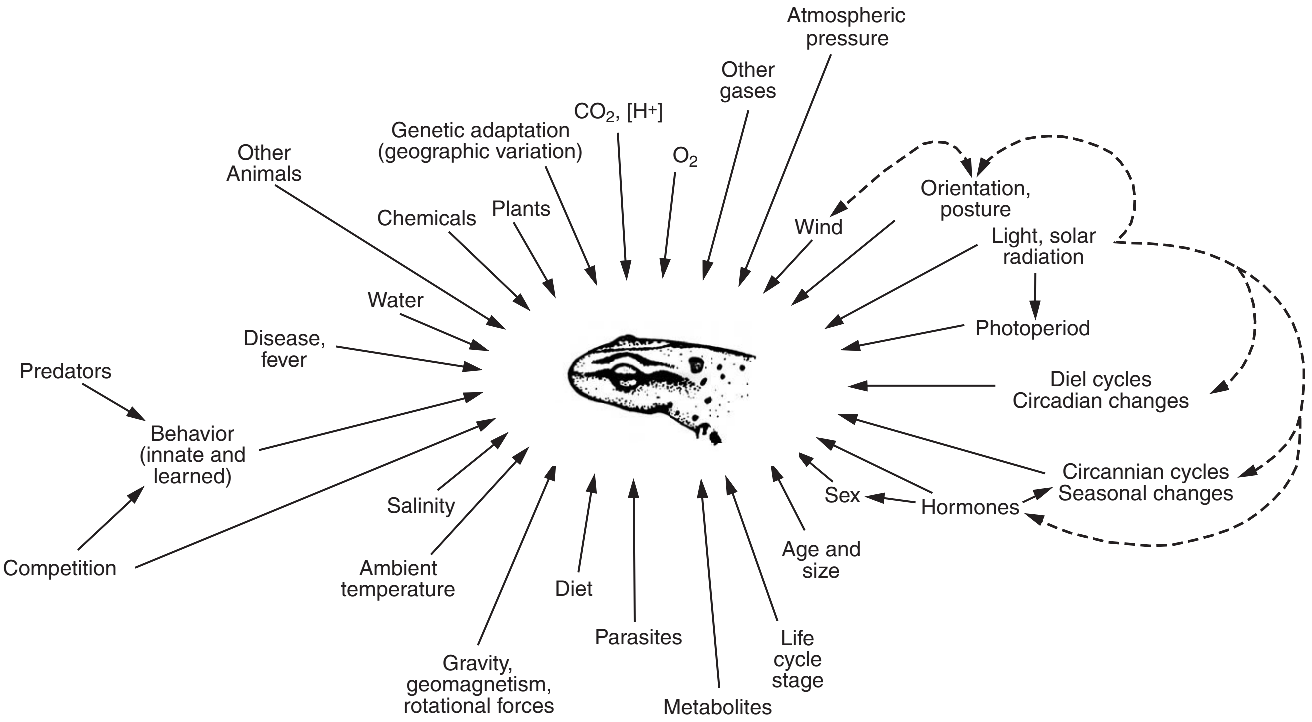


FIGURE 7.6 A multitude of factors influence heat exchange and thus body temperatures and the thermal ecology of amphibians and reptiles. The effects of some variables are direct, such as orientation and exposure during basking. Others are indirect. Predators, for example, can interfere with an amphibian's or reptile's ability to use basking sites, thereby forcing it to maintain activity at suboptimal temperatures. Adapted from Hutchison and Dupré (1992).

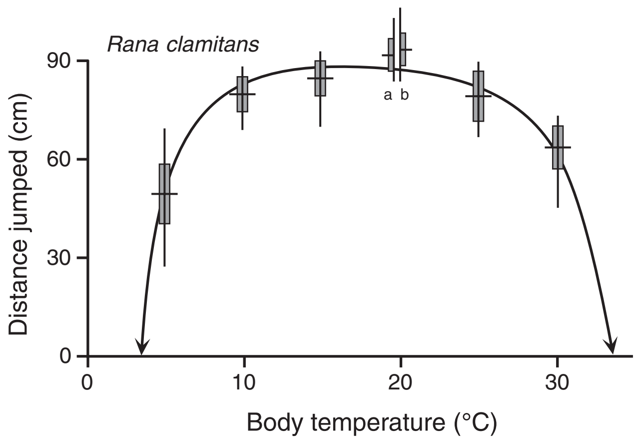


FIGURE 7.7 Green frogs, *Rana clamitans*, jump varying distances depending upon their body temperature, but do most poorly at low and high temperatures. "a" and "b" refer to different sets of samples at 20°C. Adapted from Huey and Stevenson (1979).

However, geckos are an ancient group and nocturnalism appears ancestral, suggesting that this explanation is unlikely. Likely, a trade-off exists between nocturnal and diurnal activities. The cost to survival and fitness of nocturnality is sufficiently low that shifting diurnal activities, such as digestion, that operate most efficiently at high temperatures, to lower temperatures does not incur a fitness cost.

Evolutionary studies suggest that thermal physiology and performance have evolved together in 11 species of lacertid lizards (Bauwens et al., 1995). Species that have narrow distributions of preferred body temperatures and can achieve near-maximum sprint speeds across a wide range of body temperatures have the highest levels of performance (Fig. 7.9). As relative hindlimb length has increased evolutionarily, so has maximum sprint speed. The optimal temperature for sprinting has also evolved with maximum sprint speed. As morphology has changed evolutionarily, so has physiology and behavior. In some instances, thermal physiology does not appear to have kept pace evolutionarily with performance. Two populations of the lacertid *Podarcis tiliguerta* are separated by a 1450-m elevational gradient. Set temperatures based on laboratory studies are identical, suggesting that their thermal physiology is similar. At high elevations, lizard body temperatures average 25.4°C, whereas at low elevations they average 30.2°C. High-elevation lizards have lower sprint velocities than low-elevation lizards and do not achieve the absolute speeds reached by low-elevation lizards (Bauwens et al., 1995). The possibility exists that lizards at higher elevations do not face the same risks as lizards at lower elevations and thus selection on temperature-related performance characteristics has been relaxed at high elevations.

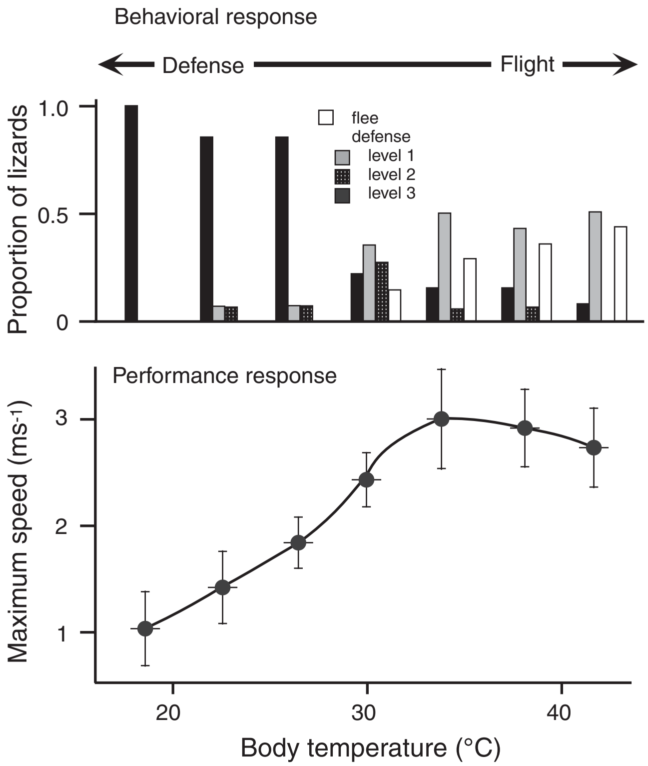


FIGURE 7.8 Body temperatures determine escape behaviors of active *Trapelus savignii*. At high body temperatures, lizards rely on running (flight) for escape, reflecting the optimization of running speeds at high body temperatures. At lower body temperatures, alternative escape behaviors become more frequent. Defense occurs at three levels: level 1, gape and lunge; level 2, upright stance, body inflated, and tongue protruding; and level 3, all of the above plus attack, lashing with tail, and leaping off substrate to bite. Adapted from Hertz et al. (1982).

The temperatures that ectotherm eggs experience can have cascading effects on performance of individuals. In addition to increasing developmental rates, higher temperatures during development can affect relative size and performance of hatchlings (Van Damme et al., 1992). In some species, the effects appear to be carried through at least part of the juvenile life history stage and possibly through life. Field-collected and laboratory-hatched eggs of the Australian skink *Bassiana duperreyi* produce hatchlings that differ in size and performance depending upon incubation regime (Elphick and Shine, 1998). Eggs incubated on a cycle around 20°C ("cold incubated") hatch later and produce smaller hatchlings relative to original egg size than those incubated on a cycle around 27°C ("hot incubated"). The hot-incubated lizards are relatively heavier and have longer tails than those from the cold incubator. Hot-incubated lizards perform better in sprint speed trials and maintain their superior performance for at least 20 weeks (the entire study). Whether these incubation-mediated phenotypic differences among offspring translate into differences in

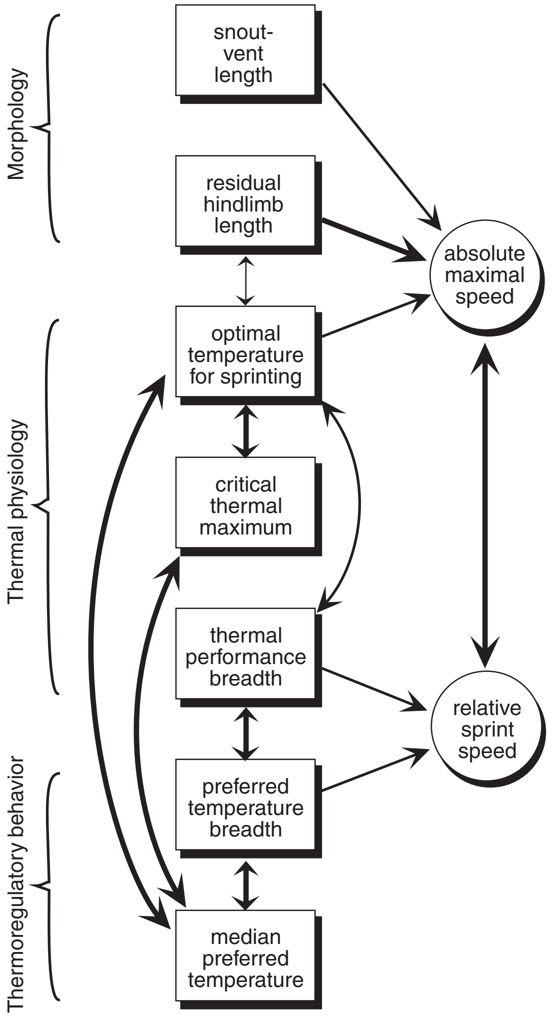


FIGURE 7.9 Morphology, physiology, and behavior have evolved together among 13 species of lacertid lizards. Relative hindlimb length (residual hindlimb length) is correlated with absolute maximal running speed, which correlates with relative sprint speed. Attributes of thermal physiology are also correlated. Heavy lines indicate significantly correlated traits and, because the analysis is based on phylogenetically independent contrasts, the effects of phylogenetic relatedness have been accounted for. Adapted from Bauwens et al. (1995).

individual fitness remains to be determined. However, some details of the study suggest that they do. Survival among all study animals was low, but hot-incubated lizards survived better than cold-incubated lizards in the laboratory trials. Relative size and performance in natural populations likely influence individual fitness through effects on time to sexual maturity, body size at sexual maturity, and ability to compete for high-quality mates.

Control of Body Temperature

Most amphibians and reptiles control their body temperatures within relatively narrow ranges while active (Table 7.2). Much of this control is behavioral, the result of short-term movements or posturing to maximize heat gain or loss. Among amphibians, behavioral thermoregulation is difficult to separate from behavioral mechanisms for water conservation because water loss is temperature dependent and amphibians have few mechanisms for reducing water loss. In many salamanders, for example, behavioral control of temperature does not occur (Feder and Lynch, 1982). In amphibians without cutaneous control of evaporative water loss, body temperatures are only slightly above environmental temperatures because of evaporative cooling. Most reptiles and many frogs rely on behavioral mechanisms to thermoregulate. Because sun exposure and temperatures of natural environments vary spatially and temporally, behaviors resulting in thermoregulation vary accordingly (e.g., Fig. 7.2). Microhabitat selection and adjustments in time of activity account for much of the control of body temperature (Table 7.2).

Many salamanders, particularly plethodontids, do not thermoregulate behaviorally, at least in the same ways that many frogs and most reptiles do (Feder and Lynch, 1982). Body temperatures of tropical plethodontids along an elevational gradient parallel environmental temperatures and change seasonally with environmental temperatures. Sympatric tropical species of plethodontids do not differ in body temperatures, indicating that niche segregation by temperature does not exist. Maximum body temperatures of tropical and temperate-zone plethodontids are similar, but temperate-zone species have lower minimum body temperatures because temperate-zone microhabitats experience cool periods that tropical ones do not experience. One explanation for the apparent lack of behavioral thermoregulation in these salamanders is that they cannot exploit warm terrestrial microhabitats because they are too dry, except possibly in the moist tropical lowlands. Likewise, they would have difficulty exploiting warm aquatic microenvironments such as those in the moist tropical lowlands because of the oxygen deficiency of warm water. Because they lack lungs, gulping air to gain oxygen while in low-oxygen water is not an alternative. They are thus restricted to relatively cool terrestrial microhabitats and maintain temperatures similar to those microhabitats. Most other salamanders have body temperatures similar to their microhabitats most of the time. Ambystomatid salamanders, for example, spend most of their lives underground. When they migrate to ponds to breed, migrations take place during rainy nights that offer no opportunities for behavioral thermoregulation.

Some frogs regulate body temperatures by basking in sun (e.g., Fig. 7.2). Bullfrogs (*Rana catesbeiana*) vary in body temperatures from 26 to 33°C while active (Lillywhite, 1970) even though environmental temperatures vary more widely. During the day, they gain heat by basking in sun and lose heat by a combination of postural adjustments and use of the cold pond water as a heat sink. At night when water temperatures are low, bullfrogs move from shallow areas to the center of the pond where water is relatively warmer. In the morning, they return to the pond edge to bask and gain heat. Although bullfrogs clearly cannot maintain high body temperatures at night, they behaviorally select the warmest patches in a relatively cool mosaic of the nighttime thermal landscape, thereby exercising some control over their body temperatures. Similar observations have been made on other frog species (see Hutchison and Dupré, 1992).

An alternative to moving between microsites to gain and lose heat is to use water absorption and evaporative water loss to moderate body temperatures. By having a portion of the body against moist substrate, a frog can absorb water to replace water lost by evaporative cooling, thereby maintaining thermal stability even though environmental temperatures may be relatively high (see Fig. 6.6). Likewise, by regulating evaporative water loss, some frogs are capable of maintaining body temperatures in cooling environments by reducing evaporative water loss (Withers et al., 1982).

Control of evaporative cooling to stabilize body temperatures during periods of high ambient temperatures occurs in other ways as well. The best known examples are the waterproof frogs *Phyllomedusa* and *Chiromantis* which allow body temperatures to track environmental temperatures until body temperatures reach 38–40°C, when skin glands begin secretion and evaporative cooling allows the frog to maintain a stable body temperature even if environmental temperature reaches 44–45°C (Shoemaker et al., 1989).

Control of body temperatures in diurnal lizards and snakes often involves behavioral shifts throughout the day. Some populations of the South American tropidurine lizard *Tropidurus hispidus* live on isolated granitic rock outcrops in the Amazon rain forest that receive direct sunlight. The rain forest acts as a distribution barrier; the lizards do not enter the shaded forest. During the day direct sunlight causes the rock surfaces to heat up to nearly 50°C, which is above the critical thermal maximum for most animals. The lizards forage and interact socially on the rock surfaces, maintaining relatively constant body temperatures throughout the day by moving between rock patches exposed to sun and shady areas (Fig. 7.10). During morning, lizards bask on relatively cool rocks to gain heat. During afternoon, lizards use relatively cool rocks in shade as heat sinks to maintain activity temperatures.

Snakes differ from most lizards in that their surface to volume ratios are high as the result of their elongate and

TABLE 7.2 Examples of Body Temperatures of Amphibians and Reptiles

Species	Minimum voluntary	Maximum voluntary	Mean	No. species
Salamanders				
Cryptobranchidae	9.8	28.0	—	1
Sirenidae	8.0	26.0	24.0	3
Amphiumidae	—	—	24.0	1
Salamandridae	4.5	28.4	16.0	4
Temperate ambystomatids	1.0	26.7	14.5	9
Tropical ambystomatids	10.5	30.0	19.0	12
Temperate aquatic plethodontids	2.0	22.0	11.3	9
Temperate terrestrial plethodontids	−2.0	26.3	13.5	28
Tropical plethodontids	1.8	30.0	14.2	43
Frogs				
Ascaphus	4.4	14.0	10.0	1
Pelobatidae	12.2	25.0	21.4	2
Leptodactylidae	22.0	28.0	24.7	5
Bufo	3.0	33.7	24.0	17
Hylidae	3.8	33.7	23.7	14
Gastrophryne	15.5	35.7	26.5	2
Rana	4.0	34.7	21.3	12
Lizards				
Anguidae	11.0	34.7	23.0	3
Anniellinae	13.8	28.3	21.0	1
Chamaelonidae	21.0	36.5	21.0	2
Gekkonidae	15.0	34.0	24.9	3
Gerrhosaurinae	19.0	41.0	33.3	1
Helodermatidae	24.2	33.7	27.2	1
Iguanidae	18.0	46.4	36.7	50
Lacertidae	35.0	41.5	38.4	3
Scincidae	13.2	39.5	30.4	16
Teiidae	27.0	45.0	40.5	9
Xantusiidae	11.5	32.2	23.1	4
Snakes				
Boidae	12.2	34.0	25.1	3
Colubridae	9.0	38.0	26.8	41
Viperidae	17.5	34.5	27.0	12
Pelamis platurus	—	—	24.9	1
Turtles				
Chelydridae	5.0	24.5	—	1
Emydidae	8.0	35.2	26.7	6
Kinosternidae	16.2	28.8	23.0[1]	2
Testudinidae	15.0	37.8	30.6	3

Sources: Brattstrom (1963, 1965), Duellman and Trueb (1986), and Feder et al. (1982).

[1] Estimated.

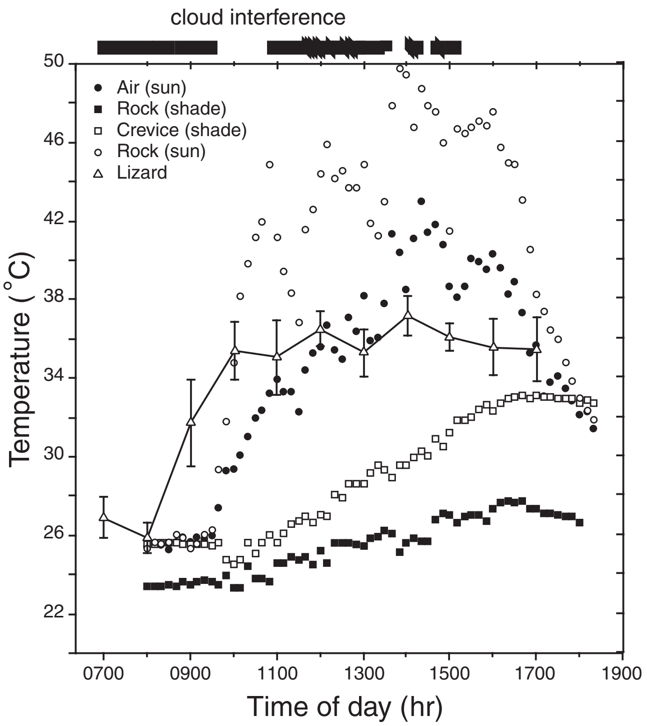


FIGURE 7.10 Many lizards regulate their body temperatures within a relatively narrow range by behavioral adjustments. During mornings when rock surfaces are relatively cool, *Tropidurus hispidus* bask in the sun to gain heat. As rock temperatures increase during the day, the lizards spend more time on shaded rock surfaces or in crevices, using cool portions of their habitat as heat sinks. Late in the day when exposed rock surfaces cool, lizards shift most activity to open rock surfaces that remain warm and allow the lizards to maintain high body temperatures longer. Adapted from Vitt et al. (1996b).

relatively slender morphology. Morphology, and more specifically, how morphology is used, can have large effects on heat exchange (Lillywhite, 1987). Postural adjustments change exposure of body surfaces; a stretched out snake has much more surface area exposed than a coiled snake. Behaviorally, snakes seek out microhabitats with appropriate temperatures. For example, file snakes (*Acrochordus arafurae*) are able to maintain body temperatures within a range of 24–35°C by selecting microhabitats within that range and avoiding other microhabitats (Shine and Lambreck, 1985).

Even though many laboratory and field studies of reptilian thermal ecology and physiology suggest that the species under study thermoregulate with some degree of accuracy, comparisons of environmental temperatures and set temperatures are necessary to reach that conclusion. The high-elevation tropical lizard *Anolis cristatellus* lives in open habitats and basks in sun to gain heat. During summer and winter, body temperatures of the lizards are higher than environmental temperatures, which indicates that they thermoregulate (Fig. 7.11). However, in summer, environmental temperatures are higher than in winter, and as a result the lizards are able to achieve higher body temperatures much more easily than they do in the same environment during winter. Even though their body temperatures are variable in both summer and winter, in summer their body temperatures more closely approximate set temperatures. *Anolis gundlachi* lives in a forest environment at low elevations where opportunities to bask and gain heat are limited. Its body temperature is much lower than that of *A. cristatellus.* However, because its set temperature is nearly identical to environmental temperatures, no thermoregulation is necessary for the lizards to maintain body temperatures near their set temperature, and for the same reason body temperatures vary little from set temperatures; they are maintained with a high degree of accuracy.

Physiological processes that facilitate heat gain and loss occur in the skin, cardiovascular system, and excretory system (Table 7.3). Limited heat production can occur by muscular activity (see below), and the hormone thyroxin can cause heat production through its effect on metabolism. Peripheral and central temperature sensors determine physiological and whole-animal responses to temperature change, and species are variously tolerant to high and low temperatures.

Temperature control by heat production is rare in amphibians and reptiles. Among the best examples of heat production are in brooding pythons and leatherback seaturtles. Female pythons increase their body temperatures while brooding eggs by contracting muscles of the body (Hutchison et al., 1966). Some of the heat is transferred to the developing clutch, which then develops at a faster rate. Body temperatures, muscle contraction rates, and oxygen consumption rates of female *Python molurus bivittatus* increase above that of nonbrooding snakes during the time that the snakes brood their eggs (Fig. 7.12). Higher-temperature-mediated development rates during incubation translate into earlier hatching. Combined laboratory and field studies on Australian pythons (*Morelia spilota*) show that brooding not only influences developmental rates, but also offspring quality (Shine and Fitzgerald, 1996).

Leatherback seaturtles (*Dermochelys coriacea*) approach mammalian endothermy on a diet of jellyfish. They maintain body temperatures of 25–26°C in 8°C seawater by a combination of elevated metabolism, large body size, thick insulation, and thermally efficient regulation of blood flow to skin and appendages (Frair et al., 1972; Spotila et al., 1997). Their dark skin may permit some heat gain through solar radiation, but their primary heat source is from muscular activity. Metabolic rates of leatherbacks are higher than what would be predicted on the basis of body size alone (Paladino et al.,

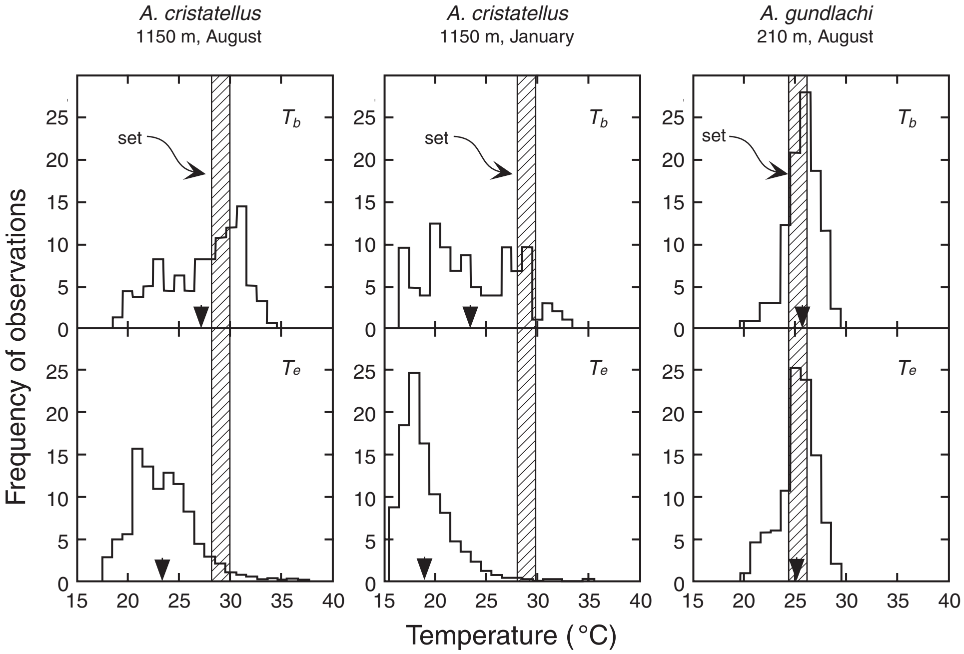


FIGURE 7.11 Precision of thermoregulation in *Anolis* lizards. The upper panels show body temperatures of lizards; the lower panels show operative environmental temperatures; and the crosshatched bars show set or preferred temperatures of the lizards. Means are indicated by arrows. Similarity of body temperatures to set temperatures indicates accuracy of thermoregulation. The accuracy of thermoregulation varies with season in *Anolis cristatellus* as the result of shifts in environmental temperatures. The accuracy of thermoregulation is high in *Anolis gundlachi* even though it does not thermoregulate. In this case, the environmental temperatures are nearly identical to set temperatures of the lizards. Adapted from Hertz et al., 1993.

1990). Heat is retained by a thick, oil-filled skin (an equivalent insulator to the blubbery skin of whales) and counter-current heat exchange in the circulatory system of the limbs. As a consequence, they can enter much cooler marine environments than most reptiles. The same mechanism permits the turtles to lose heat when in warm waters. Other seaturtles are not nearly as efficient at thermoregulation. Green seaturtles and loggerheads typically maintain body temperatures only 1–2°C above temperatures of surrounding water.

Costs and Constraints of Thermoregulation

Even though physiological and behavioral processes are maximized within relatively narrow ranges of temperatures in amphibians and reptiles, individuals may not maintain activity at the optimum temperatures for performance because of the costs associated with doing so. Alternatively, activity can occur at suboptimal temperatures even when the costs are great. Theoretically, costs of activity at suboptimal temperatures must be balanced by gains of being active (Huey and Slatkin, 1976). Costs are varied and not well understood; they include risk of predation, reduced performance, and reduced foraging success.

The desert lizard *Sceloporus merriami* is active during the morning at relatively low body temperatures (33.3°C), inactive during midday when external temperatures are extreme, and active in the evening at body temperatures of 37.0°C (Grant, 1990). Although the lizards engage in similar behavior (e.g., in morning and afternoon, social displays, movements, and feeding) metabolic rates and water loss are greater and sprint speed is lower in the evening when body temperatures are high. Thus, the metabolic and performance costs of activity occur in the evening when lizards have high body temperatures. However, males that are active late in the day apparently have a higher mating success resulting from their prolonged social encounters. The costs of activity at temperatures beyond those optimal for performance are offset by the advantages gained by maximizing social interactions that ultimately impact individual fitness.

Biophysical models can be useful for evaluating costs and benefits of thermoregulation in ectotherms. Microclimate data can be used to model physical parameters necessary to maintain energy balance, and data on body temperatures and activity of free-ranging animals can be used to test the models (e.g., Porter and Gates, 1969).

TABLE 7.3 Behavioral, Morphological, and Physiological Factors Influencing Heat Exchange in Amphibians and Reptiles

1. Behavior
    - Microhabitat selection
    - Temporal adjustments of activity
    - Postural adjustments
    - Huddling or aggregation
    - Burrowing
2. Integument
    - Modification of reflectance by color change
3. Cardiovascular system
    - Capacity for vasomotor activity including peripheral vasomotion
    - Vascular shunts
    - Cardiac shunts
    - Countercurrent systems
    - Temperature-independent control of cardiac output
4. Evaporative cooling
    - Water loss from skin
    - Panting; water loss from oral or buccal surfaces
    - Respiratory water loss
    - Salivation; increased buccal evaporation
    - Urination on self to increase surface evaporation
5. Heat production
    - Shivering thermogenesis
    - Increase in cellular metabolism by hormonal stimulation
6. Temperature sensors
    - Peripheral
    - Central
7. Tolerance of hyperthermia or hypothermia
    - Marked capacity for hypothermia
    - Modest tolerance of hyperthermia

Source: Bartholomew (1982).

The Galapagos land iguana, *Conolophus pallidus*, shifts habitats from the hot season to the garua (cool) season (Christian et al., 1983). The two habitats differ in wind speed and substrate and air temperatures. Temperatures in the hot season habitat (plateau) are high during the day, but decline earlier in the day than those of the garua season habitat, the cliff face. The lizards select cooler microhabitats and maintain cooler body temperatures during the garua season than during the hot season even though microhabitats with warmer temperatures are available during the garua season (Fig. 7.13). Lower cool season temperatures reflect a change in thermoregulation because warm temperatures are available year round. What the lizards gain by operating at suboptimal body temperatures during the garua season is more time at relatively high, but not the highest, temperatures. In both seasons, their body temperatures are maintained at levels that allow the longest period of constant temperature.

Body Size

Rates of heat gain or loss decrease with increasing body size because in larger animals proportionately less surface area is available for heat exchange. In terrestrial lizards, for example, the critical mass is about 20–25 g, at which size physiological mechanisms can have some effect on temperature control. This is one of the many reasons that behavioral control of thermal interactions assumes such importance in small ectotherms.

DORMANCY

When environmental conditions exceed an individual's capacity for homeostasis, retreat and inactivity offer an avenue for survival. Regular cycles of dormancy are major features in the lives of many amphibians and reptiles. Climatic fluctuations are the principal force for cyclic dormancy—hot and dry conditions in desert regions and near or below freezing temperatures in temperate-zone areas are examples. Seasonal fluctuations in food resources may drive dormancy in some tropical areas, although this remains unproven. Dormancy behaviors are commonly segregated into hibernation for avoidance of winter cold and estivation for all others, including acyclic drought-caused dormancy. Depending upon the geographic range, individuals of some species may be dormant longer than they are active. For example, Arizona *Scaphiopus* appear to be active for about 1 month per year and Manitoba *Thamnophis* are active for less than 4 months each year.

Physiological studies of amphibian and reptilian dormancy indicate that many species alter cardiovascular function and suppress metabolic activities to conserve energy and ensure adequate oxygen to vital organs during extended periods of inactivity. Metabolic rates are lower than if rates were slowed just by temperature effects. The physiology of estivation is less clear; metabolic rates generally do not drop below rates expected on the basis of temperature alone, although water loss rates are variously reduced.

Hibernation

Hibernation is a behavioral response to changing seasons (Case, 1976b). Although hibernation in mammals is often associated with changes in resource availability

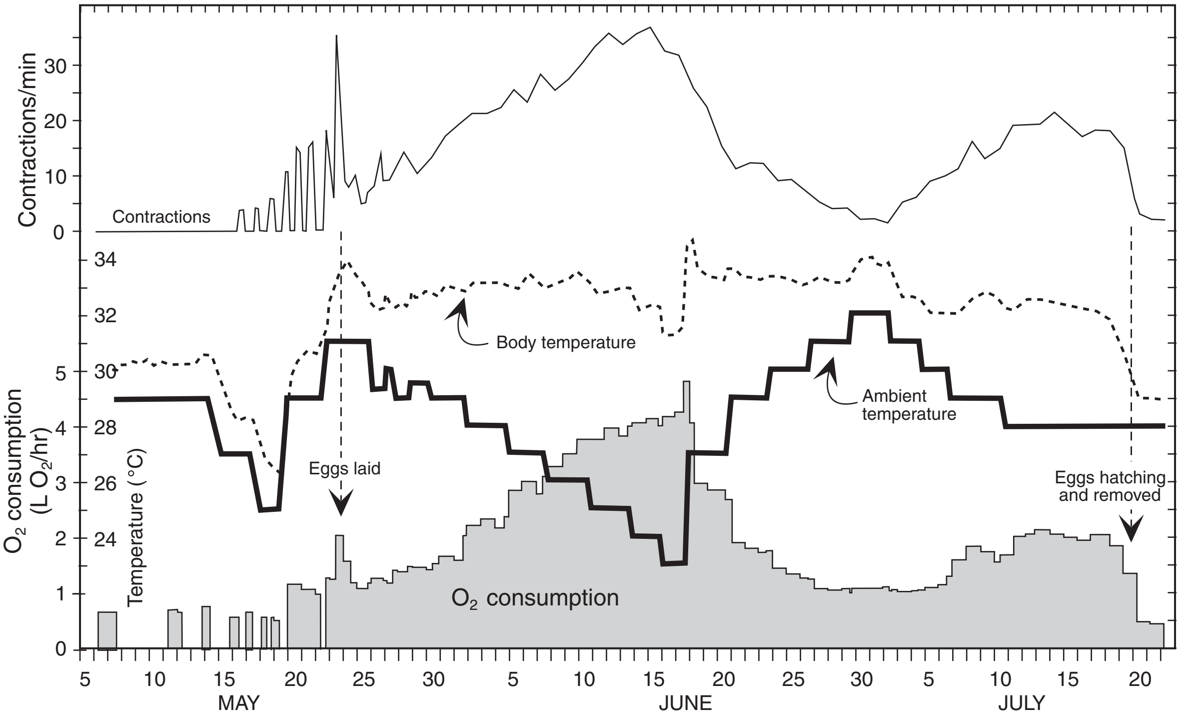


FIGURE 7.12 Brooding temperature in a python. *Python molurus bivittatus* generates heat by rapid contractions of skeletal muscle while brooding eggs. The rate of muscle contractions increases, oxygen intake increases, and CO_2 production increases during egg brooding. Adapted from Van Mierop and Barnard (1978).

caused by cold temperatures, hibernation in amphibians and reptiles most likely is a direct response to cold temperatures and secondarily to changes in resource availability (Gregory, 1982). During hibernation, activity ceases for the most part, body temperatures are determined by temperatures in the hibernation site, and physiological processes are reduced to levels the same or lower than those predicted on the basis of temperature. Limited activity can occur, depending on immediate thermal conditions in the environment. In most instances, limited activity during hibernation involves feeding, mating, gestation, or other important life processes.

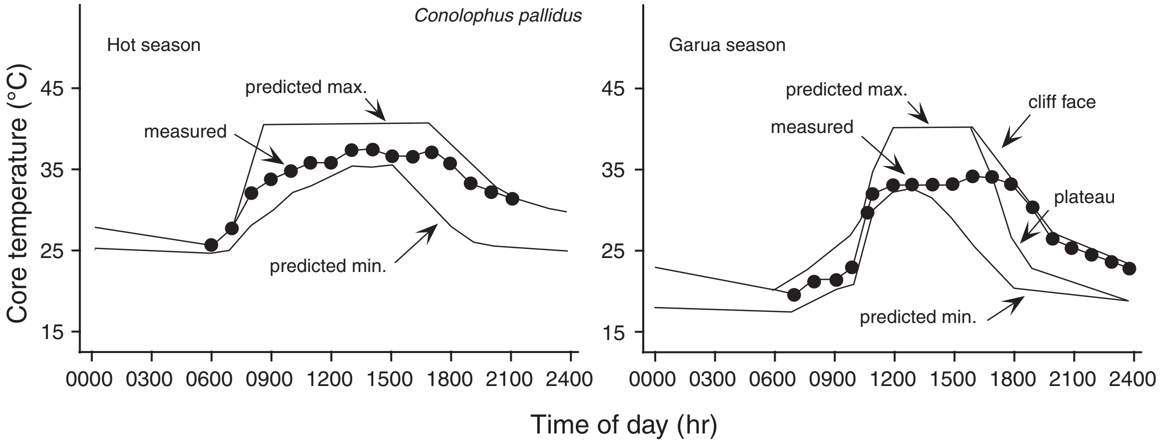


FIGURE 7.13 Biophysical models can estimate the thermal limits available to an ectotherm in a specific habitat. When coupled with temperature data from free-ranging Galapagos land iguanas (*Conolophus pallidus*), trade-offs between achieving optimal temperatures and remaining active for longer periods at suboptimal temperature demonstrate that the physical environment can determine patterns of space use. Adapted from Christian et al. (1983).

As winter approaches in temperate zones, most amphibians and reptiles seek shelter where the minimum environmental temperatures will not fall below freezing. Some amphibians and turtles avoid subfreezing temperatures by hibernating on the bottoms of lakes and streams. Because water reaches its greatest density at 4°C and sinks, animals resting on or in the bottom usually will not experience temperatures less than 4°C. Amphibians and reptiles hibernating on land are less well insulated by soil and must select sites below the frost line or be capable of moving deeper as the frost line approaches them. The few terrestrial hibernators that have been followed do move during hibernation. Box turtles (*Terrapene carolina*) begin hibernation near the soil surface, reach nearly 0.5 m deep during the coldest periods, and then inch toward the surface as environmental temperatures moderate. Hibernating snakes (*Elaphe, Crotalus*) move along thermal gradients in their denning caves and crevices, always staying at the warmest point.

Many aquatic hibernators rest on the bottom of ponds or streams rather than buried in the bottom. While such sites might expose them to predation, hibernation in open water permits aquatic respiration (extrapulmonary) and apparently is sufficient to meet some or all of the oxygen expenditures during dormancy in both amphibians and reptiles. In normoxic water, the oxygen demands of lunged anurans and salamanders are easily met by cutaneous respiration during hibernation. Cutaneous respiration also provides sufficient oxygen for some hibernating reptiles (*Chrysemys picta, Sternotherus odoratus, Thamnophis sirtalis*). Experiments on garter snakes hibernating submerged in a water-filled hibernaculum demonstrate that the submerged snakes use aerobic metabolism but at a more energy conservative rate than terrestrial hibernating conspecifics. In normoxic waters, turtles also remain aerobic through cutaneous and perhaps buccopharyngeal respiration; however, if buried in anoxic or hypoxic environments such as mud, the hibernating animals switch to anaerobiosis. Survival is possible because of high tolerance for lactic acid build-up, and in some instances, submerged turtles may shuttle between normoxic and anoxic sites. When in the normoxic ones, they can shift to aerobiosis and to some extent flush the excess lactic acid. This might explain observations of turtles swimming below the ice of a frozen pond.

Freeze Tolerance

Most temperate-zone amphibians and reptiles are able to survive brief periods of supercooling (−1 to −2°C). Freezing (formation of ice crystals within the body) is lethal to all but a few species because ice crystals physically damage cells and tissue. Intracellular freezing destroys cytoplasmic structures and cell metabolism. Extracellular freezing also causes physical damage, but the critical factor is osmotic imbalance. As body fluids freeze, pure water freezes first, increases the extracellular osmotic concentration, and dehydrates the cells. Intracellular dehydration disrupts cell structure and, if extreme, causes cell death. Extracellular freezing also blocks fluid circulation and the delivery of oxygen and nutrients to the cells. The damage from freezing causes the animal's death upon thawing.

Intracellular freezing is lethal for all animals. A few species of turtles (*Terrapene carolina*, hatchling *Chrysemys picta*) and frogs (*Pseudacris crucifer, Hyla versicolor, Pseudacris triseriata, Rana sylvatica*) are "freeze tolerant" and survive extracellular freezing. The frogs hibernate in shallow shelters, and although snow may insulate them, body temperatures still drop to −5 to −7°C, causing them to freeze. Ice crystals appear beneath the skin and interspersed among the skeletal muscles; a large mass of ice develops in the body cavity. As much as 35–45% of the total body water may become ice and yet the frogs survive. When frozen, a frog's life processes are suspended; breathing, blood flow, and heart-beat stop. These frogs tolerate the large volume of body ice by producing and accumulating cryoprotectants (= antifreeze) within the cells. The cryoprotectants are either glycerol (*H. versicolor*) or glucose (the three other species), which protects and stabilizes cellular function and structure by preventing intracellular freezing and dehydration. These freeze-tolerant species also possess specialized proteins that control extracellular freezing and adjust cellular metabolism to function at low temperatures and under anaerobic conditions.

The frogs do not physiologically anticipate winter and begin to produce the cryoprotectants. Ice forms peripherally and triggers synthesis of cryoprotectants. The rate of freezing is slow, permitting the production and distribution of cryoprotectants throughout the body before any freeze damage can occur. As soon as the body begins to thaw, the cryoprotectants are removed from general circulation. Freeze tolerance extends into early spring at the time when the frogs begin reproductive activities. For the early spring breeders such as the spring peeper (*P. crucifer*) and the wood frog (*R. sylvatica*), this extended tolerance permits survival under the highly variable and occasionally subzero temperatures that occur during their late winter to early spring breeding season. Freeze tolerance appears to be lost gradually in association with the beginning of feeding.

Estivation

Amphibians in desert and semidesert habitats face long periods of low humidity and no rain. To remain active is impossible for all but a few species; death by dehydration occurs quickly. Arid land species retreat to deep burrows with high humidity and moist soils, become inactive, and reduce their metabolism. Inactivity may dominate an anuran's life. *Spea hammondii* in the deserts of southwestern North America spend >90% of their life inactive; they appear explosively and breed with the first heavy summer rains, and then feed for 2–3 weeks before becoming inactive for another year. Where retreats become dehydrating, some anuran species (e.g., *Cyclorana, Neobatrachus, Lepidobatrachus, Pternohyla, Pyxicephalus*) produce epidermal cocoons. The cocoon forms by a daily shedding of the stratum corneum; the successive layers form an increasingly impermeable cocoon, completely encasing the frog except around the nostrils (see Chapter 6). Some salamanders (e.g., *Siren*) burrow into the mud of drying ponds and produce similar epidermal cocoons.

ENERGETICS

The acquisition of energy in the natural world involves a complex interaction among the biophysical environment in which an animal lives, resources available and their distribution, the social system and how it might constrain access to resources and consequently mating success, and the risk involved in acquiring resources (Fig. 7.14). Energy available to amphibians and reptiles is limited by a combination of resource availability and the costs or risks of harvesting it. Once acquired, energy is used for three primary life processes: growth, maintenance, and reproduction. Energy can also be allocated to storage to be used at a later time. All other aspects of energy use (e.g., energetic support for performance, physiological processes) fall within these broad categories (Fig. 7.15). Compartmentalizing energy use makes it relatively easy to understand how various behaviors or processes contribute to the overall energy budget of an organism.

Amphibians and reptiles do not use energy produced during metabolism to maintain body temperature, and their body temperatures are low during at least portions of the day and season. Consequently, they have relatively low energetic costs of maintenance. Approximately 40–80% of energy ingested in food goes into body tissue in ectotherms, whereas about 98% of energy ingested in food of birds and mammals (endotherms) goes into temperature regulation and activity. The high densities and biomass that amphibians and reptiles achieve, even in low-resource environments, can be attributed to this. Because the conversion of food (resources) into usable energy is an oxidative process, energy can be measured by measuring the rate of use of oxygen both in the

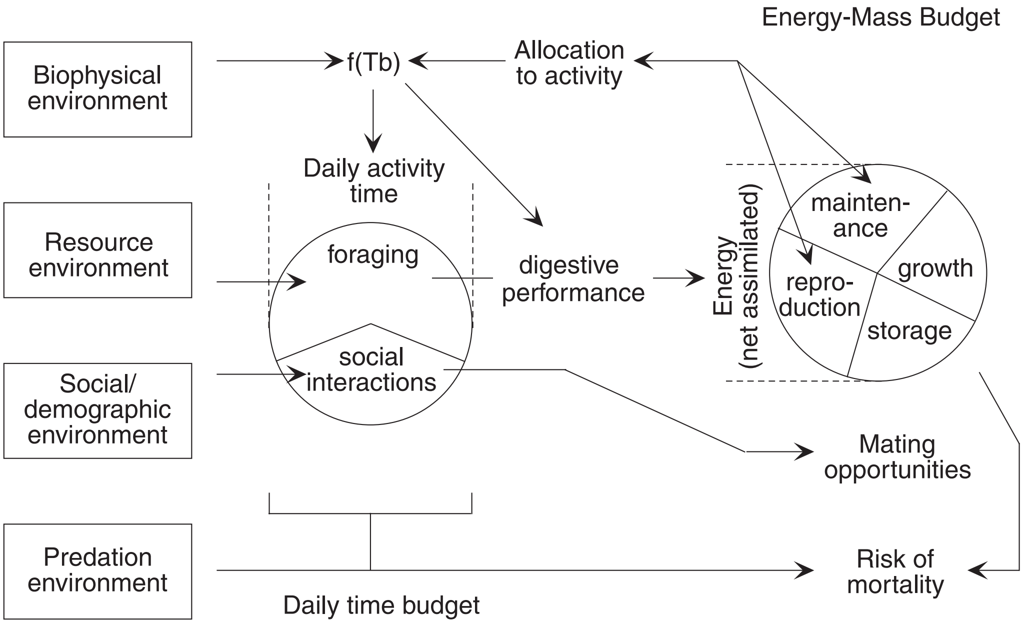


FIGURE 7.14 The ability of amphibians and reptiles to acquire the necessary energy to support life is determined by a combination of abiotic and biotic factors. Adapted from Dunham et al. (1989) and Niewiarowski (1994).

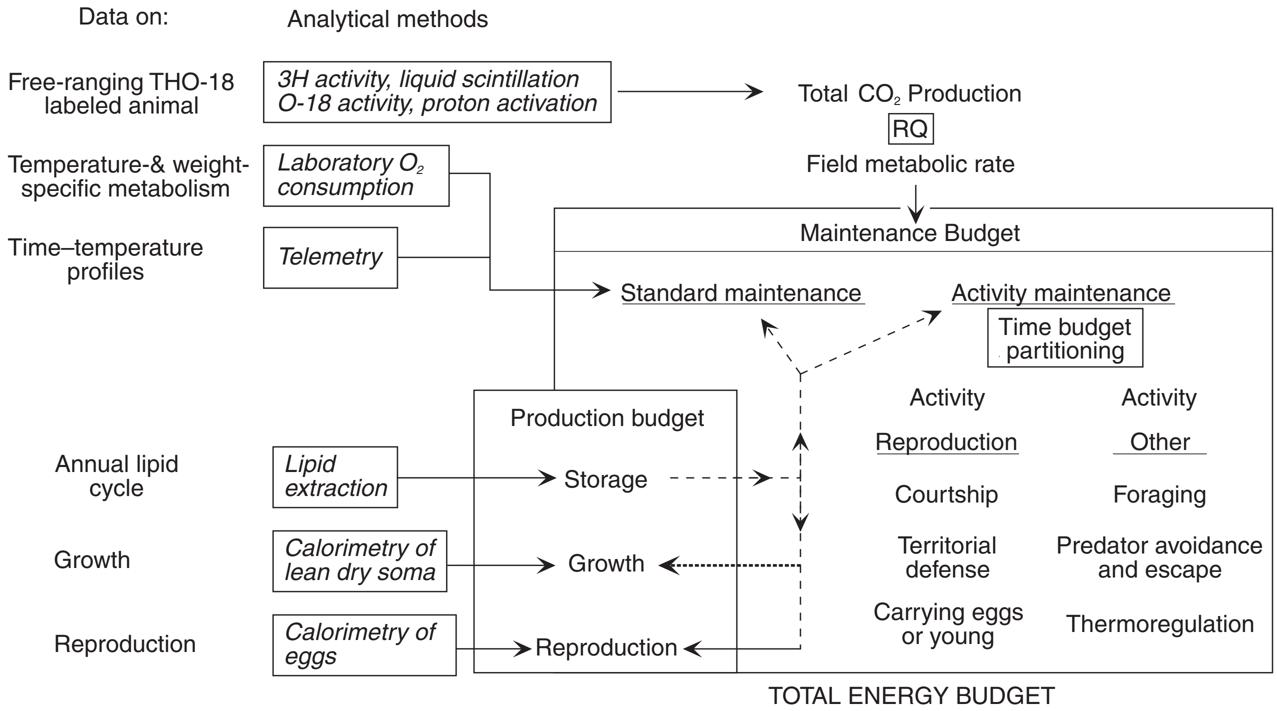


FIGURE 7.15 Schematic diagram showing the protocol for developing ecologically meaningful energy budgets for amphibians and reptiles. Analytical methods can vary depending on the species studied and the specific question asked. Complete energy budgets require partitioning of energy into growth, maintenance, storage, and reproduction. All activities belong to one of these four compartments. Adapted from Congdon et al. (1982a).

laboratory and in the field. Energetic studies typically refer to oxygen consumption for a given body mass per unit time as $\dot{V}O_2$. To standardize units for comparisons, oxygen consumption is generally presented as milliliters or liters of O_2 per gram or kilogram of body mass per hour. Standard metabolism is the minimum rate of energy consumption necessary to stay alive (usually measured when an animal is completely at rest). Resting metabolism is the rate of energy consumption of post-absorptive (not digesting food) animals when not moving but at a time of day when the animals would normally be active. Maximum metabolism is energy consumption at a high level of activity. Because rates of energy use are temperature dependent, data on metabolic rates usually contain a temperature component.

Comparing the energetic cost of specific behaviors across species without placing them in the context of a complete energy budget can be misleading. For example, if two frog species invest the same amounts of energy in reproduction as measured by the energy content or mass of their clutches, it does not follow that their reproductive investments are equal. One might be a large-bodied species that invests very little of its annual energy budget in a single reproductive event. The other might be a very small species that invests a major portion of its annual energy into a single reproductive event. Comparisons of energy use among individuals within species can be much more illuminating because trade-offs will be more evident and extraneous variables (e.g., size) can be minimized. An individual that invests more in a reproductive event than other individuals must harvest more resources to support the additional reproductive investment, divert more energy away from maintenance, or use stored energy that would otherwise be available for maintenance at a later time.

Similar to other physiological processes, the use of energy is related to temperature and body size (Fig. 7.16). Because metabolism in most animals is supported by oxygen, oxygen consumption can be used as a measure of metabolism. Not surprisingly, level of activity influences metabolic rate independent of temperature. Thus warmer ectotherms use more energy, as do more active ones. Body size also influences energy use; larger ectotherms in general use more energy than smaller ones. The energetic cost for a wide variety of behaviors has been studied in many amphibians and reptiles. These include locomotion, prey handling, foraging, and social interactions.

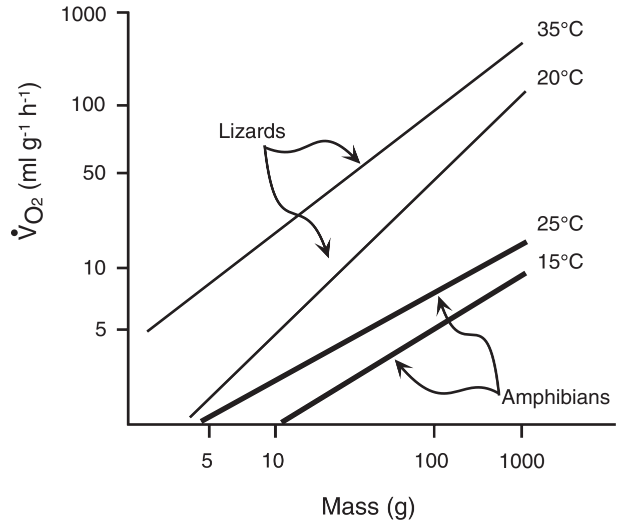


FIGURE 7.16 Effects of body mass and temperature on the rate of oxygen uptake (metabolic rate) in a reptile and an amphibian under two different thermal regimes. Amphibians have lower metabolic rates than reptiles even after the effects of size and temperature are removed. Data from Bennett (1982) and Whitford (1973).

When resting metabolism is known, it is relatively easy to measure the energetic cost of various behaviors. The difference between the metabolic rate associated with the behavior and the rate of resting metabolism estimates the energetic cost of the activity. Because rates are temperature dependent, temperature must be controlled. Examples of activities of amphibians and reptiles that require significant amounts of energy include reproductive related behaviors, prey acquisition, escape, foraging, and locomotion.

Like most frogs, males of the spring peeper (*Pseudacris crucifer*) call to attract females. While at rest, males use 0.108 ml of oxygen per gram of body mass per hour,—a rate similar to that of females at rest (Taigen et al., 1985). During forced exercise, males have higher metabolic rates than females (0.110 ml/[g · hr] versus 0.91 ml/[g · hr], respectively). Males use more energy while calling (1.51 ml/[g · hr]) than they do while exercising; energy used for calling by males can be considered a cost of reproduction. The energy used for call production increases with the rate of calls produced (Fig. 7.17). The rate of call production is the primary determinant of mating success in males; females are attracted to males with the highest calling rates (Forester and Czarnowsky, 1985). Thus the high energetic cost of calling in spring peepers has a high payoff in terms of reproductive success.

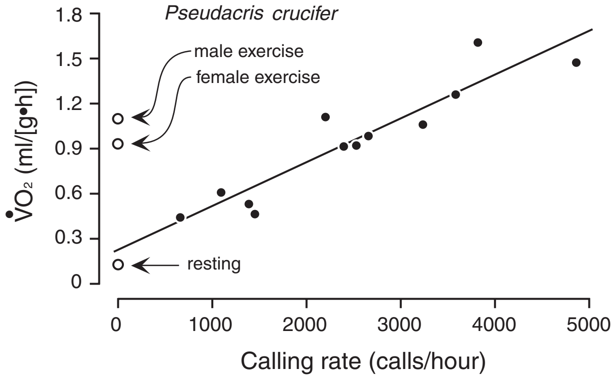


FIGURE 7.17 Male spring peepers (*Pseudacris crucifer*) expend considerable energy calling to attract females during the breeding season. The rate of calling is related to reproductive success, which explains why males expend extra energy to call at higher rates. Adapted from Taigen et al. (1985).

Moving from place to place requires the use of energy, and different animals have different ways of moving. In general, body mass alone explains much of the variation in energetic costs of locomotion for obvious reasons. Because locomotion involves distance moved, the energetic cost of locomotion, which is called the net cost of transport, is measured as oxygen used per unit body mass per kilometer (e.g., O_2· g · km]). In general, amphibians have lower costs of transport than reptiles but great variation exists among species, some of which is tied to the specific type of locomotion. Snakes provide a nice example of the cost of transport because morphology is relatively conservative and there are no limbs to consider. The four kinds of locomotion used by most snakes, lateral undulation, concertina, sidewinding, and rectilinear, differ considerably in terms of energy requirements. Concertina locomotion requires seven times more energy than lateral undulation. Sidewinding, which appears to have a high level of activity associated with it, requires much less energy than lateral undulation or concertina locomotion (Fig. 7.18). The snake moves by arching its body and moving its body through the arch; a relatively small portion of the body touches the substrate at any one time, resulting in little resistance (Fig. 7.19; Secor et al., 1992).

Most energetic studies of behavior in amphibians and reptiles were conducted in the laboratory until the development of a technique using doubly labeled water. Animals are injected in the field with water that has a heavy oxygen atom (^{18}O) and a heavy hydrogen atom (^{3}H). By sampling blood periodically and examining the decay in the ^{18}O, rates of energy use can be calculated (Nagy, 1983a). The decay in ^{3}H provides an estimate of water flux. A number of particularly interesting estimates of energy use by free-ranging reptiles have provided new insights into trade-offs in energy use.

Two snakes, the sidewinder (*Crotalus cerastes*) and the coachwhip (*Masticophis flagellum*), occur together over a

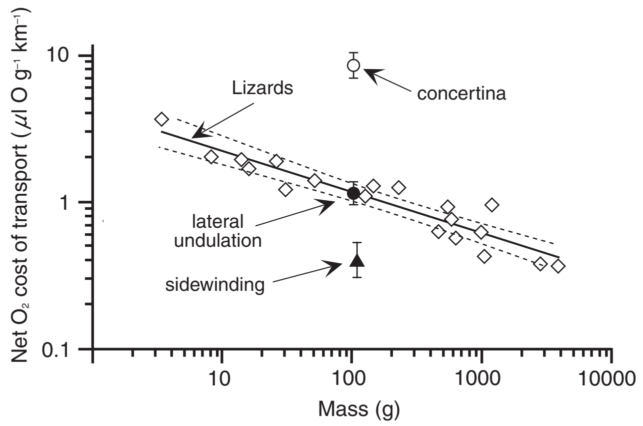


FIGURE 7.18 The net cost of transport for snakes using lateral undulation is similar to that of lizards during locomotion. Concertina locomotion is much more expensive energetically, while sidewinding has a low energetic cost. Adapted from Secor et al. (1992).

large part of the Mojave and Sonoran Deserts of western North America. The sidewinder is a sit-and-wait or ambush forager that remains for extended time periods in a single place waiting for potential prey to pass by. When a prey item passes, it strikes, envenomates, kills, tracks, and swallows the prey. The coachwhip is an active or wide forager that moves considerable distances during the day in search of prey that it captures and swallows, usually alive (Fig. 7.20). Daily energy expenditure in both species varies with season, partially as the result of seasonal changes in temperature (Secor and Nagy, 1994). Even though slight differences are apparent between the two species in standard metabolic rates (coachwhip higher at all temperatures), large differences are apparent in energy used for other activities, much of which can be attributed to foraging (Fig. 7.21). The energetically expensive foraging of coachwhips is offset by increased rates of energy acquisition. Sidewinders feed primarily on small rodents and lizards whereas coachwhips feed on a wide variety of vertebrates, including sidewinders! Coachwhips spend more time foraging, move more frequently, and have higher prey capture rates than sidewinders, accounting for differences in energy uptake and use.

Synthesis

Water balance, respiration, thermoregulation, and energetics are tightly linked in ectothermic vertebrates. For amphibians, rates of water loss can be extremely high and most species select microhabitats that minimize water loss. Such microhabitats are usually relatively cool or enclosed. Most amphibians take in large amounts of water and produce dilute urine, although there are some notable exceptions. One consequence of activity at low temperatures and of ectothermy in general is that metabolic rates are low (no metabolic cost of heat production). For many reptiles, activity occurs at high body temperatures, but during periods of inactivity, body

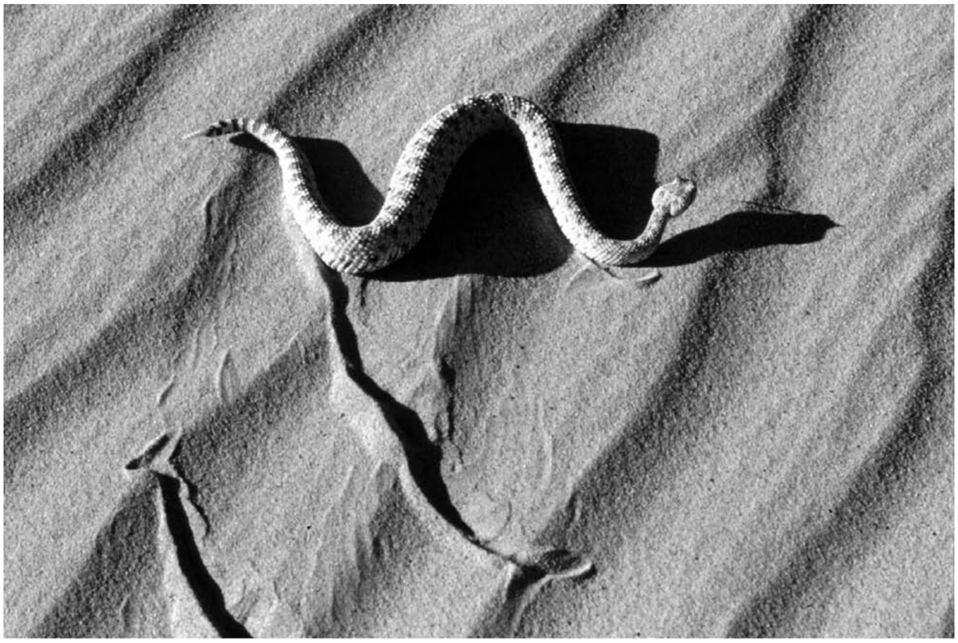


FIGURE 7.19 The sidewinder *Crotalus cerastes* during locomotion on a sand dune. Photograph by C. Mattison.

FIGURE 7.20 The sidewinder *Crotalus cerastes* (left) is a sit-and-wait predator investing little energy in prey search whereas the coachwhip, *Masticophis flagellum* (right), is an active forager that spends considerable energy searching for prey. The coachwhip is eating an adult *Dipsosaurus dorsalis.* Photograph of *C.c.* by S. C. Secor, and *M.f.* by J. M. Howland.

temperatures are much lower. Reptiles in general take in much less water than amphibians and are capable of retaining more of what they take in. As a result, they produce relatively concentrated urine, often including uric acid as a concentrated waste product. Like amphibians, metabolic rates of reptiles are low because there is no cost of heat production (with a few exceptions); however, overall, reptilian metabolic rates are higher than those of amphibians. Because nearly all energy acquired is directed into low-cost maintenance, growth, reproduction, and storage, amphibians and reptiles can occur at high densities in environments that limit densities of homeothermic vertebrates that expend much of their ingested energy on heat production. They can also persist through long periods of energy shortages.

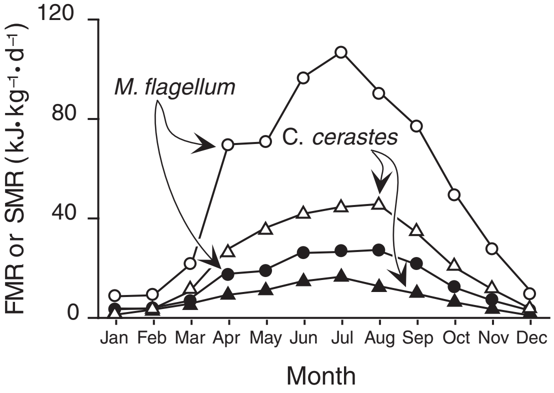


FIGURE 7.21 The sidewinder, a sit-and-wait predator, expends considerably less energy under natural field conditions than the coachwhip, an actively foraging predator. Year-long profiles of daily energy expenditures (averaged by month) are illustrated. Open symbols indicate field metabolic rates (FMR) based on doubly labeled water measurements and closed symbols indicate standard metabolic rates (SMR). Adapted from Secor and Nagy (1994).

Although the interplay between temperature, water economy, and energetics is well documented from a physiological perspective, the correlated evolution of these important physiological traits is only beginning to be appreciated. The evolutionary history of geckos in the genus *Coleonyx* exemplifies the possibilities an evolutionary approach to the interplay between water economy, temperature, and metabolism can have in understanding physiological processes. The ancestor of *Coleonyx* in North America appears to have had a relatively low body temperature (26°C), a high evaporative water loss rate (2.5 mg g^{-1} hr^{-1}), and a low standard metabolic rate (0.07 mg g^{-1} hr^{-1}), and lived in a relatively moist, forested habitat (Dial and Lee, 1992). Two extant species, *Coleonyx mitratus* and *Coleonyx elegans*, retain these characteristics and they are members of the earliest lineage (Fig. 7.22). During the evolutionary history of *Coleonyx*, species moved into more arid environments—ultimately into the deserts of North America. Correlated with that shift are increases in body temperatures (above 31.0°C), reductions in evaporative water loss (<0.1 mg g^{-1} hr^{-1}), and increases in standard metabolic rate (>0.15 mg g^{-1} hr^{-1}). In this example, the exact set of predictions based on a shift from mesic to xeric habitats hold true, indicating that these are indeed adaptations to life in specific environments. Finally, this example points to the importance of maintaining physiological homeostasis for amphibians and reptiles occupying diverse environments.

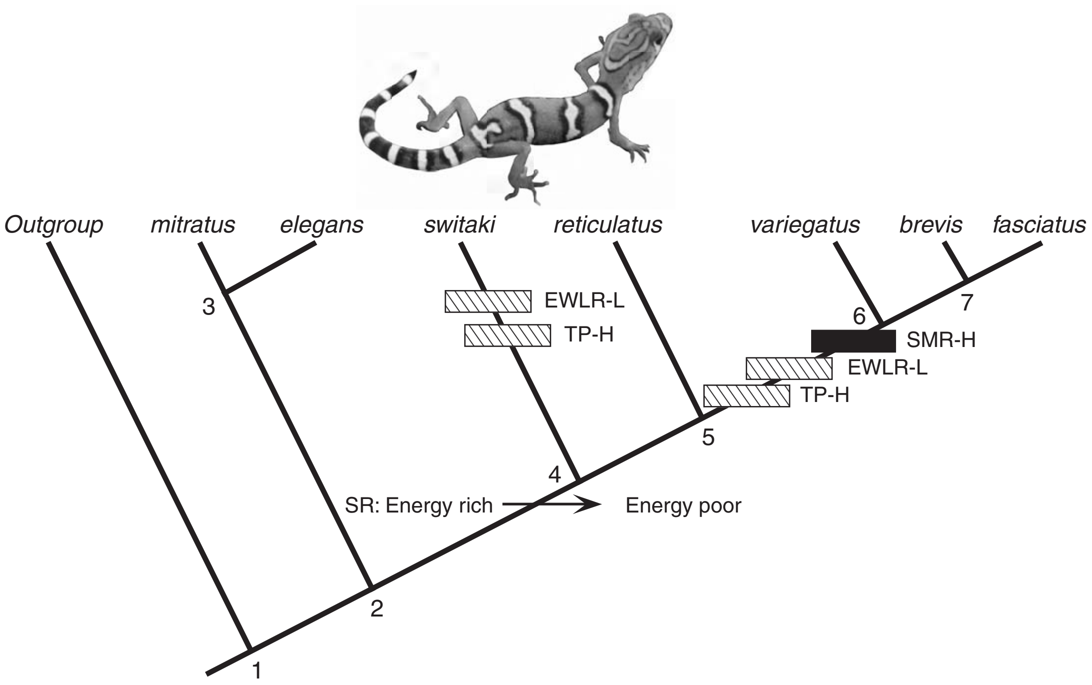


FIGURE 7.22 A hypothetical physiological-ecological character state evolution in lizards in the genus *Coleonyx*. Four equally parsimonious hypotheses were found based on physiological data alone, but when coupled with biogeographic data, the other three were rejected. EWLR, evaporative water-loss rate; TP, temperature preference; SMR, standard metabolic rate; H, high; and L, low. Solid bars indicate acquisition of a new state and cross-hatched bars indicate independent evolution of a derived state. The genera *Eubleparis*, *Hemitheconyx*, and *Holodactylus* compose the outgroup. Presumably there was a shift in the selective regime (SR) from an energy-rich to an energy-poor microhabitat during the evolutionary history of *Coleonyx*. Adapted from Dial and Grismer (1992).

ADDITIONAL READING

Bartholomew, G. A. (1982). Physiological control of body temperature. *In* "Biology of the Reptilia, Vol. 12. Physiology C. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 167–211. Academic Press, New York.

Bennett, A. F. (1980). The metabolic foundations of vertebrate behavior. *BioScience* **30:** 452–456.

Gregory, P. T. (1982). Reptilian hibernation. *In* "Biology of the Reptilia, Vol. 13. Physiology D, Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 53–154. Academic Press, New York.

Huey, R. B., and Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Amer. Zool.* **19:** 357–366.

Hutchison, V. H., and Dupré, R. K. (1992). Thermoregulation. *In* "Environmental Physiology of the Amphibia" (M. E. Feder and W. W. Burggren, Eds.), pp. 206–249. Univ. of Chicago Press, Chicago.

Lillywhite, H. B. (1987). Temperature, energetics, and physiological ecology. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 422–477. MacMillan, New York.

REFERENCES

General: Bartholomew, 1982; Bauwens et al., 1995; Bennett, 1980; Cowles and Bogert, 1944; Dawson, 1975; Garland, 1994; Huey and Slatkin, 1976; Hutchison and Dupré, 1992; Pearson and Bradford, 1976; Rome et al., 1992.

Thermoregulation: Heat Exchange with the Environment: Atsatt, 1939; Christian, 1996; Huey et al., 1989a; Hutchison and Larimer, 1960; Pearson, 1977.

Temperature and Performance: Autumn et al., 1994; Bauwens et al., 1995; Elphick and Shine, 1998; Hertz et al., 1982; Huey and Stevenson, 1979; Huey et al., 1989b; Rocha and Bergallo, 1990; Van Damme et al., 1992.

Control of Body Temperature: Feder and Lynch, 1982; Frair et al., 1972; Hutchison and Dupré, 1992; Hutchison et al., 1966; Lillywhite, 1970, 1987; Paladino et al., 1990; Shine and Fitzgerald, 1996; Shine and Lambreck, 1985; Shoemaker et al., 1989; Spotila et al., 1997; Withers et al., 1982.

Costs and Constraints of Thermoregulation: Christian et al., 1983; Grant, 1990; Huey and Slatkin, 1976; Porter and Gates, 1969.

Dormancy (Hibernation and Estivation): Case, 1976b; Gregory, 1982.

Energetics: Forester and Czarnowsky, 1985; Nagy, 1983a; Secor and Nagy, 1994; Secor et al., 1992; Taigen et al., 1985.

Synthesis: Dial and Grismer, 1992.

Part IV

BEHAVIORAL ECOLOGY

Behavioral ecology includes the ecology of movement, social interactions, foraging, and escape from predators. All of these require behavior of one kind or another. Behavioral decisions ultimately influence individual fitness because they determine whether an individual will be able to compete within the social system of its own species, avoid predators, or successfully find food. We first consider the distribution of individuals in their environments and in relation to other individuals within their populations. The mechanisms that individuals use to navigate within and between the habitats they use are briefly summarized. We follow by examining the complexities of social behavior centering on how individuals interact with other individuals within local populations. Individual amphibians and reptiles balance the primary benefit of social behavior, increased individual fitness, against the costs of acquiring the resources required to maintain activity and the potential risks of predation while carrying on these activities.

Chapter

8

Spacing, Movements, and Orientation

Exactly where individual animals live is determined by complex interactions between physiological requirements of individuals and physical characteristics of their habitats. The location of other individuals can constrain spacing patterns within bounds set by the physical environment. Movements are critical for locating food, mates, and avoiding environmental extremes and predators, and the ability to return to high-quality microhabitats, overwintering sites, and breeding sites requires systems for orientation. Animals are not distributed randomly—some places are better than others in terms of resource availability when balanced against the risk or costs of acquiring the resource. Animals do not remain in the same place—they are sensitive to gradients in resources and risk may vary with location. Because of their sensitivity to resource gradients, animals orient themselves and direct their patterns of movement in organized ways, often toward resources. The payoff for making these choices is clear: individuals that are better able to access resources while minimizing risk grow more rapidly, reproduce earlier, and, if their body size is larger as a result of their resource accruing abilities, produce more or bigger offspring (see Chapters 5 and 9). If all resources were spread uniformly in the environment or even across environments, it would be difficult for individuals or species to segregate spatially. Resources are not distributed uniformly. As a result, nearly all environments are patchy in one way or another. Even if a single resource were distributed uniformly across habitat patches, other resources would be distributed in other ways. As the number of potential resource categories increases, the likelihood that two species or two individuals would use all resources in the same way rapidly declines.

Global patterns of amphibian and reptile distribution indicate that the physical environment places limits on the spatial distribution of species. Seasnakes, for example, are largely distributed in the shallow, warm seas of southeastern Asia and northern Australia partly because they originated there and partly because the broad continental shelf areas offer a thermally appropriate habitat with a high diversity and abundance of potential prey. The absence of seasnakes in the Atlantic Ocean reflects their inability to cross cold polar currents and deep expanses of open ocean (Greene, 1997). Only a single species, *Pelamis platurus*, has traversed the Pacific and successfully colonized the coastal waters of western tropical America. This seasnake probably arrived in the eastern Pacific after the closing of the Panamanian gap (4 mybp), and hence was unable to continue its westward dispersal into the Caribbean and the Atlantic. For many crocodylians, a combination of fresh, or in some instances, brackish, water and the absence of freezing weather delimits their geographic distribution. For many amphibians, the spatial distribution of appropriate breeding sites sets limits on their distributions. Historical factors also play a role, as pointed out in Chapter 12. Past and present locations of dispersal barriers, including mountain ranges, rivers, and oceans, have excluded many taxa from invading areas where climatically they could survive and flourish. Geographic distributions of species or populations can be limited by microhabitat distributions, the presence or absence of competitors or predators, or even the availability of prey. Microhabitat specialists such as *Xantusia henshawi* are restricted to areas with exfoliating rock (Lee, 1975); flat lizards in the genera *Tropidurus* and *Platysaurus* are restricted to granitic outcrops in South America and South Africa, respectively (Vanzolini et al., 1980; Broadley, 1978). *Anolis* lizards on Caribbean islands have evolved microhabitat specialization (see Chapter 12) in response to competition with other *Anolis* and thus are limited to specific microhabitats within the same habitat (Williams, 1969). Dietary specialists occur only in microhabitats containing the prey that they eat. Horned lizards, *Phrynosoma*, which are ant specialists, do not occur in habitats lacking edible ants (see Pianka and Parker, 1975), and some, like *Phrynosoma cornutum*, may move very little while active because they sit along trails of harvester ants (Whitford and Bryant, 1979; Whiting et al., 1993). No single factor explains the geographic distribution of any species. At a local level, a multitude of factors influence spatial distributions of individuals.

LOCAL DISTRIBUTION OF INDIVIDUALS

Distribution of individuals occurs at a number of levels. In the context of community ecology, species tend to be associated with specific microhabitat patches (the "place" resource or niche discussed in Chapter 12). A relatively easy and informative exercise is to walk through a natural habitat and list the animal species and the microhabitats where they were first observed. A tabulation of these data reveals that each species tends to be associated with different microhabitats. Because microhabitats interdigitate, any given habitat can contain a large number of species that spatially overlap, but each occurs predominantly in specific microhabitats. Selection of microhabitats is enforced by competitive interactions and the risk associated with activity in unfamiliar places or patches. An individual may no longer be cryptic or may be unable to escape predators in unfamiliar patches (see Chapter 12).

Within species, individuals often move within an area that they do not defend from conspecifics, called the home range. Foraging and social activities occur in this area. Adjacent home ranges can overlap or they can be completely exclusive. A portion or all of the home range might be defended, usually against conspecifics but occasionally against other species. This defended area is the "territory," which is introduced in this chapter and discussed in the context of social behavior in Chapter 9. "Spacing" typically implies the spatial distribution of individuals within a species, and more specifically, within a local population. As a result, spacing usually focuses on home ranges and territories.

Home Ranges

Home ranges of amphibians and reptiles usually are associated with one or more resources. The resources include food, shelter, mates, thermoregulation sites, escape routes, and a host of other things. Home range size can vary between sexes, is often associated with body size, and is influenced by population density. For species living in two-dimensional habitats, such as fringe-toed lizards on sand dunes in southern California or plethodontid salamanders in the Great Smoky Mountains, the home range can easily be measured as the area that encompasses all of the outer points within which an individual occurs. This technique is called the minimum polygon method of home range determination and does not take into consideration the amount of time or the relative frequency with which an individual might use different parts of the home range. Nevertheless, it is the most widely used method of calculating home range and has many advantages. In particular, it can be calculated easily in the field, the measurements are fairly accurate if samples are adequate, and it is based on actual observations of animal occurrences (Rose, 1982). Moreover, the amount of overlap in home ranges between individuals in the population can be easily calculated. The variation in sizes of amphibian and reptile home ranges is impressive (Table 8.1). An association between body size and home range size exists across many species, but there are some exceptions. For arboreal amphibians and reptiles, measuring home range is much more difficult, and even defining it is not easy. The Amazonian lizard *Anolis transversalis*, for example, spends much of its life in the canopy of a single or a few trees. The home range is three-dimensional and thus is a volume rather than an area. Moreover, because the lizard can only move on the branches and leaves within the canopy, many gaps or unusable areas exist. Nevertheless, conceptually, a three-dimensional home range is no different from a two-dimensional one-they both represent regular use of space by individuals.

TABLE 8.1 Home Range and Resource Defense in Select Amphibians and Reptiles

				Defense		
Taxon	**Area (m^2)**	**Female area**	**Male size (mm)**	**Territorial**	**Site/resource Specific**	**Habits**
Batrachoseps pacificus	3.6	?	42	?	?	Terrestrial
Desmognathus fuscus	1.4	?	45	?	?	Semiaquatic
Salamandra salamandra	10	>	82	?	?	Terrestrial
Atelopus varius	<20	=	25	+		Terrestrial
Rana clamitans	65	=	60	+		Semiaquatic
Syrrhophus marnockii	328	=	20	+		Terrestrial
Terrapene c. triungis	52,000	=	115	–	–	Terrestrial
Trachemys scripta	397,500	<	200^a	–	±	Aquatic
Crocodylus niloticus	7,990	<	2100^b	+		Aquatic
Sceloporus merriami	535	<	45	+		Terrestrial
Varanus olivaceus	20,500	<	450	±	+	Arboreal
Xantusia riversiana	17	=	65	–	+	Terrestrial
Acrochordus arafurae	15,000	?	900	–	?	Aquatic
Carphophis amoenus	253	?	215	?	?	Semifossorial
Natrix natrix	99,000	>	700	?	?	Terrestrial

Sources: salamanders are Bp (Cunningham, 1960), Df (Ashton, 1975), and Ss (Joly, 1968). Frogs are Av (Crump, 1986), Rc (Martof, 1953), and Sm (Jameson, 1955). Turtles are Tct (Schwartz et al., 1984) and Ts (Schubauer et al., 1990). Crocodilian is Cn (Hutton, 1989). Lizards are Sm (Ruby and Dunham, 1987), Vo (Auffenberg, 1988), and Xr (Fellers and Drost, 1991 a,b). Snakes are Aa (Shine and Lambeck, 1985), Ca (Barbour et al., 1969), and Nn (Madsen, 1984).

[a] Plastron length.

[b] Total length.

Home ranges can vary through time or space, they can change radically following single events, and for some species they may not even exist. Home ranges are not defended, and parts of them may be used by other individuals. Overlap in home ranges among individuals can be considerable. During the nonbreeding season, many terrestrial amphibians (e.g., *Ambystoma maculatum, Plethodon cinereus, Bufo marinus, Rana temporaria*) have small-to moderate-sized home ranges away from water. An individual can have one or more resting and feeding sites (activity centers) within its home range but it might use a single site for a day, a week, or longer before shifting to another site. An amphibian may not visit all sites each day or even each week, but the periodic occurrence at sites and the persistent occupancy of the total area adjacent to these sites delimit the individual's home range. For species that reproduce in ponds or streams, the home range breaks down during breeding events because adults breed in aquatic sites that are not within the home range. Amphibians (e.g., dendrobatid frogs, *Eleutherodactylus, Plethodon*) generally deposit eggs or give birth within their home ranges. Some spend their entire lives in a single home range.

Shape of home ranges varies considerably and is often related to the microhabitat specificity of a species and the physical structure of the microhabitat. Semiaquatic species (*Desmognathus monticola, Rana macrodon*) are linearly distributed along stream and lake shores. As a consequence, individuals within these populations tend to have elongate, narrow home ranges along the stream edge or lakeshore. The water snake *Nerodia taxispilota* is linearly distributed along rivers, streams, and edges of ponds and lakes in the southeastern United States. Along part of the Savannah River that divides Georgia and South Carolina, these water snakes are most common adjacent to backwater areas, such as oxbow lakes and areas along the outside banks of curves in the river where water velocity is highest (Mills et al., 1995). They commonly are found on steep river banks or perched on logs and roots out of the water. During one 2-year period, each snake moved an average of 270 m, although most individuals moved very little. These snakes are capable of long travel but often remain in a relatively small area because of the availability of good perch sites. Additionally, steep banks and overhanging logs and roots provide some protection from aquatic and terrestrial predators.

The smooth softshell turtle *Apalone muticus* is linearly distributed in rivers throughout the southern and central United States. These rivers experience drastic and unpredictable fluctuations in water level, and flooding can cause major changes in the physical structure of the river channel. As a result, the home ranges of these softshelled turtles are short-lived (Plummer and Shirer, 1975). Home ranges are associated with sandbars that change periodically due to erosion, but some softshells change the location of their home ranges without any apparent change of habitat (Fig. 8.1). Some individuals often move long distances from their home ranges and then return, presumably assessing the quality of other areas in the river. Other individuals maintain approximately the same home range year after year even when the habitat structure changes.

Home size often varies among sexes and with reproductive state. Home ranges of male *Sceloporus jarrovi* are twice the size of female home ranges and increase in average size as the fall breeding season commences. In contrast, female home range size remains the same (Fig. 8.2; Ruby, 1978). The increase in male home range size is due partially to a 50% reduction in male density from summer to fall and an increase in the proportion of the home range defended by reproductive males. By the peak of the breeding season, males defend the entire home range; during this time, the home range and territory are the same.

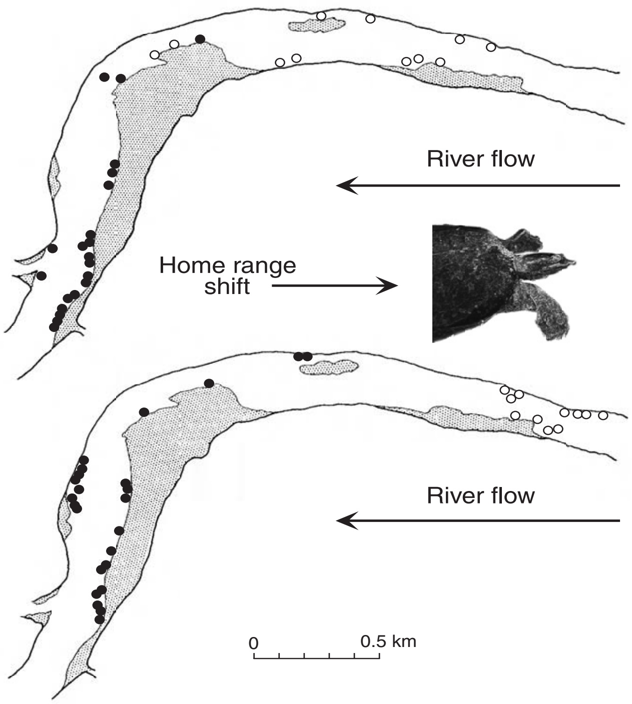


FIGURE 8.1 Shifts in the home ranges of two female *Apalone muticus* in the Kansas River. Two time periods are represented: solid circles represent early sightings during summer and open circles represent sightings approximately 1 to 2 months later (time periods are not the same for each turtle). The upper display is a subadult that shifted its home range 1363 m upstream. The lower display is an adult female that shifted its home range 1534 m upstream. Because the turtles are aquatic and live in rivers and streams, their distribution is linear. Adapted from Plummer and Shirer (1975).

In most species, home range size generally decreases as food availability or density increases (Fig. 8.3). In at least one instance, the local climate places constraints on lizard activity that feed back on the amount of space used by individuals. As in *S. jarrovi*, home ranges of male *Sceloporus merriami* are larger than those of females, but geographically close populations vary greatly in home range size (Fig. 8.4). This lizard occurs across an elevational gradient in the Chisos Mountains of west Texas. Populations at higher elevations experience a much more mesic environment than those at low elevations. Males and females at the lowest elevations at Boquillas have much smaller home ranges than individuals at higher elevations even though food availability is lowest and lizard density is highest at Boquillas. Although it appears paradoxical that lizard density could be high with low food availability, an interaction between reproductive, microhabitat, and energetic requirements accounts for the small home ranges. The environment at Boquillas is the most extreme (high temperatures, low rainfall) along the elevational gradient, and as a result, the amount of time available to each lizard for activity is reduced. Feeding rates of Boquillas lizards are low, suggesting that energy is more limited compared with higher-elevation populations. The high temperature also limits activity, and with food already in short supply, the lizards further limit their activity, which reduces home range size. The reduced activity coupled with low food availability ultimately feeds back on allocation of energy for reproduction and results in lower reproductive output. *S. merriami* is a sit-and-wait predator. In contrast, lizards that actively search for prey would be expected to have larger home ranges *Cnemidophorus*, an active forager, has a relatively large home range throughout which it searches for prey (Anderson, 1993).

The Australian elapid *Hoplocephalus bungaroides* centers its home range around retreat sites in rocky outcrops and tree hollows and remains inactive most of the time (Webb and Shine, 1997). Male home ranges of *H. bungaroides* overlap very little during the breeding season, but home ranges of females are often within the home ranges of males. Females carrying eggs move less than nonreproductive females or males, and as a result have smaller home ranges. Home range size in males and females varies among years, apparently in response to the relative abundance of their mammalian prey.

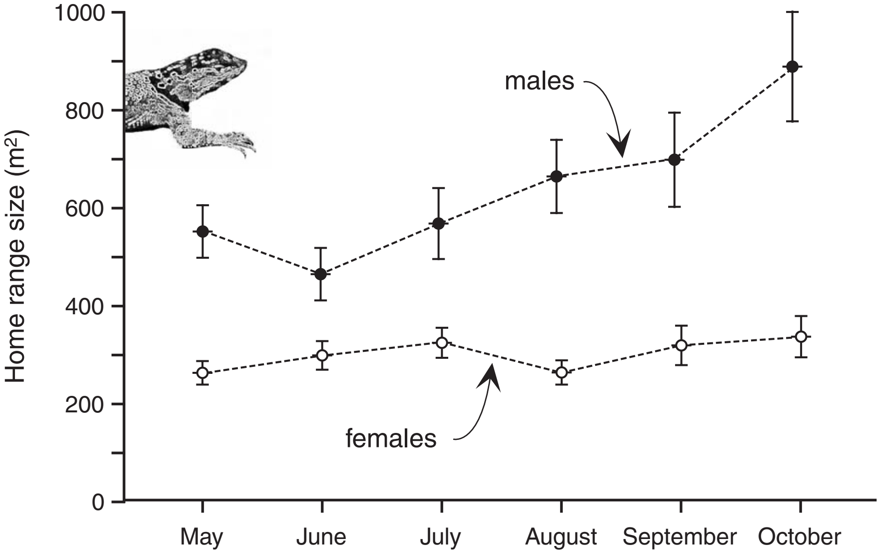


FIGURE 8.2 Seasonal variation in home range size for male and female *Sceloporus jarrovi*. Breeding occurs in fall, at which time male home ranges increase in size. Adapted from Ruby (1978).

Aquatic environments offer special challenges in terms of space use for amphibians and reptiles, not only because of their three-dimensional nature, but because they fluctuate depending on rainfall or drought. Aquatic snakes and turtles often have relatively large home ranges that can change seasonally. During particularly dry years, their entire area of activity can shift if a pond or stream dries. Most leave their home ranges for brief periods to deposit eggs. Surprisingly, one of the larger aquatic (marine) turtles, *Chelonia mydas*, has one of the smallest home ranges once it settles in an area to feed. These turtles create a submarine pasture and focus their grazing in that small area. In contrast, another seaturtle, *Dermochelys coriacea*, appears to move constantly, tracking the seasonal blooms of its jellyfish prey.

A few other patterns of space use occur in ambush–foraging species that do not fit the typical home range model because of regular long-distance shifts in primary foraging sites. Individual prairie rattlesnakes, *Crotalus viridis*, wander until they locate an area of high prey density (Duvall et al., 1985). They remain in that area

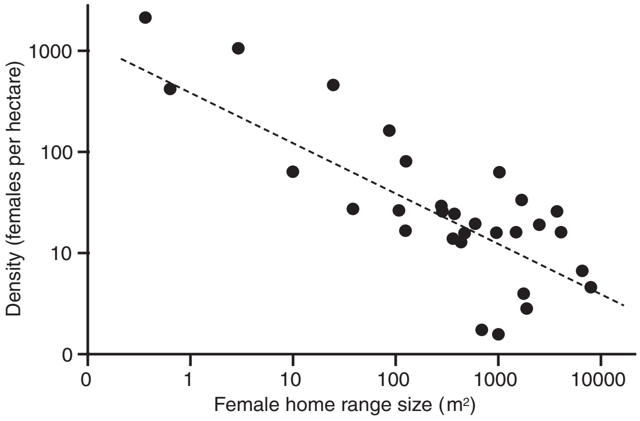


FIGURE 8.3 As female density increases, home range size decreases for most amphibians and reptiles as shown here for territorial and nonterritorial female lizards. Adapted from Stamps (1983).

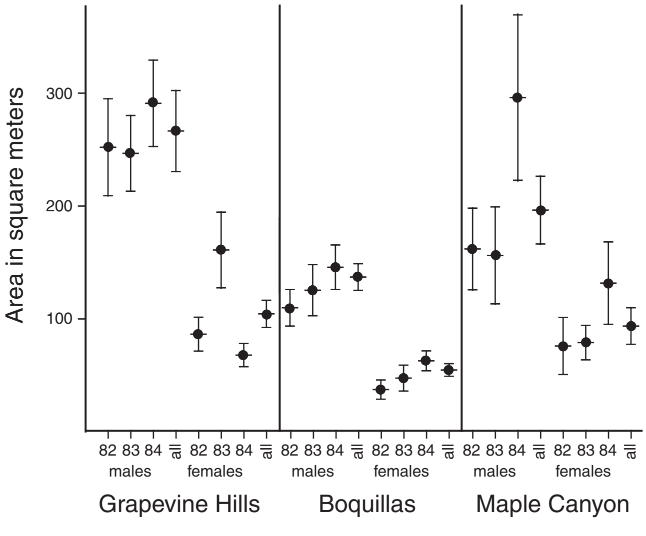


FIGURE 8.4 Home range size in *Sceloporus merriami* varies between sexes, among years, and among three different sites in the Chisos Mountains of west Texas. Boquillas, the site with the most extreme (hot and dry) environment, imposes thermal constraints on lizard activity, resulting in small home ranges. Adapted from Ruby and Dunham (1987).

until prey density reaches some lower threshold and prey capture becomes infrequent, after which they move to a new site. Likewise, the water snakes *Nerodia sipedon* appear not to have traditional home ranges (Tiebout and Gary, 1987). Because "home range" size continues to increase with the number of times an individual is captured, use of space appears to consist of a series of activity centers that shift spatially. Similar use of space has been observed in other snakes (e.g., Madsen, 1984).

Water pythons, *Liasis fuscus*, migrate seasonally to follow their prey, dusky rats (*Rattus colletti*), which shift their dry season distribution from soil crevices in the backswamp areas in the Northern Territory, Australia, to levee banks up to 12 km away during the wet season when the floodplain floods (Fig. 8.5). At the end of the wet season, the snakes return to the floodplain even though rat density remains high on the levee. Adult male rats, which reach a larger size than females, are more abundant and reach larger size on the floodplain due to higher levels of moisture and nutrients, and these are preferred (Madsen and Shine, 1996b). The snakes shift their seasonal activity to coincide with greatest abundance of their preferred prey. The bushmaster, *Lachesis muta*, moves to microhabitats where prey capture is likely, such as along the edge of a fallen log or along trails. The snake typically remains in one spot for several weeks, rarely changing position except to raise the head at night while "searching" for passing prey. After a meal, the snake remains at the site 2–4 more weeks digesting the prey, and then seeks out a new foraging site. It remains a mystery whether some sort of large, circumscribed area is involved or whether bushmasters simply move along a nonrepeating track.

The most obvious examples of age-specific differences in space use can be found in species with complex life cycles. Many larval amphibians live in aquatic environments and the adults live in terrestrial environments,

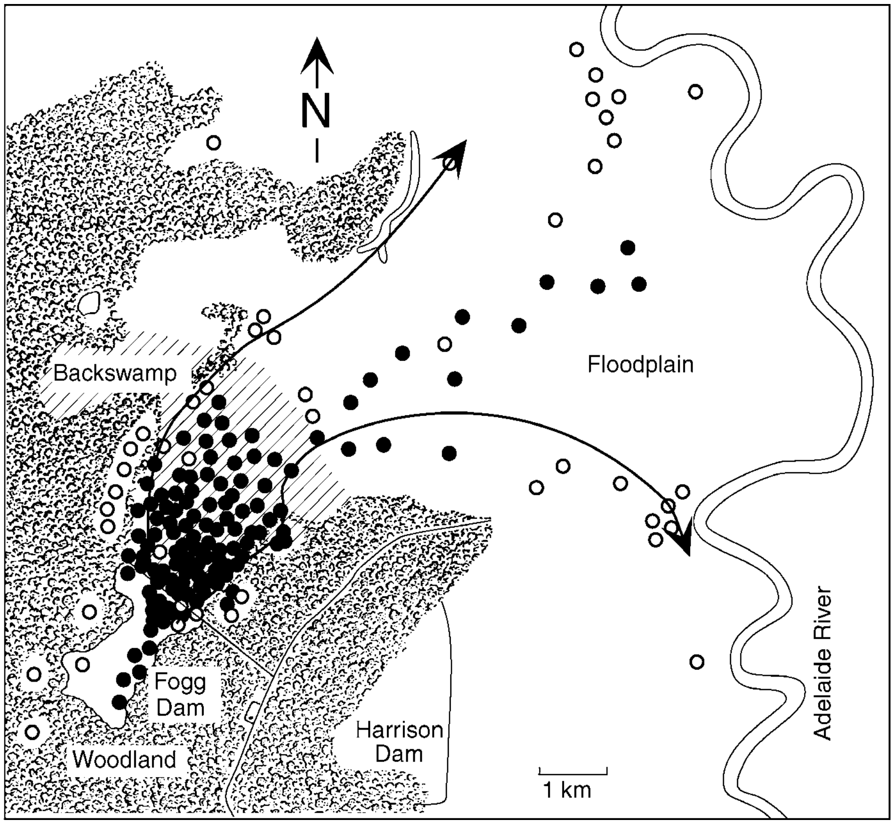


FIGURE 8.5 Locations and movements of water pythons (*Liasis fuscus*) in the Northern Territory of Australia. Solid circles indicate positions of snakes during the dry season when the floodplain is dry and the backswamp contains deep crevices; open circles indicate positions of snakes during the wet season when the floodplain is wet and the backswamp crevices are closed. Snakes move to high ground in wet season because rats become rare in low areas. Snakes move to the backswamp and dam during the dry season because rats there are larger. Arrows show movement patterns for two radio-tracked individuals (one male and one female), showing that individuals move long distances. Adapted from Madsen and Shine (1996).

so little overlap in larval and adult use of space is expected. Adults of many amphibians with complex life histories have home ranges, but whether larvae have home ranges is unclear. In arboreal lizards, juveniles use different perches than adults or disperse in response to population density. Hatchlings of the Neotropical lizard *Anolis aeneus* prefer perches averaging 1.35 cm in diameter, whereas adult females and males prefer much larger perches (8.5 and 38.6 cm diameter, respectively). Hatchling perches are closer to the ground (14.4 cm on average) than those of adult females and males (50.6 and 169.7 cm, respectively). Home range size is also much smaller for hatchlings (Stamps, 1978). Because of ontogenetic differences in perch characteristics, hatchlings occupy different microhabitats than adults.

Females of Australian sleepy lizards, *Tiliqua rugosa*, give birth within their home ranges. During spring of their first year of life, juveniles maintain home ranges that overlap much more with the home range of their mother than with home ranges of adjacent adults even though no parental care occurs (Bull and Bagurst, 1998). Juvenile home ranges are about 60% of the size of home ranges of females and the juveniles move less often and for shorter distances than adult males or females. Adult males have home ranges that average about 20% larger than those of adult females.

Territories

A territory is the portion of a home range that is actively defended against intruders, usually because there is some sort of defendable resource or something about the particular area that is better than adjacent areas. Defense results in exclusive use of the territory by the resident (Brown and Orians, 1970). In amphibians and reptiles, when territoriality occurs, males are most often territorial and females are not. In a few species, females defend a territory as well. Most often, territories defended by males contain females whose home ranges are included within the male territory. Because territoriality allows an individual to maintain control over resources, it involves competition among individuals within species for resources that ultimately contribute to individual fitness. Natural selection favors those individuals that control and use resources in a way that positively influences their reproductive success. Discovering the connection between resource control and reproductive success is seldom easy. Every aspect of territorial behavior has costs, and obviously, the gains associated with territoriality must outweigh the costs if territorial behavior is to be maintained through time.

Imagine two individual males in a population—one defends good places to forage from other males but allows females into those areas and breeds with them. The other male controls no resources and as a consequence does not attract females. However, he can easily find enough food to keep himself healthy by moving around. The territorial male, as the result of his territory defense behavior, might, hypothetically, be more vulnerable to predation. Nevertheless, he has many more opportunities for mating than the other male. He actually may not live very long, but long enough to reproduce, so that when he is killed by predators, he will have left offspring. In the meantime, the nonterritorial male remains healthy and lives a long life. Representation of his genes ends in that generation, whereas territorial genes (even with the risk attached) are passed on to the next generation. Alternatively, the long-lived, healthy male could replace a territorial male that was eliminated, shift his behavior to territorial, and achieve a high reproductive success. In this scenario, both types of male reproductive strategies are maintained in the population.

Of course, social systems and the evolution of social systems are not this simple—for example, a nonterritorial male might be able to sneak a few matings with females living within the home range of territorial males. Thus, nonterritorial genes can be passed on at a lower frequency than territorial ones. Territoriality generally is linked with mate choice and other aspects of social systems (see Chapter 9).

Given the above, a territory can be defined explicitly as any defended area that meets the following three conditions: it is a fixed area; it is defended with behavioral acts that cause escape or avoidance by intruders; and such behavioral acts result in exclusive area use with respect to rivals (Brown and Orians, 1970).

Territoriality is well known in some frogs and salamanders but unknown in caecilians. In frogs, acoustic signals serve as avoidance displays, and outright aggression can occur in threat displays. Territoriality occurs most often in frogs with extended breeding seasons and is rare or does not occur in explosive breeders or species with very restricted breeding seasons. It also occurs in frogs with extended parental care (e.g., dendrobatid frogs). In bullfrogs, males establish territories that contain good oviposition sites, which they defend with threats, displays, or wrestling matches. Large males win a majority of contests with other males, indicating that male size determines dominance (Howard, 1978a). Good oviposition sites have high embryo survival rates (Howard, 1978b). The two primary sources of mortality, developmental abnormalities and leech predation, are reduced at sites with temperatures $>32^\circ$C and enough vegetation and depth to reduce leech predation. Females are attracted to territories with a potential for low egg mortality, and because large males control these territories, they mate with more females. In this situation, the resource base for territories is high-quality egg deposition sites, and the payoff is increased reproductive success for defenders of these sites. Sneak or satellite males that are not territory holders occasionally intercept females and mate with them.

Most data on salamander territoriality is based on studies of a single clade, *Plethodon*, which is composed largely of terrestrial species. *Plethodon cinereus* marks territories with chemicals (pheromones). In the laboratory, adult male and female *P. cinereus* show "dear enemy" recognition in which they are less aggressive toward recognized enemies than they are toward unfamiliar intruders (Jaeger, 1981). Evolutionarily, this reduces energy spent in continual high-level encounters with close neighbors that are unlikely to go away but will maintain distance if reminded that a territorial holder is in place. Combat, often directed at the tail, can occur, and tails can be lost as a result of encounters. Tails are important energy stores for reproduction; consequently, the loss of a tail negatively affects reproductive success. Bites during combat are also directed at the nasolabial grooves, which are important transmitters of chemical signals (Jaeger, 1981; Jaeger et al., 1982).

The Central American dendrobatid frog *Dendrobates pumilio* lives in leaf litter on the forest floor. Males maintain territories that they aggressively defend from other males (Bunnell, 1973). Males call from tree bases or fallen logs, and the distribution of these structures determines intermale distance to a large extent (McVey et al., 1981). Many males remain in restricted areas over long time periods and when displaced experimentally, return to their territories. Females deposit eggs in terrestrial oviposition sites and males use elevated perches for calling; the location of male territories must include these resources.

Food available to individual animals varies both temporally and spatially and can influence space use. Males and females of the montane lizard *Sceloporus jarrovi* defend territories against conspecifics of the same size or sex (Simon, 1975). Territories that contain relatively more food tend to be smaller than territories with less food, independent of the differences in territory size associated with lizard body size. Adding food to the territory of *S. jarrovi* results in a shift in space use; the site where food is added becomes the center of the territory. In this instance, food availability appears to determine the location of the territory.

Evolution of Territoriality

Studies conducted on use of space by individuals within and between species reveal considerable variation in the proportions of home ranges that are defended. Some species defend the entire home range, others defend specific sites within the home range, and others do not appear to defend any part of the home range. Males of many species without territories aggressively attack other males that approach females either within the male's home range or while the resident is courting the female (see Chapter 9). Although adaptive scenarios can be devised to explain territorial defense in nearly every amphibian or reptile, similarities in behavior among closely related species often reflect common ancestry; individuals of many species behave the way their ancestors did.

A close examination of defense behavior in lizards suggests that evolutionary history determines behavioral patterns. Among studied lizards, defense is accomplished by direct combat, threats, or simple avoidance (Stamps, 1977). Combat involves biting, wrestling, or any behaviors involving physical contact between two individuals. Threat refers to aggressive communication in which no physical contact is made. Threats most often involve push-up displays, throat expansion, or high-intensity erection and contraction of the dewlap. Avoidance defense is based on indirect displays such as chemical signals. Push-up displays are presented from a distance where the primary goal is to assert presence. Other examples of avoidance displays exist as well. The size of the area defended can range from all or part of the home range to none of it (Table 8.2). An examination of the distribution of home range defense on a lizard phylogeny shows that there has been an overall reduction in the proportion of the home range defended throughout the evolutionary history of lizards (Fig. 8.6). This phylogenetic analysis shows that territoriality (defense of all or part of the home range) is ancestral to all lizards and that adaptive scenarios are not necessary to explain territoriality in the Iguania and Gekkonidae. The loss of territoriality within the scleroglossans (particularly the Teiidae, Lacertidae, Anguidae, and Varanidae) most likely reflects the consequences of a switch from a sit-and-wait foraging mode to an active or wide-foraging mode (see Chapter 10).

Other Patterns of Space Use

Many amphibians and reptiles brood or guard nests, and remain near the eggs until the eggs hatch (e.g., Figs. 4.22 and 4.23). The space the brooding parent uses is much smaller than the home range and is not necessarily within the home range used during the nonbrooding season. Females of the four-toed salamander, *Hemidactylium scutatum*, brood eggs in clumps of peat moss along slow-moving streams, remaining restricted to the nest for an extended time period. Female broad-headed skinks, *Eumeces laticeps*, brood clutches of eggs in

TABLE 8.2 Ten Behavioral Categories for Lizards Based on Aggressive Defense of Resources

	Defense area		
Defense style	All or part of home range	Specific site (basking, shelter)	No area (self)
Combat	Type I	Type IV	Type VII
Threat	Type II	Type V	Type VIII
Avoidance	Type III	Type VI	Type IX
Type X[a]			

Source: Adapted from Martins (1994).

Note: Each category is defined by the intersection of defense style and defense areas.

[a] Type X consists of affiliative aggregations or random distribution of animals.

partially decomposed pockets within hardwood logs, rarely leaving until after the eggs hatch.

Aggregations occur in a wide variety of amphibians and reptiles for a number of reasons (Table 8.3). All aggregations represent nonrandom use of space, and most often are centered around scarce resources. For amphibians, the most obvious examples are aggregations of adults in ponds or other bodies of water during breeding events (e.g., Marquis et al., 1986). Spadefoots arrive by the thousands to breed in temporary ponds as do many other explosive-breeding frogs (Duellman and Trueb, 1986). Tadpoles of a variety of species form dense "schools" that move about in ponds, presumably to offset predation (e.g., Caldwell, 1989). A variety of species of salamanders, including *Plethodon glutinosus, Ambystoma macrodactylum,* and *Ambystoma tigrinum*, aggregate when the terrestrial environment becomes excessively dry (e.g., Wells and Wells, 1976; Anderson, 1967; Gehlbach et al., 1969). Garter snakes aggregate in large numbers for both overwintering and mating (Aleksiuk and Gregory, 1974). In fall, *Sceloporus jarrovi* aggregate along crevices in mountains of southeastern Arizona to overwinter. They frequently bask in sun along the crevices to gain heat even though they are territorial during the activity season (Congdon et al., 1979). Snakes and lizards aggregate by default at talus slopes used as nesting sites in northern Oregon. Fifty-one lizard eggs, 294 snake eggs, and 76 snakes were found in a patch of talus with an area of 150 square feet (Brodie et al., 1969). These are but a few examples of aggregations in amphibians and reptiles (Fig. 8.7).

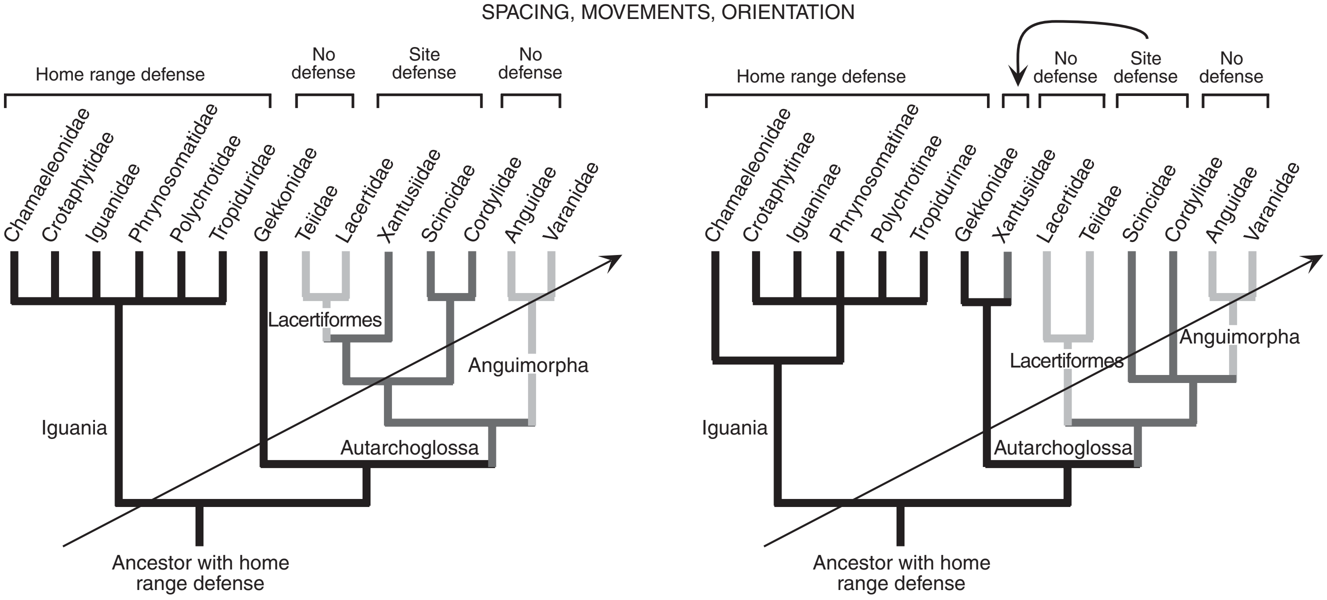


FIGURE 8.6 Phylogeny for lizards showing the evolutionary distribution of "home range" defense. The ancestor of all lizards presumably defended the entire home range, with an overall reduction in area defended as lizards diversified. Variation of shading on evolutionary lineages corresponds to headings across the top, and the arrow denotes the direction of evolutionary trends. The taxonomic rearrangement in lizards (right) slightly changes the interpretation of Martins' (1994) original figure (left), but the overall trend is the same. Adapted from Martins (1994).

TABLE 8.3 Examples of Social, Nonreproductive Aggregations of Amphibians and Reptiles

Taxon	Purpose
Salamanders, seven mixed species	Hibernation
Plethodon glutinosus	Estivation
Salamandra salamandra	Hibernation
Bufo tadpoles	Schooling
Hyla meridionalis, Pelodytes, Triturus, Podarcis	Hibernation
Limnodynastes, juveniles	Water conservation
Xenopus laevis tadpoles	Schooling
Terrapene ornata	Hibernation
Terrapene ornata and *Kinosternon flavescens*	Hibernation
Crocodilian hatchlings	Reduce predation
Alligator mississippiensis	Feeding
Amblyrhynchus cristatus	Sleeping
Diadophis punctatus	Water conservation (?)
Pelamis platurus	Feeding
Storeria dekayi	Water conservation (?) and hibernation
Thamnophis (3 species), 3 other snake genera, *Ambystoma*, and *Pseudacris*	Hibernation
Typhlops richardi	Water conservation (?)

Sources: Amphibians are s (Bell, 1955), Pg (Humphries, 1956), Ss (Lescure, 1986a), B (Wassersug, 1973), Hm (Van den Elzen, 1975), L (Johnson, 1969), and Xi (Wassersug, 1973). Reptiles are To (Carpenter, 1957), c and am (J. Lang, 1989), Ac (Boersma, 1982), Dp (Dundee and Miller, 1968), Pp (Kropach, 1971), Sd (Noble and Clausen, 1936), T (Carpenter, 1953), and Tr (Thomas, 1965).

MOVEMENTS, HOMING, AND MIGRATIONS

Most amphibians and reptiles move relatively little during their entire lifetime except when they are breeding. Individual box turtles, *Terrapene c. carolina*, in Maryland, for example, moved very little over 30 years or more and remained in the same home range (Stickel, 1950, 1989); similar observations have been made on many other species. Individuals move to forage or change foraging positions, pursue mates, defend territories, deposit eggs, or escape predators. Most of these movements take place within the individual's home range. The benefits of moving are offset by the costs of moving (usually energy or risk of mortality). For species with cryptic morphology or coloration, moving upsets crypsis and can accrue a survival cost. Active or wide-foraging species tend to move considerably more and expend more energy doing so within their home ranges than do species that use the sit-and-wait foraging mode (Anderson and Karasov, 1981; Huey and Pianka, 1981a). The former's alert behavior and rapid response to predators offset the cost of exposure.

Both extrinsic and intrinsic factors influence movements of amphibians and reptiles (Table 8.4). Herpetologists rapidly learn to take advantage of environmentally induced patterns of movements; amphibians, in particular, can be collected or observed in great numbers on rainy nights during spring in temperate zones and on the first rainy nights during tropical wet seasons. Rattlesnakes (particularly subspecies of *Crotalus viridis*) occur in large numbers when they aggregate for overwintering. Long-term studies on slider turtles have identified factors causing movements in turtles (Table 8.5). These factors likely apply to most species of amphibians and reptiles. Movements outside of the home range carry additional risks compared to movements within the home range, largely because traveling occurs in areas with which the individual has little or no familiarity. When these movements occur, they usually are related to breeding, finding food or water no longer available in the home range, or overwintering, or are in response to catastrophes (e.g., flooding).

The most apparent dichotomy in movement patterns on a daily basis is diurnal versus nocturnal movement. Most salamanders and frogs are nocturnal, but some species such as cricket frogs (*Acris*) are both diurnal and nocturnal. Movements of winter-breeding amphibians occur nearly exclusively at night even though weather conditions during the day at the same time of year are favorable for breeding (Pechmann and Semlitsch, 1986). The absence of daylight appears to trigger movements in *Pseudacris crucifer, Pseudacris ornata, Pseudacris nigrita*, and *Rana sphenocephala,* and both temperature and moisture determine the specific nights on which breeding will occur. On nights with low temperatures or no rainfall, breeding migrations do not occur. The risk of movement during daytime for these frogs may be tied to diurnal predators like birds. Dendrobatid frogs are diurnal and sleep at night, often perched within 0.5 m of the ground on leaves of small plants. Brightly colored species (e.g., *Dendrobates, Phyllobates*) offset predation by having noxious or poisonous skin secretions and advertising their toxicity with aposematic coloration, whereas other species (e.g., *Colostethus*) offset diurnal predation by cryptic coloration and behavior (see Chapter 11).

Depending on species, turtles can be diurnal or nocturnal. Box turtles (*Terrapene*) and tortoises (*Geochelone*) are strictly diurnal, as are many aquatic turtles (e.g., *Apalone, Graptemys*). Some species, like *Chelydra serpentina*, appear to be active during the day and at night. Crocodylians are active during both day and night, but

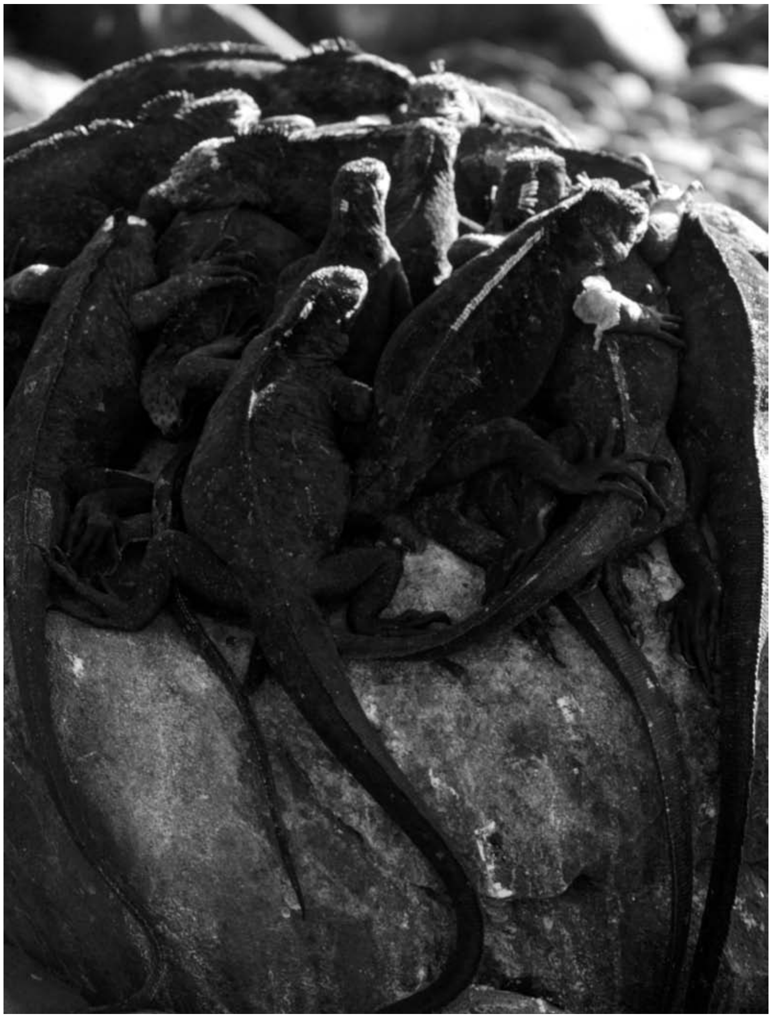


FIGURE 8.7 A basking aggregation of marine iguanas, *Amblyrhynchus cristatus*. Photograph by K. Miyata.

much of their diurnal activity involves basking. *Caiman crocodilus* in the Amazon of Brazil, for example, bask on sandy banks of rivers and ponds during the day and actively search through their aquatic habitats for prey at night. When water floods the forest during the wet season, caimans enter the flooded forest in search of stranded prey. Among lizards, most are diurnal (e.g., all iguanians, teiids, gymnophthalmids), some are nocturnal (e.g., many gekkonids), and some vary their diel activity, at least on the surface, with season (e.g., helodermatids). Among snakes, nearly every possible diel pattern of activity occurs. Most desert snakes are nocturnal but some, like *Masticophis flagellum*, are strictly diurnal. Likewise, many tropical snakes are nocturnal, but some species, including all species of whipsnakes in the genus *Chironius*, are diurnal (Fig. 8.8).

In the Mojave Desert of southern California, male sidewinders (*Crotalus cerastes*) move an average of 185 m each night while active, whereas nongravid females move only 122 m (Secor, 1994). Individuals are active on about 60% of the nights during their activity season. Greatest movements of adult males occur during spring and fall mating seasons, which suggests that they are searching for females. Activity ranges of individuals vary from 7.3 to 61 ha; males, females, and juveniles have similar activity ranges. Sidewinders appear to move randomly until fall when their movements are directed toward overwintering sites. Overwintering sites are usually located in rodent burrows at the interface between sand and alluvial habitat patches.

Freshwater turtles leave their aquatic habitats to dig nests, search for mates, overwinter, or locate new aquatic habitats when their original stream or pond dries up. Six turtle species, *Trachemys scripta, Kinosternon subrubrum, Pseudemys floridana, Sternotherus odoratus, Chelydra serpentina*, and *Deirochelys reticularia*, are long-time

TABLE 8.4 Factors That Influence Movements of Individual Amphibians and Reptiles

Environmental	Population	Individual
Daily temperature patterns	Density	Sex
Seasonal temperature patterns	Sex ratio	Body size
Humidity/rainfall	Age structure	Age
Habitat type or condition	Size structure	Physiological condition
Catastrophic events	Disease/parasitism	Reproductive state
		Recent experience

Source: Adapted from Gibbons et al. (1990).

residents of Ellenton Bay, a freshwater pond located approximately two miles from the Savannah River in South Carolina. Adults of four other species, *Pseudemys concinna, Clemmys guttata, Chrysemys picta*, and *Kinosternon baurii*, occasionally enter Ellenton Bay (Tuberville et al., 1996). Juveniles of the latter four species have never been observed at the pond, and, with the exception of *P. concinna*, a majority of nonresident turtles were males (100% for *K. baurii* and *C. picta*, 80% for *C. guttata*). Only a single female *P. concinna* has entered the pond. Most of the nonresident turtles are males because long overland movements by males increase their probability of encountering females in other aquatic habitats, whereas females have less to gain by long-distance moves, particularly considering the potential costs of increased risk of predation by terrestrial predators. Overland ventures by *T. scripta* vary from 0.2 to 9 km, resulting in sightings of turtles in ponds other than their home ponds (Fig. 8.9). Many of the turtles return to their home ponds, indicating that these movements are not immigrations.

TABLE 8.5 Causes and Consequences of Movements at the Intrapopulation and Interpopulation Level for Turtles

Category	Purpose	Primary benefits gained by moving
Intrapopulational (short range)	Feeding	Growth; lipid storage
	Basking	Increased mobility due to body temperature increase; reduction of external parasites; enhanced digestion
	Courtship and mating (adults only)	Reproductive success
	Hiding, dormancy	Escape from predators or environmental extremes
Interpopulational (long range)	Seasonal	
	Seeking food resources	Growth; lipid storage
	Nesting (adult females)	Direct increase in fitness
	Mate seeking (adult males)	Direct increase in fitness
	Migration (hibernation, aestivation)	Survival
	Travel from nest by juveniles	Initiation of growth
	Departure from unsuitable habitat	Survival

Source: Adapted from Gibbons et al. (1990).

In Malaysia, the semiaquatic snake *Enhydris plumbae* occurs in water buffalo wallows, slow-moving streams, rice paddies, and a variety of other aquatic habitats (Voris and Karns, 1996). Most individuals move very little, and 44% do not move at all (Fig. 8.10). The snakes are active day and night but are observed on the surface at night. A partial explanation for the low movement in *E. plumbae* is that many occur in small, isolated bodies of water (buffalo wallows), but even those in rice paddies move very little.

Studying movement behavior of salamanders, especially terrestrial species, is logistically difficult. By inserting tiny tantalum-182 tags in the abdomen of salamanders, individuals can be located in the habitat even though they may be buried in soil or leaf litter. A scintillation system detects radioactivity of the tags from 2 m away. The technique appears particularly suitable for short-term studies because the isotope has no apparent effect on salamander physical condition and the tags remain in place for about a month (Semlitsch, 1981). This technique is not useful for longer time periods because salamanders lose body weight, suffer skin lesions, and often lose the tags after about 40 days. An early study using the technique revealed that some salamanders are capable of orientation and subsequent homing when displaced. Males of *Plethodon jordani* occupy home ranges that are about three times larger than those of females (Madison and Shoop, 1970). Salamanders displaced between 22 and 60 m from their home ranges return to within 7 m of their capture site, which indicates that they are capable of orientation. Because the displaced salamanders climbed up on vegetation, air-borne chemical cues were implicated in orientation. Homing studies on *Desmognathus fuscus* in Pennsylvania add support to the hypothesis that chemical cues are involved in homing. These salamanders maintain small home ranges along a stream for extended time periods. Four groups of

FIGURE 8.8 Although most tropical snakes are nocturnal, some, such as the tropical whipsnake, *Chironius fuscus*, are strictly diurnal. Photograph by L. J. Vitt.

salamanders were displaced to discover the possible cues used in homing behavior: one group was a normal, nontreated group; the second was an anosmic (olfactory system nonfunctional) group; the third group was blind; and the fourth group was a sham-treated control group (Barthalmus and Bellis, 1972). The anosmic group did not return to original home ranges, whereas varying numbers of the other treated groups did return, lending support to the hypothesis that chemical cues are involved in the orientation and homing process (see below).

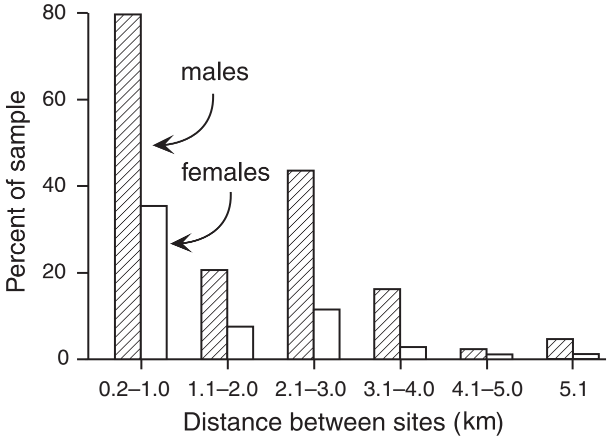


FIGURE 8.9 Long-range movements based on straight-line distances of *Trachemys scripta* between aquatic habitats in South Carolina. Travel between Ellenton Bay and Lost Lake was primarily over land. Exchanges in Par Pond could have been by a shorter overland route or a longer route through water. Adapted from Gibbons et al. (1990).

Among the most striking movements by extant amphibians and reptiles are seaturtle migrations from birth site to feeding grounds as juveniles and, many years later, back to nesting beaches as adults. Green seaturtles, *Chelonia mydas*, emerge from eggs at Tortuguero, Costa Rica, enter the Caribbean Sea, and migrate throughout most of the Caribbean (Fig. 8.11). Their long journeys and ability to return to the beaches where they hatched suggest a complex navigational system (see below).

Mass Movements

Mass movements occur in some amphibians and reptiles. The use of terrestrial drift fences around amphibian breeding ponds has made it relatively easy to monitor the movements of amphibians, some of which are startling. Ambystomatid salamanders and many frogs, especially those that are explosive breeders, move en masse to and from breeding ponds. Metamorphs leaving breeding ponds often do so en masse as well. During a single year (1970), 2034 individuals of 14 species of frogs moved in or out of one permanent pond, and 3759 individuals of 13 species of frogs moved in or out of another temporary

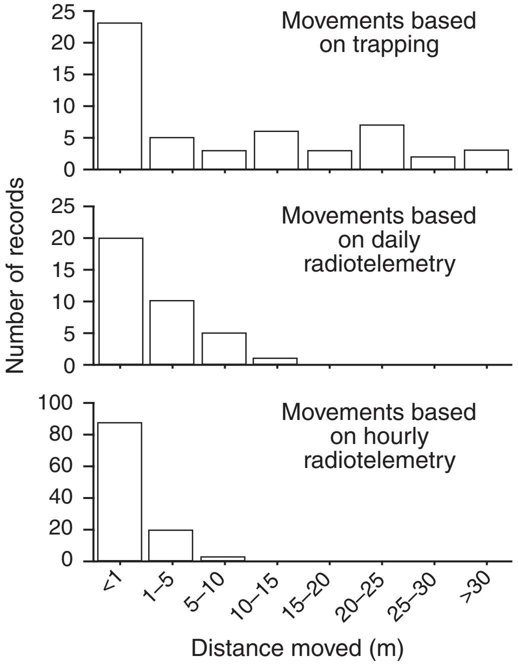


FIGURE 8.10 The snake *Enhydris plumbea* in Malaysia (Borneo) moves very little. The method of collecting movement data influences the results and might lead to misleading conclusions in species that move considerable distances. Adapted from Voris and Karns (1996).

pond in South Carolina (Gibbons and Bennett, 1974). However, the numbers of amphibians migrating into and out of ponds during breeding and metamorphosing events vary considerably among species and years. The salamander *Ambystoma opacum*, for example, did not enter or leave a small pond in South Carolina from 1970 to 1980, but in 1987, nearly 300 adult females entered and more than 800 metamorphs exited the pond (Pechmann et al., 1991). In the same pond over a 12-year period, patterns of movement among species were not concordant (Fig. 8.12).

Seaturtles and large freshwater turtles (*Podocnemis*) arrive at nesting beaches by the hundreds over a few nights. Garter snakes and rattlesnakes enter and leave hibernacula in large groups. Thus mass movements are common and generally appear related to breeding events or overwintering. These and the above examples largely represent directed and cyclic movements away from the home ranges used during the activity season.

Dispersal

Dispersal is undirected movement to locations unknown by the dispersing animal and commonly refers to juveniles leaving the home ranges of their parents to find a home of their own. Habitat instability, intraspecific competition, and inbreeding depression are considered the primary evolutionary driving forces resulting in dispersal (Fig. 8.13). Whether or not individuals should disperse is based on the relative costs and benefits of doing so (Clobert et al., 1994). Costs to dispersal include increased predation risk associated with entering unknown and unfamiliar habitats, potential difficulties finding resources (food, shelter), and potentially increased aggression from unfamiliar conspecifics. Benefits include opportunities to discover better resources, increased likelihood of outbreeding, and potentially reduced local competition. In populations of the European lizard *Lacerta vivipara*, more than 50% of juveniles disperse, whereas very low numbers of yearlings or adults disperse (Clobert et al., 1994). Dispersal of juveniles is greater when population density is high in their population of origin. High population density is an indicator of a temporally high-quality environment. High-quality environments produce offspring that are better able to compete because of relatively larger size and condition. By dispersing, these juveniles offset disadvantages associated with inbreeding. In low-quality environments, only the most competitive juveniles will survive, whether or not they disperse. These survivors will be the individuals with the best set of characteristics for the poor environment. By not dispersing and mating with other individuals that survived and thus carrying traits for survival under poor conditions, individuals with traits associated with success in the poor habitat will be favored. Even though inbreeding is potentially high, it is selective and consequently typical costs of inbreeding are relaxed compared to benefits juveniles gain by remaining in their place of origin (philopatry). In this example, a complex interaction between variation in the local environment and the costs and benefits of dispersal with respect to inbreeding determines whether juveniles should or should not disperse.

Amphibian metamorphs and hatchling seaturtles are two examples of cohorts that leave their natal sites but will return in subsequent years to breed. They do not appear to know where they are going as hatchlings, but innate navigational mechanisms will allow them to return later in life.

Metamorphosing amphibian larvae move into and through the habitat of their parents, most becoming part of the local populations. Dispersal distance usually is small, and the juveniles occupy home ranges in vacant spots among adults or in peripheral locations. Similar dispersal occurs in reptiles and direct-developing amphibians, although dispersal can occur later as large juveniles make the transition into the breeding population.

Among animal species with polygynous mating systems, males generally disperse farther than females, partly because males compete for females and partly because females often disperse less as the result of their

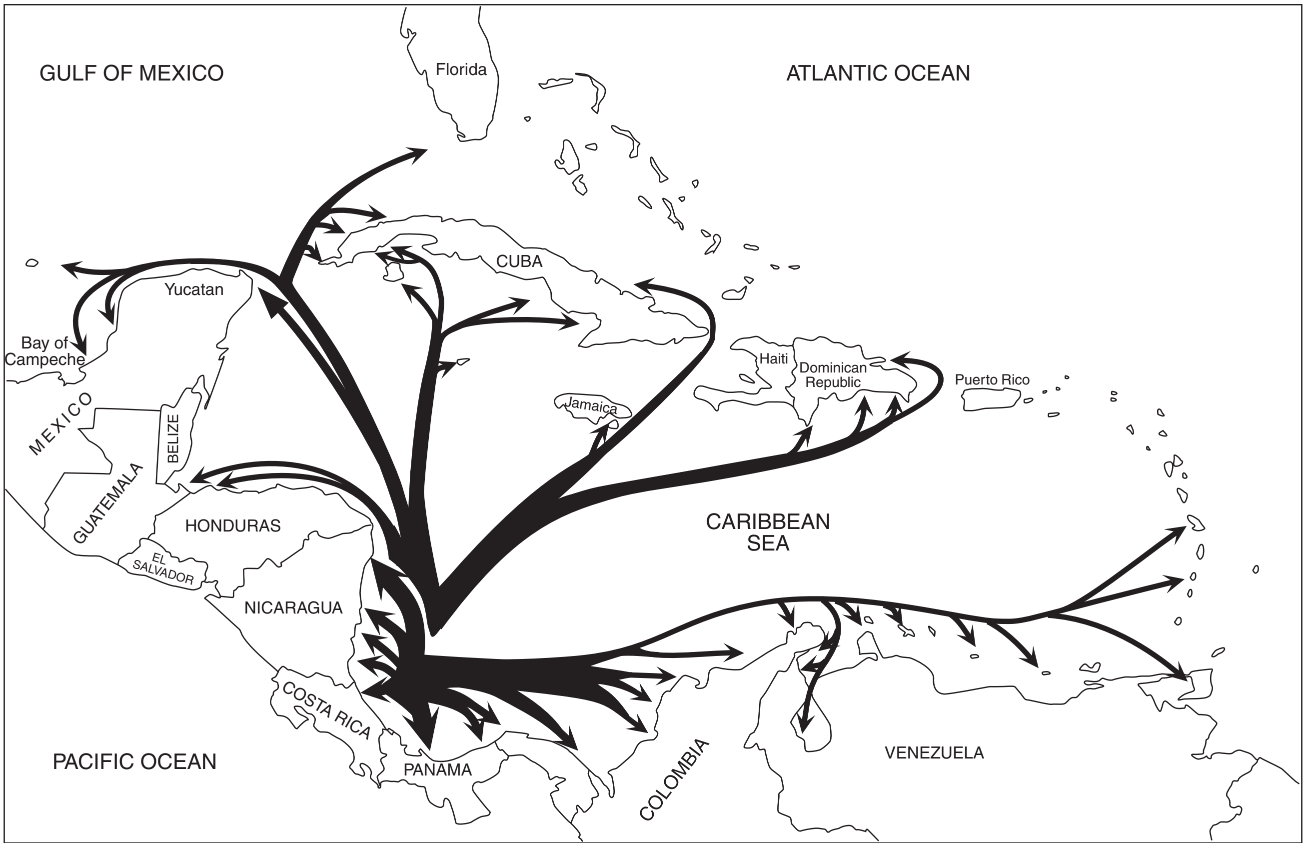


FIGURE 8.11 Green seaturtles travel from their nesting beaches throughout the Caribbean Ocean to reach feeding areas as far north as Cuba. Adapted from Bowen and Avise (1996).

association with resources or refugia from predators (Stamps, 1983). Male *Uta stansburiana* disperse during their first year of life, and in some cases, females disperse equally as far as males (Doughty et al., 1994). Females appear to disperse until they locate good territories. Some males disperse farther than females because they have to go farther to find unoccupied territories.

Homing and Orientation

Homing refers to the ability of displaced individuals to return to their original location. Implicit in any discussion of homing is the idea that animals must be able to sense the direction they are moving. Amphibians and reptiles that migrate, particularly during breeding events or just before and after overwintering, generally do not move randomly. Amphibians migrating into and out of breeding ponds enter and leave by relatively predictable pathways, as do rattlesnakes moving to overwintering den sites (e.g., Dodd, 1994; Dodd and Cade, 1998). Orientation can involve visual, olfactory, auditory, or even magnetic cues, each of which requires a different system for reception (Fig. 8.14). Orientation requires some sort of map and a compass. If the compass is based on celestial cues such as the sun, then a clock is necessary to reset the compass as the sun's azimuth changes seasonally.

Salamanders generally cannot home from more than about 30 m, but the newt *Taricha rivularis* in California can home for up to 2 km. Some individuals can home from about 8 km. Some turtles can home from only 0.5–1 km (*Clemmys guttata*), but others home over 500 km (seaturtles). Crocodylians can home for up to 2 or more kilometers. In the few lizards studied, relocation to distances of about 200 m or less results in good homing ability, but at a greater distance, the lizards do not return.

Many amphibians and reptiles return to specific shelters following both short- and long-distance movements. Movements of the snake *Hierophis viridiflavus* in Italy can be divided into single-day loops in which the snake leaves its shelter and returns by the end of the day, complex loops in which the snake moves greater distances over several days using temporary shelters, and large loops involving movements up to 3 km and lasting up to a month (Ciofi and Chelazzi, 1994). Single-day loops are

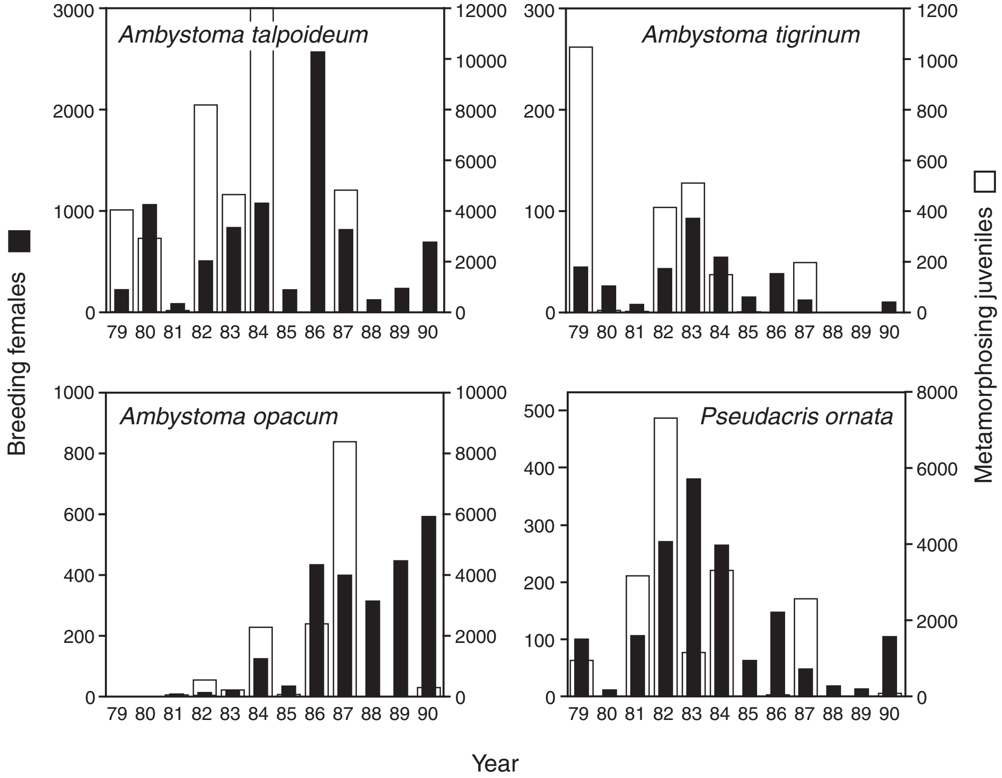


FIGURE 8.12 The number of breeding females and metamorphosing larvae of three salamander species and one frog species varies impressively from year to year in the small Rainbow Bay in South Carolina. Migration patterns of amphibians using the same breeding sites are not synchronous. Adapted from Pechmann et al. (1991).

primarily excursions for basking, complex loops appear to associated with foraging, and large loops appear associated with reproductive activity (Fig. 8.15).

Landmarks

Within home ranges, most amphibians and reptiles use local landmarks. The repeated use of the same perches, foraging areas, and overnight retreats indicates that individual reptiles and amphibians recognize landmarks within their home ranges. The existence of home ranges and territories is also evidence for the ability of individuals to recognize local landmarks. On a larger spatial scale, many species appear able to recognize the kinds of habitats they live in and orient to those. Some *Anolis* lizards are known to use elevated vantage points to survey their immediate habitat. In a simple but effective experiment, three species of *Anolis* were placed on artificial elevated posts from which they could see two vegetation types, a grass–bush habitat and a forest habitat (Kiester et al., 1975). *Anolis auratus* and *Anolis pulchellus* chose the grass–shrub habitat, whereas *Anolis cristatellus* chose the forest habitat. Because the choices correspond with the natural habitats of the lizards, the study reveals that these species used the habitat structure as a landmark or cue to direct their movement.

Orientation and homing ability varies among lizards, even in the same habitat. In open habitats of southern Idaho, horned lizards, *Phrynosoma douglassi*, seem unable to find their original home range when displaced, yet adult sagebrush lizards, *Sceloporus graciosus*, are able to orient toward and return to their original home ranges (Guyer, 1991). Horned lizards may not maintain home ranges for long because their movements follow the movements of their ant prey. Since home ranges and defense of all or part of the home range (territories) are ancestral in lizards (Martins, 1994), horned lizards have apparently lost these abilities (to orient and return to home ranges).

When disturbed, many amphibians and most reptiles rapidly retreat along what appear to be well-known escape routes. This too demonstrates their familiarity with local landmarks. Directed long-distance movement, such as annual migrations of prairie rattlesnakes to den sites, also suggests the importance of local landmarks in orientation and navigation.

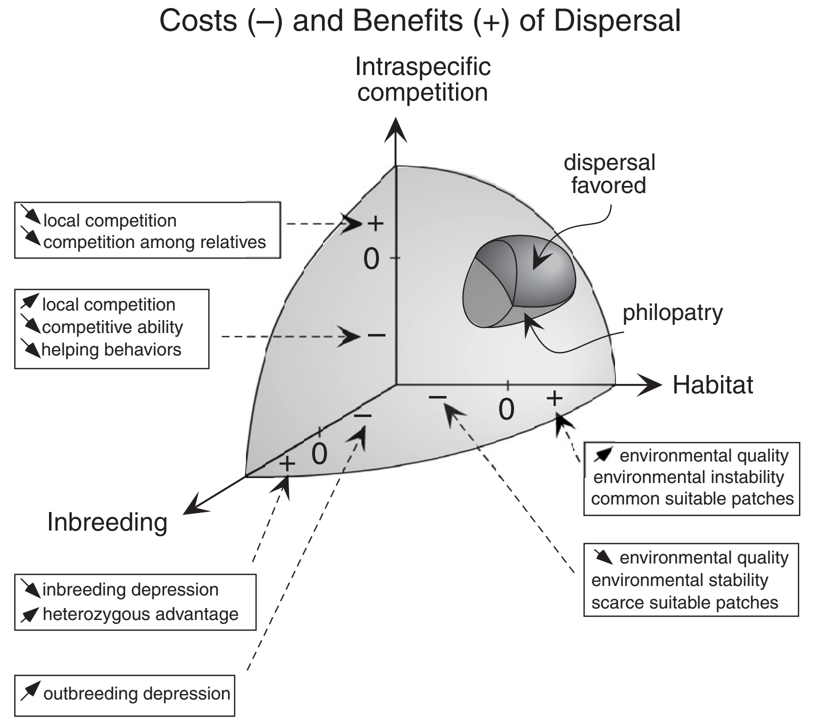


FIGURE 8.13 Model showing the relationships between costs and benefits of dispersal. The curved surface represents points where costs and benefits of dispersal are at equilibrium. Dispersal behavior will be selected above the plane whereas philopatry will be selected below the plane. The three-dimensional volume represents a species in which some individuals (e.g., juveniles) disperse and others (e.g., adults) remain where they are. Adapted from Clobert et al. (1994).

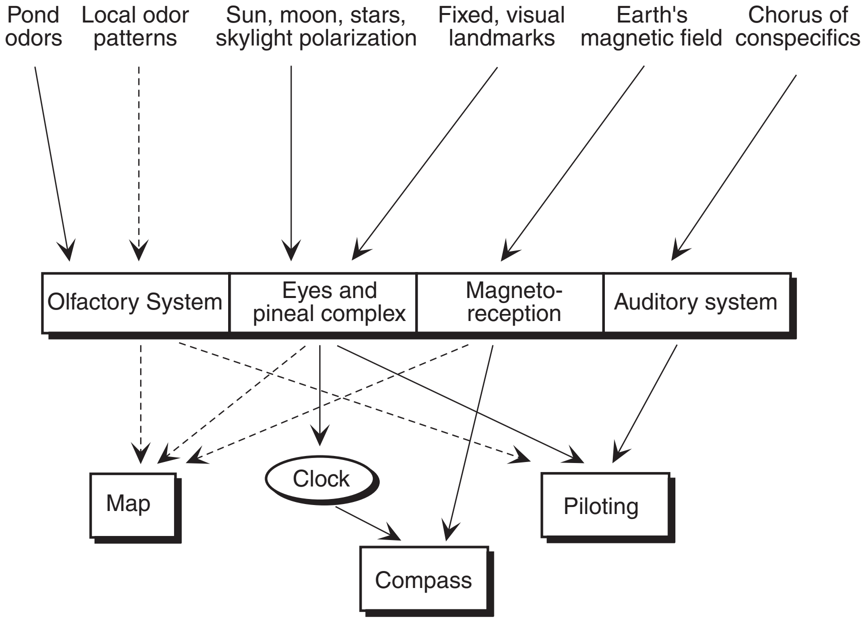


FIGURE 8.14 Relationships among cues, sensory systems, and the mechanistic basis of orientation and navigation for anurans. These relationships may be similar for most amphibians and reptiles. For terrestrial species, odors might be associated with den sites or daily retreats. Adapted from Sinch (1990).

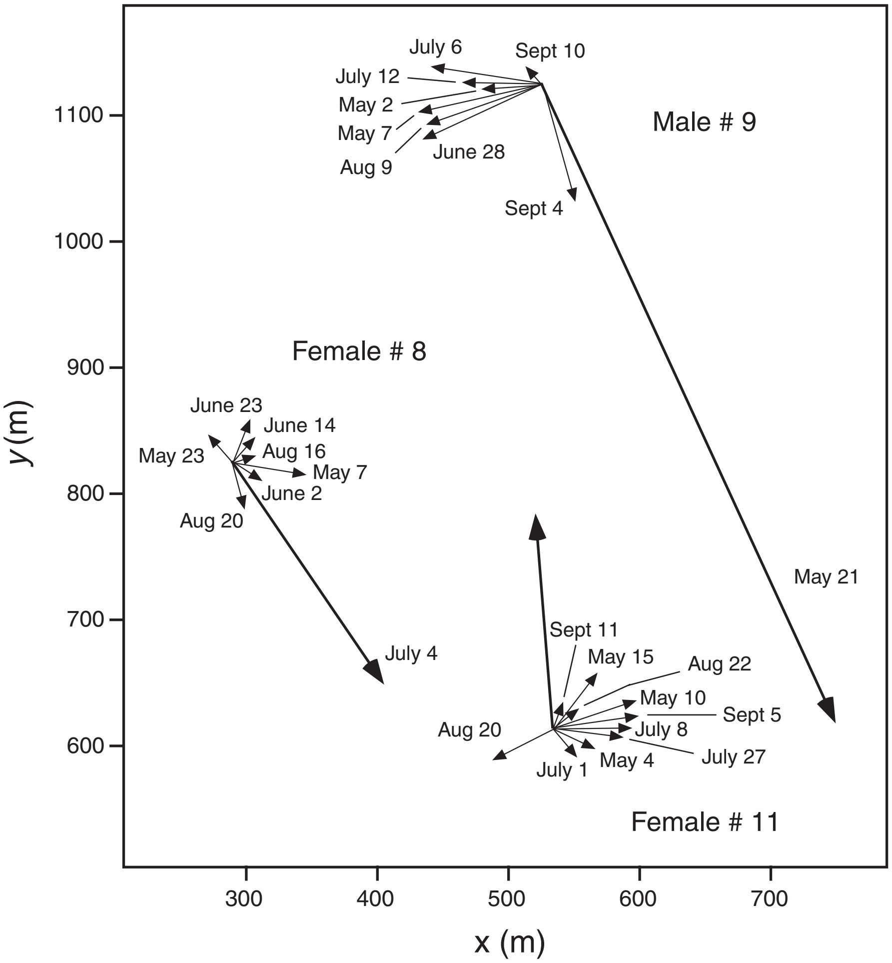


FIGURE 8.15 Movement activity of three individual *Hierophis viridiflavus.* Short arrows indicate typical 1–day or complex movements, and the heavier, long arrows indicate large loops. The tip of each arrow indicates the most distant point reached by the snake during each excursion. Adapted from Ciofi and Chelazzi (1994).

x–y Orientation

The interface between aquatic (or marine) and terrestrial environments provides a landmark for orientation by animals that use the interface. Many frogs, for example, typically jump into the water at approximately 90° to the shoreline; their jumps are nonrandom with respect to physical characteristics of the environment. The advantages to orientation toward or away from shorelines are clear. For adult amphibians that sit along the shore, escape into the water is important for avoiding terrestrial predators; for larvae facing metamorphosis, orientation toward shore is critical for emergence into the terrestrial environment; and for adults during breeding migrations, orientation toward breeding sites is crucial to find aquatic environments for egg deposition. This type of orientation is termed *y*-axis orientation. Linear cliff faces, river banks, and a host of other physical characteristics of the environment might also serve as the basis for *x–y* orientation in terrestrial species. For aquatic amphibians, the *x* axis is the shoreline and the amphibians tend to move perpendicular (90°, the *y* axis) to it (Fig. 8.16). Of course shorelines can face any direction. For example, a circular pond has portions that face every possible direction of the compass. Amphibians use the sun and its trajectory, which are predictable, to set their *x–y* compass based on the particular shoreline that they use. When landscape views are taken away, frogs and tadpoles retain their ability to orient perpendicular to the *x* axis as long as they can view the sky (e.g., Ferguson, 1967; Goodyear, 1971; Goodyear and Altig, 1971; Tracy, 1971). Some evidence suggests that turtles may also use the sun to set an *x–y* compass (Gibbons and Smith, 1968).

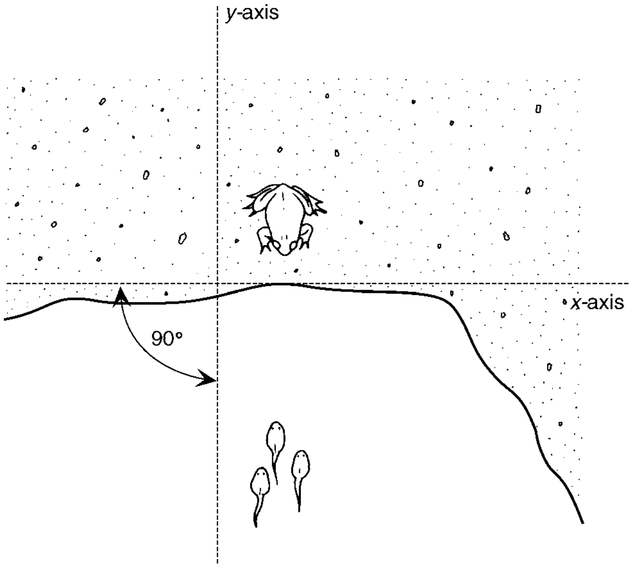


FIGURE 8.16 *y*-axis orientation is a type of celestial orientation. The animal establishes a homing axis (*y*) perpendicular to an identifiable physical attribute of its home (e.g., shoreline, the *x* axis). Normal escape response is into the pond for the frog being approached by terrestrial predators or to shallow water for tadpoles being approached by aquatic predators; return follows the compass direction of the *y* axis. Adapted from Adler (1970).

Orientation by Polarized Light

Light radiates outward from the sun. As the light waves enter the earth's atmosphere, the atmosphere deflects some light waves into a plane perpendicular to the original plane of entry. This scattering or deflection is polarization, and the scattered component (i.e., polarized light) travels in a single plane along a path called the *e*-vector. Because the *e*-vector always remains perpendicular to the sunlight's entry plane rather than to the earth's surface, the orientation of the *e*-vector plane relative to every spot on earth changes constantly as the earth rotates. For amphibians or reptiles that see polarized light, this changing orientation offers a directional clue. In addition, an inverse relationship exists between reflection and polarization—over water surfaces and damp soils, reflectance is low and polarization is high; over drier soils, reflectance is high and polarization is low (Coulson, 1974; Yeomans, 1995). Variation in polarized light over wet versus dry landscapes provides amphibians and reptiles with means to differentiate between wet and dry areas and to move to their preferred habitat.

Much indirect evidence and some clever laboratory experiments suggest that some amphibians and reptiles use polarized light in orientation and navigation. The emydid turtle *Trachemys scripta*, when displaced on sunny days to terrestrial sites 300 m away from their home ranges in a pond, orient toward the pond even though they cannot see it (Yeomans, 1995). On cloudy days, turtles fail to orient, indicating that the clouds, which stop polarized light, interfere with the ability of turtles to orient. The outer segments of cones in the eyes of *T. scripta* are capable of differentially absorbing polarized light (Liebman and Granda, 1971), further suggesting that the mechanism for locating ponds may be detection of polarized light reflected from aquatic habitats.

The pineal body of salamanders and possibly lizards is a polarized light receptor (e.g., Adler and Taylor, 1973; Taylor and Adler, 1973; Adler and Phillips, 1991). Both blinded and normal-sighted *Ambystoma tigrinum* orient to a shoreline once their internal compass has been set based on a vector of polarized light. When light is blocked from the top of the head by opaque plastic, these salamanders orient incorrectly, thus implicating the pineal in orientation based on polarized light (Adler, 1976).

Orientation by Chemical Cues

Many habitats (e.g., ponds) and retreat sites have characteristic odors that can be used by amphibians and reptiles for orientation and navigation. In southern California, the toad *Bufo boreas* breeds during spring in ponds and lakes. The toads spend the remainder of the year dispersed in the surrounding terrestrial environment. When displaced 50–200 m from a pond on clear nights, adults orient to the pond and return; on cloudy nights they also orient to the pond but not as precisely (Tracy and Dole, 1969). Blinded toads also orient to the pond but the possibility exists that they use alternate light receptors. However, when olfactory nerves are severed and the toads rendered anosmic, the toads orient randomly on clear nights even though celestial cues are available. Thus, even in the presence of celestial cues, loss of olfactory senses removes the toads' ability to orient. Because a host of environmental factors can affect the dispersion of chemical cues in natural habitats (e.g., wind), it is likely that once chemical cues are detected, they are used to set an internal compass. Once the compass course is set by chemical cues, frogs can use celestial cues to navigate.

Olfactory cues also appear important in orientation and navigation in some salamanders. Observations that salamanders retain the ability to home accurately without celestial cues suggest that olfactory cues are used, particularly on overcast or rainy nights (Ferguson, 1971). Displaced *Plethodon jordani* that are blinded return to home sites, suggesting that olfactory cues serve as orientation and navigation cues (Madison, 1969). Early studies on *Taricha rivularis,* in which these salamanders were rendered anosmic by damaging the olfactory nerves, showed a reduction in the homing ability, thus demonstrating that the olfactory system is involved in orientation (Grant et al., 1973). The salamander *Ambystoma maculatum* migrates on cloudy and rainy nights yet locates ponds. A clever experiment, in which salamanders were placed in arenas with two paper towels, one soaked in water and mud from their home pond and the other soaked with water and mud from non-home ponds, revealed that *A. maculatum* discriminates between the two odor sources, preferentially orienting toward the odor from home ponds (McGregor and Teska, 1989). These results are consistent with field observations that when *A. maculatum* are placed in unfamiliar ponds, they often migrate back to their home pond (e.g., Shoop, 1968).

Magnetic Orientation

The eastern red-spotted newt (*Notophthalmus viridescens*) is well known for its accurate homing behavior. This newt apparently detects its geographic position based on information associated with its home site (i.e., a "map") and a sense of direction ("compass"). One possible basis for such a map is the spatial variation in the magnetic field. The newts may have two different magnetoreception mechanisms that explain differences between their orientation responses to shoreline and those to their home pond under different conditions of light (Fig. 8.17). One mechanism involves visual centers in the brain that appear to respond to directional magnetic stimuli. Because visual centers are involved, this mechanism depends on light. The other mechanism involves the trigeminal nerve system, which is independent of visual input and thus does not require light. The possibility exists that a highly sensitive magnetite-based receptor responds to polarity of the magnetic field, and, if present in newts, would explain their ability to home. Such receptors have been found in other vertebrates.

Alligators and seaturtles appear capable of orienting on the basis of magnetic cues as well (Lohmann et al., 1996; Rodda, 1984, 1985; Rodda and Phillips, 1992). Seaturtles are renowned for their keen abilities to navigate, and because much of their environment is open ocean, landmarks are largely unavailable. Loggerhead seaturtles (*Caretta caretta*) that hatch in Florida, for example, appear to circle the north Atlantic Ocean and

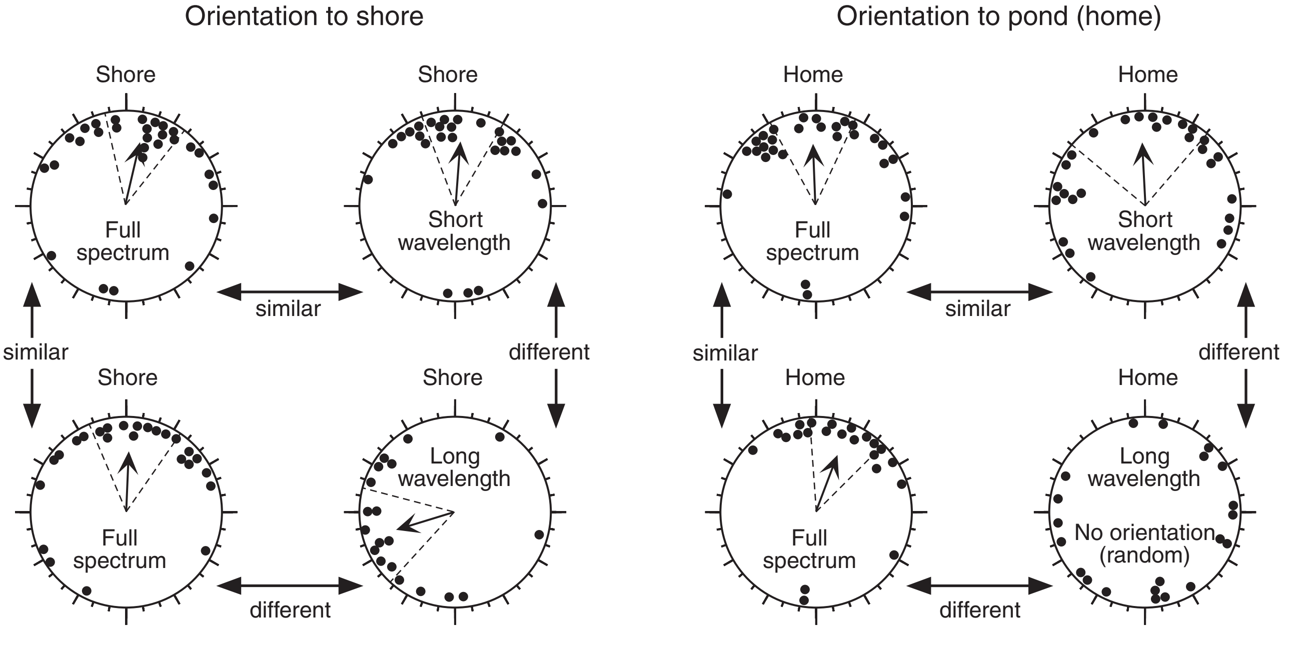


FIGURE 8.17 Diagrammatic summary of experiments on orientation toward shore and toward the home pond for eastern red-spotted newts. In both sets of experiments, controls are those with a full spectrum of light available. On the left, newts oriented toward shore in both of the controls and when under short-wavelength light. Under long-wavelength light, newts oriented approximately 90° counterclockwise from the shore, and their pattern of orientation was significantly different from both their controls and the newts under short-wavelength light, demonstrating the light dependency of shoreline magnetic orientation. On the right, newts oriented toward their home ponds in both controls and under short-wavelength light, but oriented randomly under long-wavelength light, demonstrating the light dependency of home pond magnetic orientation. Adapted from Phillips and Borland (1994).

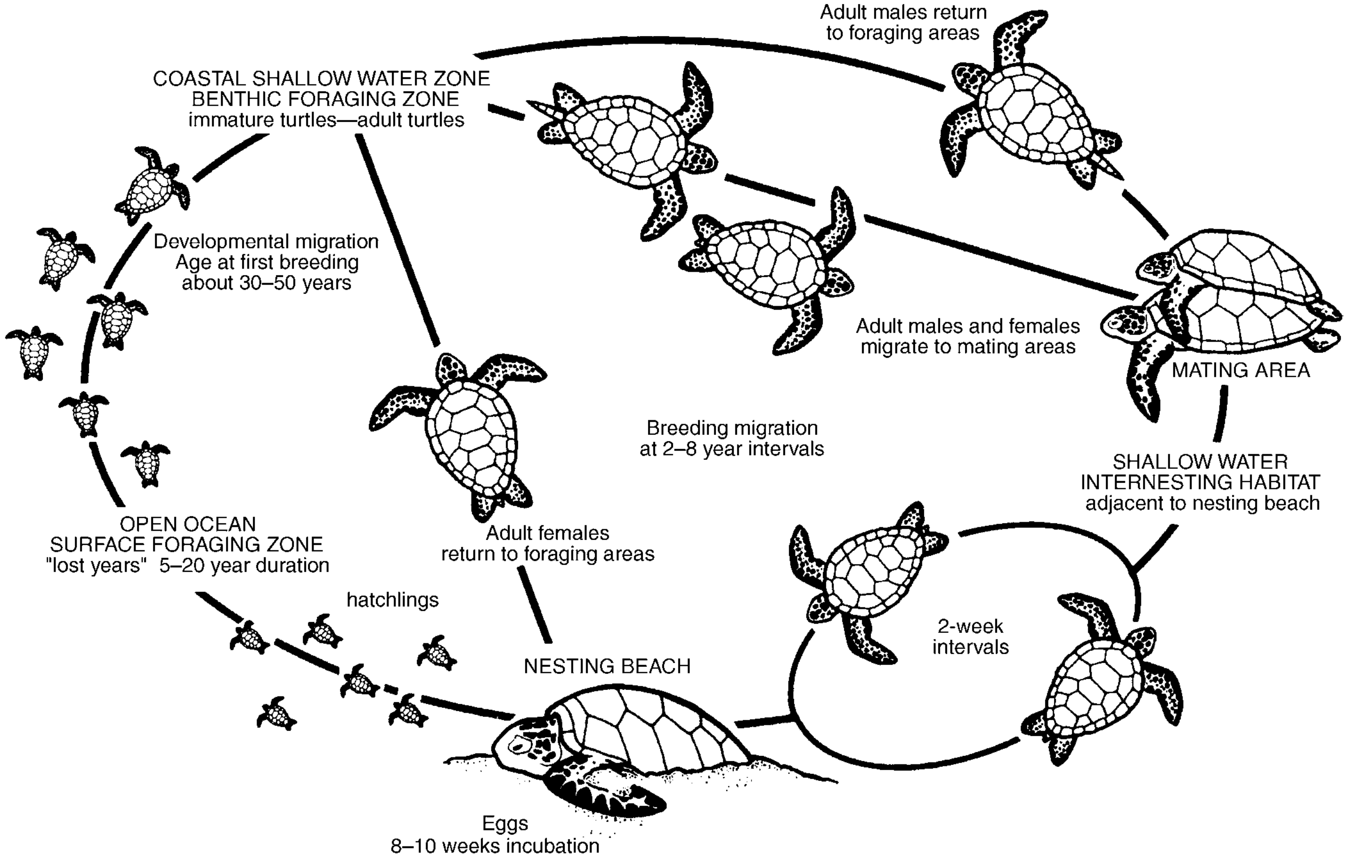


FIGURE 8.18 Life cycle of the green seaturtle showing the course of movements throughout life and possible cues used for orientation during each life history stage. Adapted from Miller (1996).

return several years later as juveniles to the American coastline. One population of green seaturtles (*Chelonia mydas*) nests on beaches of Ascension Island, more than 2200 km east of their feeding grounds off the coast of Brazil. The regular return of adults to the tiny island attests to their capability for precise orientation and navigation. Studies on mitochondrial DNA have shown that females in this population and other populations return to the beaches where they hatched (Bowen and Karl, 1996). Magnetic orientation likely is involved in open ocean navigation. In laboratory experiments, hatchlings orient to magnetic fields, to wave action, and even to chemical cues (Grassman et al., 1984; Lohmann, 1992; Lohmann et al., 1996). When leaving the beach following hatching, the hatchlings first orient on light from the moon and stars reflecting off the ocean, which takes them to the water. Once in the water, they orient on incoming waves and move perpendicular to them, which takes them out to sea. When the small turtles intersect the Gulf Stream, they are carried by currents around the Sargasso Sea (Fig. 8.18). Magnetic cues appear to be used for navigation while at sea. Once they reach maturity, at an age of 30–50 years, the adult females return to beaches for nesting.

ADDITIONAL READING

Adler, K. (1970). The role of extraoptic photoreceptors in amphibian rhythms and orientation: A review. *J. Herpetol.* **4:** 99–112.

Clobert, J., Massot, M., Lecomte, J., Sorci, G., Fraipont, M., and Barbault, R. (1994). Determinants of dispersal behavior: The common lizard as a case study. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 183–206. Princeton University Press, Princeton, NJ.

Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F., and Salmon, M. (1966). Orientation, navigation, and natal beach homing in sea turtles. In "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 107–135. CRC Press, Boca Raton, FL.

Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. *In* "Lizard Ecology. Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 169–204. Harvard University Press, Cambridge, MA.

REFERENCES

Spacing, Movements, and Orientation: Introduction: Broadley, 1978; Greene, 1997; Lee, 1975; Pianka and Parker, 1975; Vanzolini et al., 1980; Whitford and Bryant, 1979; Whiting et al., 1993; Williams, 1969.

Local Distribution of Individuals: Home Ranges: Anderson, 1993; Bull and Bagurst, 1998; Duvall et al., 1985; Madsen, 1984; Madsen and Shine, 1996b; Mills et al., 1995; Plummer and Shirer, 1975; Rose, 1982; Ruby, 1978; Stamps, 1978; Tiebout and Gary, 1987; Webb and Shine, 1997.

Territories: Brown and Orians, 1970; Bunnell, 1973; Howard, 1978a,b; Jaeger, 1981; Jaeger et al., 1982; McVey et al., 1981; Simon, 1975.

Evolution of Territoriality: Stamps, 1977.

Other Patterns of Space Use: Aleksiuk and Gregory, 1974; Anderson, 1967; Brodie et al., 1969; Caldwell, 1989; Congdon et al., 1979; Duellman and Trueb, 1986; Gehlbach et al., 1969; Marquis et al., 1986; Wells and Wells, 1976.

Movements, Homing, and Migrations: Anderson and Karasov, 1981; Barthalmus and Bellis, 1972; Huey and Pianka, 1981a; Madison and Shoop, 1970; Pechmann and Semlitsch, 1986; Secor, 1994; Semlitsch, 1981; Stickel, 1950, 1989; Tuberville et al., 1996; Voris and Karns, 1996.

Mass Movements: Gibbons and Bennett, 1974; Pechmann et al., 1991.

Dispersal: Clobert et al., 1994; Doughty et al., 1994; Stamps, 1983.

Homing and Orientation: Adler, 1976; Adler and Phillips, 1991; Adler and Taylor, 1973; Bowen and Karl, 1996; Ciofi and Chelazzi, 1994; Coulson, 1974; Dodd, 1994; Dodd and Cade, 1998; Ferguson, 1967, 1971; Gibbons and Smith, 1968; Goodyear, 1971; Goodyear and Altig, 1971; Grant et al., 1973; Grassman et al., 1984; Guyer, 1991; Kiester et al., 1975; Liebman and Granda, 1971; Lohmann, 1992; Lohmann et al., 1996; Madison, 1969; Martins, 1994; McGregor and Teska, 1989; Rodda, 1984, 1985; Rodda and Phillips, 1992; Shoop, 1968; Taylor and Adler, 1973; Tracy, 1971; Tracy and Dole, 1969; Yeomans, 1995.

Chapter

9

Communication and Social Behavior

Every organism constantly interacts with other organisms. The interactions include predation, eating, physiological responses to disease organisms, and numerous others. Social behavior is an interaction with one or more conspecifics, that is, individuals of the same species, and occasionally between individuals of different species. Social interaction may be a regular feature of an individual's daily life, particularly for individuals living in groups or occupying adjacent territories, or they may occur once a day, once a week, and even only once a year during the reproductive season in a low-density species. Whatever their frequency, social interactions require some form of communication. Amphibians and reptiles communicate through a variety of senses: visual, chemical (nasal and vomeronasal), acoustic, and tactile. In many instances, communication involves more than one sense working together, synchronously or sequentially.

The evolution of an organism's signal production is intimately interwoven with the evolution of its signal receptors. One system cannot change without adjustments in the other, or communication is lost and interactions fail. Frogs have an impressive array of vocalizations, most of which are used for mate attraction. Frogs have an equally impressive and sophisticated acoustic reception system that allows them to discriminate among species and among individuals. Skinks and other scleroglossan lizards can recognize conspecifics and often individuals exclusively by chemical cues. The primary benefit of high-resolution communication is the ability to identify and locate mates in a complex environment, such as a multispecies frog chorus in a densely vegetated marsh, and to discriminate critically among mates, that is, to recognize a high-quality male among the numerous calling males and to select the "best" one. Signal production has an energetic cost, but further, it has a potential life-threatening cost. If a conspecific can locate another conspecific by the communication signal, so can a predator. In the Neotropics, one group of predaceous bats locates male frogs by "homing in" on the frog's advertisement call (Ryan et al., 1981).

Social interactions are integral to an individual's survival and ultimately influence an individual's evolutionary fitness (Halliday and Tejedo, 1995). The diversity of amphibians and reptiles has again allowed many species to serve as model organisms for the study of the evolution of communication and social behavior. The focus below is first communication and then sexual behavior because interactions and an individual's choices associated with mate choice have a more immediate and direct effect on individual fitness than a decision or interaction in the context of other types of social behavior. Other aspects of social behavior are presented in Chapters 4, 10, and 11.

COMMUNICATION

Strictly speaking, communication is defined as ‘‘the cooperative transfer of information from a signaler to a receiver’’ (Alcock, 1998). Consequently, if a male frog calls and his call is not received by another frog, or a snake produces chemical cues that are not detected by another snake, communication has not occurred. Further, the signal and reception systems of most reptiles and amphibians are controlled by sex hormones and, thus, are most effective during the breeding season.

Visual communication uses either body movement, or a series of movements, or the flashing of a body part having a distinctive color or shape. In amphibians and reptiles, limb movements, headbobs, rapid shuttling movements, and open mouth threats compose the most common signals. Visual communication is best known for iguanian lizards but occurs in many other amphibians and reptiles, often in combination with other signals. Although visual displays are most often directed at specific individuals, assertion or advertisement displays can be performed by territorial males to reinforce their territory status to all males or to attract females within sight. Among reptiles, the combination of an approach with headbobs occurs in so many groups that it likely is an ancestral trait and may reflect an ancient solution to the identification of gender and conspecifics at a distance (e.g., Ruby and Niblick, 1994). Many reptile species are sexually dimorphic in coloration, suggesting the importance of color in species and gender recognition. Because some seasonal color changes are tied to reproductive events and under the control of androgens, color also signals an individual’s reproductive condition. Most studied reptiles have color vision, which further suggests that color is used in communication.

Acoustic communication uses sound. Acoustic communication is best known in anurans, but crocodylians, some turtles, and some lizards (Gekkonidae) regularly use sound (Table 9.1). Sounds for social communication are produced by rubbing body parts together (some gekkonids, some viperids) and slapping the body against surfaces such as water (crocodylians), although vocal sounds are most prominent. These sounds (vocalizations) are produced by airflow over the vocal cords. Many frogs have vocal sacs to enhance sound transmission.

TABLE 9.1 Vocalizing Taxa of Amphibians and Reptiles, Exclusive of Anurans

Taxon	Frequency
Ambystomatidae	+
Ambystoma maculatum	
Amphiumidae	+
Cryptobranchidae	++
Andrias davidianus	
Dicamptodontidae	++
Dicamptodon ensatus	
Plethodontidae	++
Aneides lugubris	
Salamandridae	+
Triturus alpestris	
*Sirenidae	++
Siren intermedia	
TESTUDINES	+
*Testudinidae	++
Geochelone gigantea	
*Alligatoridae	+ + +
*Crocodylidae	+ + +
Gavialidae	+ + +
*Sphenodontidae	+ + +
Agamidae	+
Brachysaura minor	
Anguidae	+
Ophisaurus	
Chamaeleonidae	+
Chamaeleo goetzei	
Cordylidae	+
Cordylus cordylus	
*Eublepharinae	+ + +
Coleonyx variegatus	
*Gekkoninae	+ + +
Gekko gecko	
Lialis burtonis	
*Iguanidae	+
*Lacertidae	++
Gallotia stehlini	
Scincidae	+
Mabuya affinis	
Teiidae	+
Cnemidophorus gularis	

Sources: Salamanders through *Triturus* (Maslin 1950); *Siren* (Gehlbach and Walker, 1970); turtles (Gans and Maderson, 1973); *Geochelone* (Frazier and Peters, 1981); crocodylians, (Garrick et al., 1978); gharial (Whitaker and Basu, 1983); tuatara (Gans et al., 1984); *Anolis* (Milton and Jenssen, 1979); and lizards (Böhme et al., 1985).

Note: Families marked with an asterisk have one or more species presumably using vocalization for intraspecific communication. The frequency of vocalization within a family or higher group is subjectively estimated: + + +, more than 50% of species; ++, moderate; +, rare (one, or few species in a speciose group). Some examples of voiced species are included.

Chemical communication uses odors, either volatile ones (nasal) or surface adherent ones (vomeronasal), and the odors are derived from glandular secretions. Chemical communication has been studied most intensely in salamanders and skinks; it is used widely by other scleroglossan lizards (including snakes), in some iguanians, and likely in caecilians. In amphibians and reptiles, most and perhaps all chemical communication relies on vomeronasal receptors. Odor chemicals are picked up by the tongue or the surface of the head and transported to the nasal sac in amphibians and the roof of the mouth in reptiles, and then ultimately to the vomeronasal organ (Fig. 10.4). Crocodylians lack vomeronasal organs, and hence lack this route for chemical communication; however, crocodylians produce glandular secretions during the reproductive season and likely communicate chemically.

Tactile communication occurs when one individual rubs, presses, or hits a body part against another individual. Tactile communication is common in turtles and snakes (e.g., ritualized combat in viperids) but also occurs commonly in amphibians and many lizards. Often, tactile communication occurs after visual, acoustic, or chemical contact has been established. Because most species of amphibians and reptiles use a combination of signals during social communication, each group is reviewed separately.

Caecilians

Most social communication in caecilians appears to be chemically mediated. Caecilians have a specialized chemosensory organ, the tentacle (see Fig. 15.2 and Chapter 2), which evolved from elements of the orbit and nasal cavity (Billo and Wake, 1987). During metamorphosis, the eye is covered by skin or bone, and its nerves and muscles degenerate. Paired tentacles develop anterior to the eyes, and the lumen of each tentacle is continuous with Jacobson's organ. During burrowing, caecilians close their nostrils and use the tentacles to detect odors. Relatively little is known about caecilian reproductive behavior, but mate location may depend upon pheromones.

Salamanders

Salamander courtship relies heavily on chemical signals. They are an essential component of the often elaborate and ritualized courtship behaviors of many salamanders (Verrell, 1989). Visual and tactile cues are also essential in salamander courtship (Fig. 9.1). Salamanders use pheromones to distinguish between species and to locate conspecifics; additionally odors identify the reproductive status and sex of conspecifics and stimulate sexual activity in females (Houck and Sever, 1994). The pheromones are produced by numerous types of courtship glands found only in males. Gland development is mediated by sex hormones. The courtship glands do not appear until sexual maturity, and most atrophy during the nonbreeding season.

In plethodontid salamanders, mate location is aided by "nose-tapping," during which a male repeatedly touches his snout to the substrate. The snout bears a pair of nasolabial grooves; these small grooves extend from the upper lip to the nares. Odors from the substrate move along the groove by capillary action and through the nares into the vomeronasal organ. In the hemidactyliines, each groove extends to the tip of a small papilla (cirrus) that protrudes from the lip beneath each naris.

Courtship glands are most common in the Salamandridae and Plethodontidae. Males of the eastern North American newts (*Notophthalmus*) have a genial gland on each side of the head. When a male encounters a receptive female, he moves beside her and then performs a series of tail undulations that waft the pheromone toward her snout. Shortly afterward, courtship continues and the female accepts the male's spermatophore. If a male finds an unreceptive female, he captures her by clasping her neck with his enlarged hindlimbs. This amplexus may last for three hours, and during this period, the males places his genial glands against the female's snout. The gland's secretions induce the female's sexual receptiveness and allow courtship to proceed to spermatophore transfer (Verrell, 1982).

Plethodontid salamanders have two general types of courtship glands, the mental gland on the chin and the caudal glands on the back at the base of the tail. Among the diverse plethodontids, there are five types of mental glands and even more diverse secretion-delivery behaviors. In some taxa, males slap or rub the mental gland directly on the females' nares. Male *Desmognathus* have enlarged premaxillary teeth. During courtship, a male drags his enlarged teeth across the female's neck or back, lacerating her skin and simultaneously releasing secretions from his mental gland, thereby directly delivering the pheromone to her circulatory system. The secretions induce sexual activity in the female.

The caudal gland secretions maintain a female's receptivity during courtship. Caudal glands lie atop the male's tail, where their secretions are in direct contact with female's snout during the tail-straddling walk. In this critical phase of courtship, the female straddles the male's tail as they walk in tandem. The secretions ensure that the female follows the male and is thus more likely to pick up his spermatophore at the end of the courtship walk (Houck and Sever, 1994). This elaborate courtship involves suites of closely integrated morphological and behavioral characters and has many variations

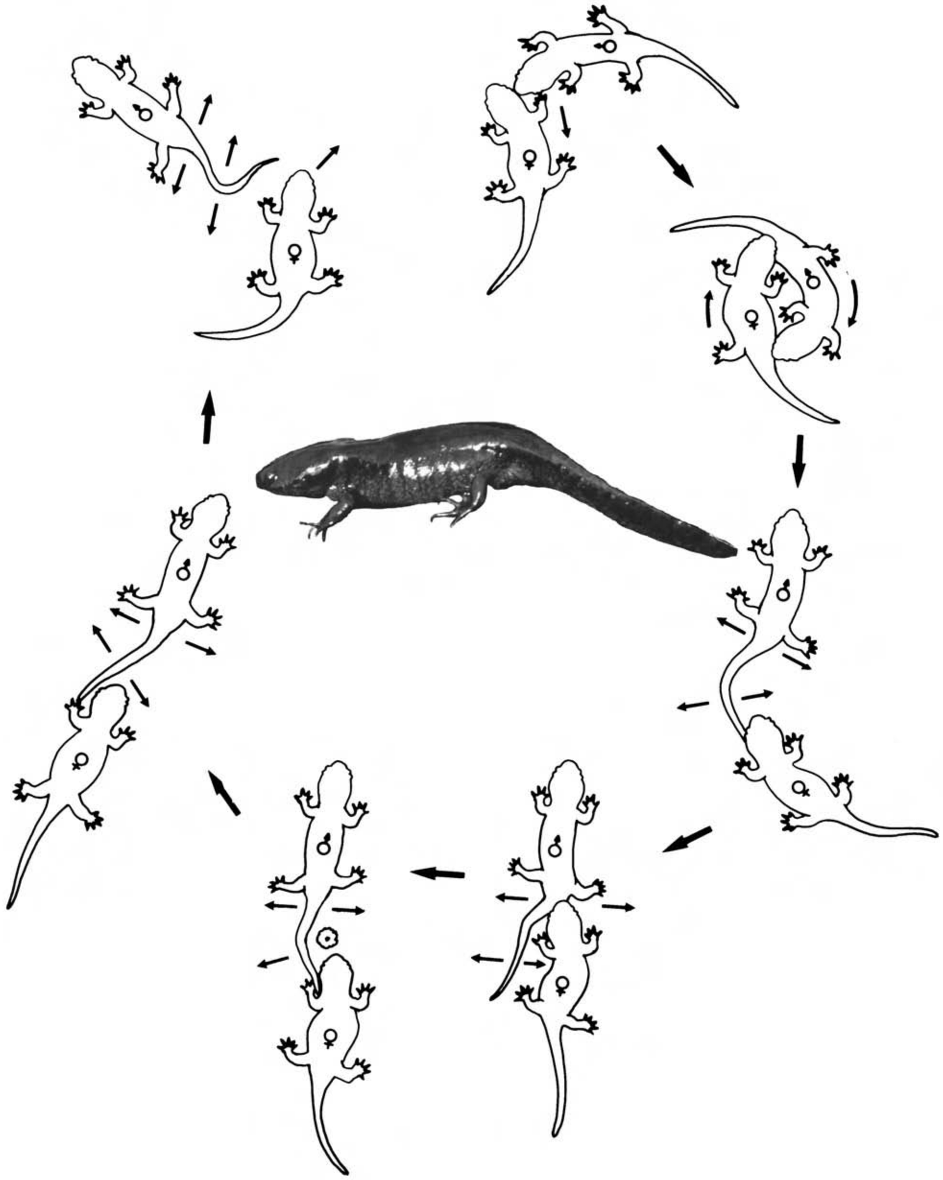


FIGURE 9.1 Courtship sequence of the mole salamander, *Ambystoma talpoideum*. The sequence begins at top center and proceeds clockwise. The male rubs the female; the female nudges the male's cloaca (bottom right), stimulating him to deposit a spermatophore (bottom left); the female briefly examines the spermatophore and then moves over it, picks up the sperm packet with her cloaca, and departs. Adapted from Shoop (1960).

among the more that 200 species of plethodontids, including the loss of the mental gland and associated behaviors.

Even though chemosensory cues are critical components of the elaborate courtship of salamanders, tactile signals are also essential and critical elements. Many salamanders nudge, butt, slap, or rub parts of their bodies against each other. As noted above, these tactile behaviors deliver pheromones to the courted female and elevate her reproductive readiness and receptiveness. Some taxa bite vigorously, and in two species, biting holds the female during courtship. In the salamandrid *Triturus*, the male whips his tail vigorously and the force of water movement is the tactile stimulation, and may even push the female away. In some cases, the tail touches the female. This tail-whipping behavior presumably increases the female's receptivity to the male (Halliday, 1977).

Frogs

Acoustic signals are the primary mode of communication in frogs, many of which breed at night. The absence of light and the anuran force-pump breathing mechanism may have been major selective factors in the evolution of vocalization (Haddad and Giaretta, 1999). Each species of anuran has distinct vocalizations, and individual frogs produce a variety of calls, depending on the behavior in which they are engaged. Frog calls segregate into four broad categories, and of these, the advertisement call is most complex (Table 9.2). In many species, different parts of an advertisement call serve different functions. Each part of a call and the various call attributes convey specific information from the signaler. Each component can vary among individual males, and this variation forms the basis for the selection and evolution of call characteristics (Table 9.3).

TABLE 9.2 Broad Categories of Call Types in Frogs

Call type	Function
I. Advertisement call	The primary function of this type of call is the attraction of conspecific gravid females. Because the advertisement call has other funtions, it is further categorized below.
A. Courtship call	The call a male makes to attract a conspecific female that is gravid and ready to mate.
B. Territorial call	The call produced by a male that is defending a territory when a second male vocalizes in or near, or intrudes into, his territory.
C. Encounter call	The call made by a male in response to the approach of another male.
II. Reciprocation call	Calls are occasionally given by a female in response to the mating call of the male; these calls are rare, and female frogs of most species do not call.
III. Release call	Call given by male that is amplexed by another male; the call is usually accompanied by vibrations of the body. This kind of call is common in explosive-breeding frogs, such as *Bufo*, in situations where many males are active at one time and amplexus is nondiscriminatory.
IV. Distress call	Loud catlike scream given by females of some species of frogs when grasped by a predator. Frogs in clades not closely related, including *Hyla lanciformis, Leptodactylus pentadactylus, Hemiphractus fasciatus, Rana catesbeiana, Rana sphenocephala*, and *Hyla boans*, among others, produce distress calls, indicating that the ability to give these calls has evolved independently several times.

Source: Adapted from Duellman and Trueb (1986).

TABLE 9.3 Components of Acoustic Signals Produced by Ampibans and Reptiles

Call component	Description
Call or call group	A discrete acoustical signal; may be a single note in some species or a series of notes.
Call rate	The number of calls produced per minute.
Note	An individual unit of energy, such as a single pulse or a trill.
Note repetition rate	The number of notes per unit time.
Pulses	Notes may be pulsed or unpulsed; examples of a pulse that can be heard are those forming the trill of a toad, which is made up of individual pulses.
Pulse rate	The number of pulses per second or millisecond.
Spectral frequency	The pitch of a call. In many species, a series of evenly spaced harmonics can be seen on the sound spectrogram. The harmonic with the greatest emphasis is called the dominant frequency, whereas the lowest-pitched harmonic is the fundamental frequency.

Source: Adapted from Duellman and Trueb (1986).

Frogs produce sound by passing air over their vocal cords, as do all tetrapods. Frogs are unusual in having vocal sacs for sound resonation. Usually only male frogs have vocal sacs, but not all species that vocalize have sacs. The shape and size of vocal sacs vary among frogs. Primitive frogs have loose folds on the sides of the mouth that are air-filled during calling; these may represent primitive vocal sacs. The vocal sac is an outpocketing of the buccal cavity and communicates with it by paired vocal slits. Frogs possess three basic types: a median subgular sac; paired subgular sacs; and paired lateral sacs. The median subgular sac is the most common type and is found in many groups of frogs (Fig. 9.2).

Sound production must be coordinated with ventilation of the lungs, which is accomplished by a force-pump mechanism (see Chapter 6). Sound is a type of energy that produces pressure waves, and the wave components can be depicted in a sound spectrogram (Fig. 9.3). From the spectrogram, numerous characteristics of the call can be measured and used to compare vocalizations of different species or to study variations of calls of individual males in a chorus. Call rates, note repetition rates, and the spectral frequencies are call parameters that vary among species and among individuals (Table 9.2). Various environmental parameters cause attenuation of sound transmission. Type of substrate and amount of vegetation through which sound must travel, as well as call frequency, temperature, and humidity affect the distance that sound is transmitted.

FIGURE 9.2 A calling graceful treefrog (*Litoria gracilenta*) from Australia. This frog has an exceptionally large median subgular vocal sac. Photograph by S. J. Richards.

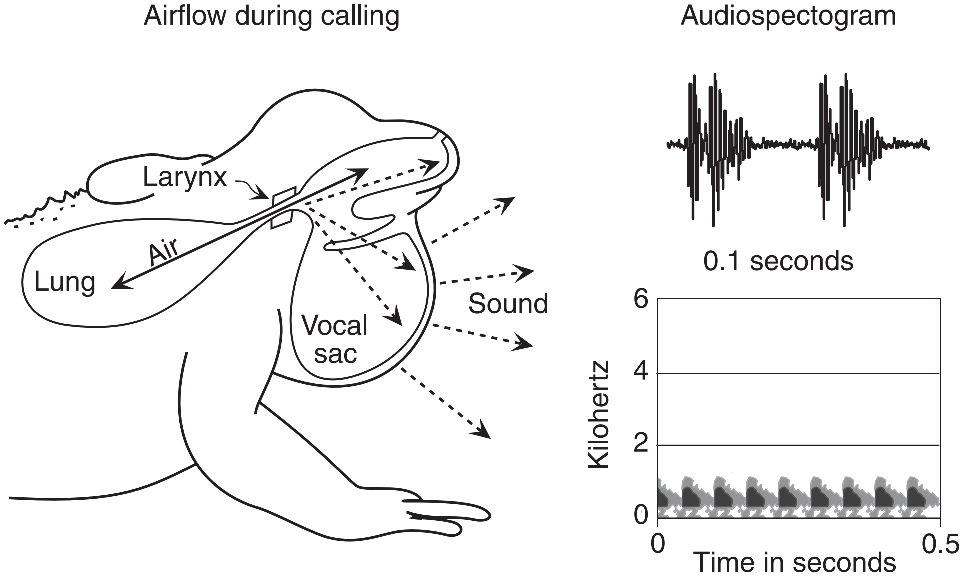


FIGURE 9.3 Sound production and call structure of the marine toad *Bufo marinus*. Sound production (left) uses aspects of the respiratory ventilation cycle without releasing air to the outside. Before calling begins, the buccopharyngeal force pump inflates the lungs and vocal sacs. Then with nostrils closed, the body muscles contract, pushing a pulse of air through the larynx, vibrating the vocal cords. Sound radiates outward and is resonated by the vocal sac. The call of *B. marinus* is a deep, long trill of many continuous pulses (>50) and lasts several seconds. The waveform (right top) and spectrogram (right bottom) show the energy envelope and pulse structure of brief segments of a call. Each pulse lasts about 0.03 s; the dominant frequency is 500–1000 Hz. Morphology adapted from Martin and Gans (1972). Redrawn and reprinted, with permission of Wiley-Liss, a subdivision of John Wiley and Sons, Inc., 1972. Call analysis courtesy of W. R. Heyer.

Reproduction in frogs is largely dependent on male vocalizations for mate attraction, territory defense, and other male–male interactions. The importance of vocal signaling for anuran reproduction and the relative easy access to breeding frogs have encouraged the intense and rigorous investigation of all aspects of the anuran signaling system. These studies range from the simple description of male calling behavior and call structure to detailed neurological investigations and behavior experiments. Older studies emphasized the description of individual species' vocalizations and how calls serve as species-isolating mechanisms and reduce interspecific mating. The comparatively recent emphasis on mating systems and an individual's reproductive success has led to the study of those aspects of frog calls that females use to discriminate among individual males and that males use in aggressive encounters with one another.

Many studies of frog vocalizations have used playback techniques in artificial settings to learn how female frogs react to male calls. In general, females respond to conspecific calls and ignore heterospecific calls. Male vocalization, although stereotyped in some respects, is more variable that once thought. In the Neotropical *Hyla ebraccata*, females prefer males with a faster call rate and multinote calls. In male–male interactions of the same species, males produce graded aggressive calls; as males get closer to each other, the duration of the first note of the call increases (Wells, 1988). Males also show plasticity in their response to the presence of an advertisement or encounter call of conspecific males. In dense choruses, male *Pseudacris regilla* allow conspecific males to vocalize at a shorter distance before reacting with an encounter call. Females strongly prefer advertisement calls over encounter calls. Therefore in a chorus, an individual male is more likely to attract a female by producing advertisement calls and by reducing his encounter-call challenges to other males (Brenowitz and Rose, 1999).

In other studies, synthetic calls are produced to mimic advertisement and other vocalizations. Components of a call can be removed, changed in frequency, or otherwise modified in order to determine which components are most attractive to females. For example, male *Physalaemus pustulosus* (Leptodactylidae) produce calls with two parts—a whine and a chuck (Ryan, 1985). Studies of marked individuals reveal that frogs can vary the complexity of their calls by producing only the whine or the whine with a variable number of chucks (up to six). Females prefer more complex calls, choosing males that give one or more chucks over those that produce only a whine. Males use complex calls only when they are in high-density choruses; when calling in isolation or in low-density choruses, males produce only the whine. The cause of this reproductive trade-off is the bat *Trachops cirrhosus*; complex calls provide this predaceous bat with location cues (Ryan et al., 1982). When competition among males for females is high, a male must risk predation to increase his probability of attracting a female, but when competition is low, a simple call may attract a female without increasing his risk of predation.

A number of frog species, including some exclusively nocturnal ones, use a combination of acoustic (see below) and visual communication (Haddad and Giaretta, 1999). Visual signals include a variety of movements of the body and the limbs. These signals include hand waving, foot raising and lowering, foot flagging, leg stretching, and toe undulations. In addition, the body can be raised and lowered, inflated, or swayed from side to side, and color changes may occur in calling males or in territorial females. Visual communication in frogs is undoubtedly more common than reported because the signals in some cases are subtle and not recognized by human observers. To date, visual communication has been reported in seven anuran clades (Lindquist and Hetherington, 1996). Some displays are remarkably similar among distantly related clades, suggesting independent evolution. Many of these species are diurnal and live in or adjacent to noisy mountain streams.

In some taxa, only males produce visual signals, but in others, both males and females use them. The leptodactylid *Hylodes asper* is a torrent-living frog; males vocalize and subsequently use a foot-flagging display to attract an approaching female (Fig. 9.4). Males raise a hindleg and hold it above the body; the light-colored toes are spread and the foot becomes a flag against the dark background of the frog's habitat (Haddad and Giaretta, 1999). The female may signal a response by stretching one or both legs behind her. Males use the foot-flagging behavior and other limb movements to signal to other males that attempt to intrude into their territories. Male *Hyla parviceps* use a similar foot-flagging display in response to the close approach of a conspecific male (Fig. 9.4). Male *Atelopus zeteki* use a stereotypic hand wave presumably to signal territorial occupancy to conspecifics (Lindquist and Hetherington, 1996).

The tiny pumpkin toadlet, *Brachycephalus ephippium* (Brachycephalidae), is a diurnal, bright orange frog that inhabits leaf litter in Brazilian coastal rain forest. Males use an up-and-down arm display to inform other males of territorial intrusion. Visual displays are coupled with vocalizations. Most often, the intruder retreats and no physical contact ensues. Breeding occurs away from water in *B. ephippium* and its weak advertisement call is lower than the background noise of the forest. Presumably, the low call and daytime activity patterns contributed to the evolution of its visual signals (Pombal et al., 1994). Some dendrobatid frogs are also diurnal and

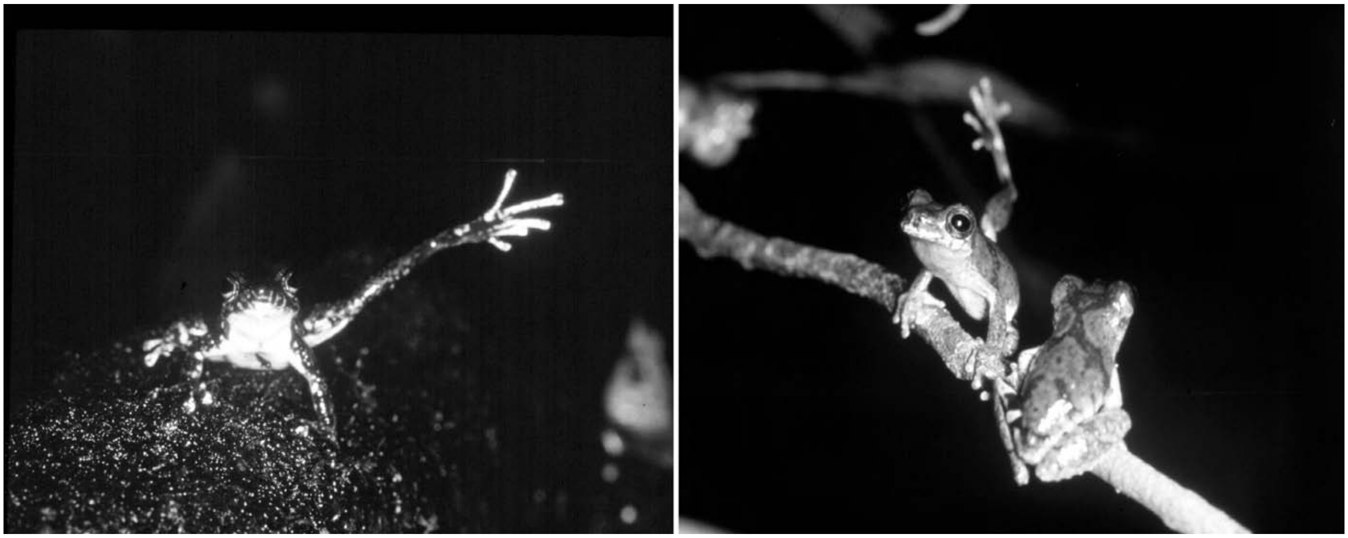


FIGURE 9.4 Foot flagging in the Brazilian torrent frog, *Hylodes asper* (Leptodactylidae; left) and *Hyla parviceps* (Hylidae; right). Photographs by W. Hödl.

brightly colored. One species, *Epipedobates parvulus*, uses leg-stretching displays (Wevers, 1988). The cryptically colored dendrobatids use various types of visual displays. Both male and female *Colostethus trinitatis* use visual displays during social interactions, and, in addition, this species exhibits sex role reversals. Females of *C. trinitatis* establish territories around boulders and rocks in streambeds. Females perch on top of large boulders and challenge intruders that enter their territories by adopting an upright posture and pulsating their bright yellow throats. If the intruder ignores the visual signal, physical contact results; the frogs may stand on their hindlimbs and grapple (Wells, 1980). Females attack males, males carrying tadpoles, and other females, but most aggression is directed toward other females. Males of *C. trinitatis* use rapid color change as a visual signal. Males are light brown until they begin to call; while calling, they become uniform black, losing their stripes and other markings. Two adjacent calling males, both black, may engage in grappling fights; the loser immediately becomes light brown. Females, but not males, are territorial; males use color to court females from a distance, thereby avoiding attacks from nonreceptive females. A receptive female signals her reproductive readiness by leaving her territory and approaching a calling male.

Frogs often use tactile cues to distinguish gender, particularly in explosively breeding species (Fig. 9.5). The larger body of a gravid female provides the tactile cue that identifies her gender and reproductive state to a male. In prolonged breeding species, a female approaches a calling male, and typically, the male continues to call until touched or nudged by the female. In some poison frogs (*Dendrobates*), females follow calling males during courtship; eventually, the female strokes the male's legs, head, or chin with her forefeet, and this signals her readiness to oviposit and stimulates the male to release sperm. In *Hyla rosenbergi*, each male constructs a basin of mud or sand at the edge of a small forest stream and calls from a platform in the basin. A female approaches and inspects the basin while the male continues to call. Only after the female touches the male does he cease calling and initiate amplexus (Kluge, 1981).

Turtles

Tortoises and turtles use combinations of visual and chemical signals during social interactions. Visual displays involve headbobs (tortoises) and displays of patterns and colors on the forelimbs, neck, and head (emydid turtles). When two tortoises interact and at least one is a male, the male first performs headbobs or sways the head back and forth (Auffenberg, 1965). If both are male, the other one responds with a similar behavior; the interaction can escalate into butting, biting, and other aggressive acts. In desert tortoises, *Gopherus agassizii*, the interactions include all aforementioned acts, and two males, having interacted during the day, may spend the night in the same burrow only to continue the interaction the following day (Fig. 9.6). When males interact with females, the sequence begins in the same way, but when the female retreats instead of producing headbobs in response to the male's headbobs, the male continues to approach, intensifies his headbobbing, and then circles the female. After a series of

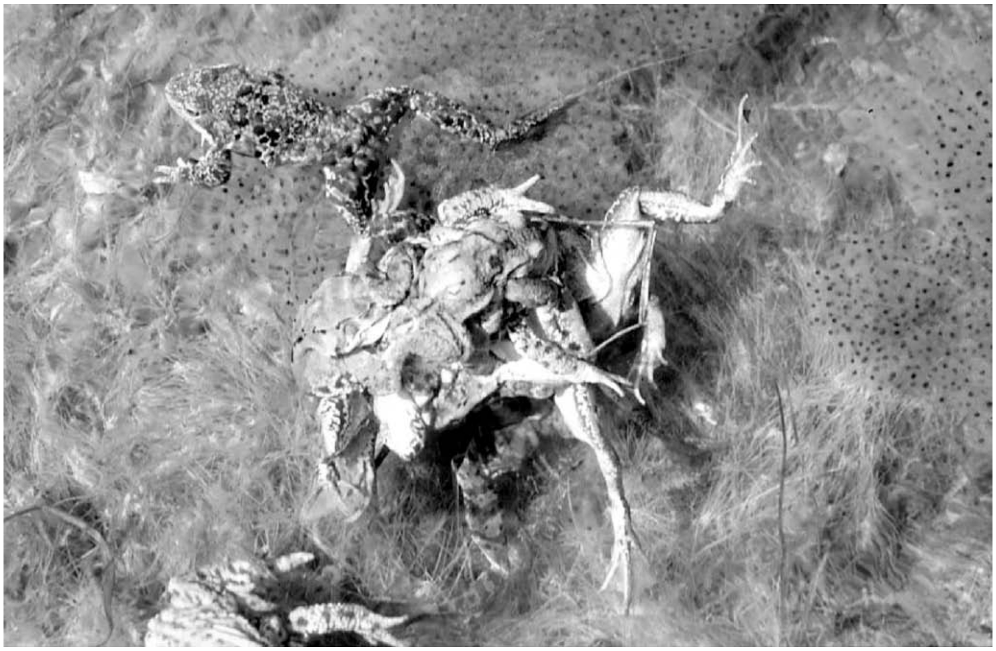


FIGURE 9.5 Scramble competition in the frogs *Bufo bufo* and *Rana temporaria* during an explosive breeding event. Photograph by W. Hödl.

behaviors including biting or ramming, the male attempts to mount the female, scratching her shell, grunting, and moving his head in and out of his shell. This behavior sequence may or may not result in copulation. Even though the initial social cues are visual, the tactile signals may ultimately initiate copulation.

In some emydid turtles, the male maneuvers around a female in the water and eventually positions himself to expose his color and striping pattern to the female. Male color patterns are species specific and presumably provide the first level of species identification. While face to face, males gently bump heads with females (a tactile cue). Following this behavior, the male attempts to position himself on the back of the female with his head above and oriented down above the head of the female (Jackson and Davis, 1972). The male extends his forelimbs with their elongate claws downward and begins a rapid chewing motion with the jaws. This behavior is followed by rapid vibratory movements of the forelimbs in front of the female's head. The limbs are vibrated in a fanlike fashion but do not touch the female.

Many turtles have Rathke's glands on the bridge of the shell. These glands produce aromatic chemicals. Other turtles (e.g., testudinids, some emydids, *Platysternon*) have mental glands that are active during the breeding season. Cloacal secretions may also play a role in social communication; however, the precise function of secretions and pheromones is poorly known. Rathke's gland secretions may allow muskturtles, *Sternotherus odoratus*, to find and follow one another in the water (Mason, 1992). Anecdotal observations of turtle behavior indicate that pheromones are likely involved in many social interactions (Halpern, 1992). Experimentally, reproductive behavior in *Emys orbicularis* was reduced by more than 60% by cutting the olfactory or vomeronasal nerves, indicating that the reception of chemical cues is involved in reproductive behavior (Boiko, 1984).

Crocodylians

Visual signals, often in combination with auditory signals, are common in crocodylian communication. Visual signals predominate in short-distance interactions, whereas auditory cues are primarily used in long-distance communication. In alligators and some crocodiles, the behavioral sequences are similar. When an intruder enters a male's territory, the resident approaches the intruder with his head and tail partially above the water's surface (''head emergent–tail arched posture''; Garrick and Lang, 1977) to signal his alertness. Chases, lunges, and real or mock fights follow. After most chases, the territorial male inflates his body (''inflated posture''). Depending on species, narial geysering (water forced out of the nares) occurs during male–male confrontations or, as in alligators, geysering occurs with ''headslaps,'' in which the head is raised out of the water and then slapped against the surface.

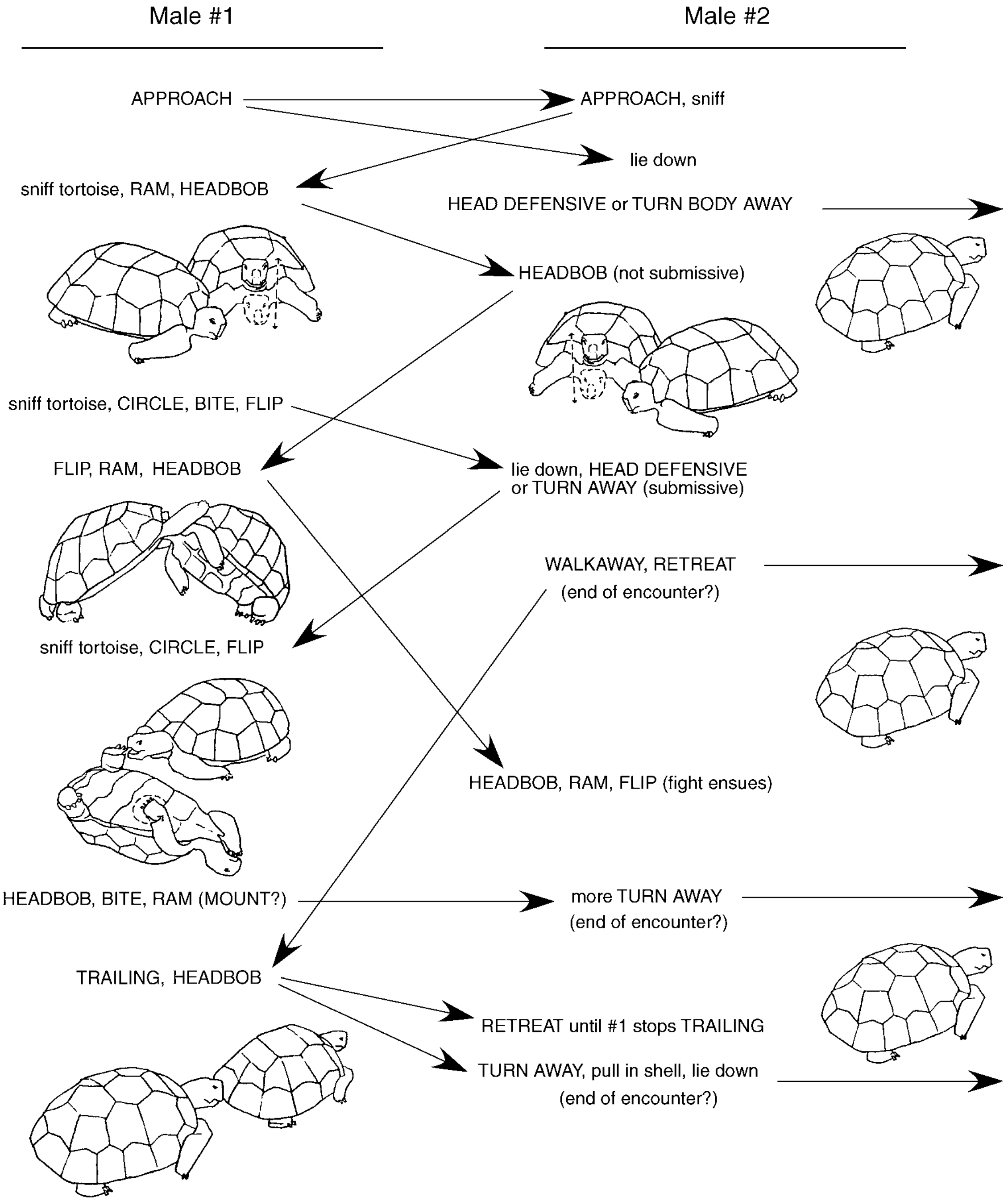


FIGURE 9.6 Sequence of behaviors that occur during an aggressive encounter between two male desert tortoises (*Gopherus agassizii*). Common alternative sequences are indicated by arrows. Terms in capital letters indicate specific behaviors that have been described. Adapted from Ruby and Niblick (1994).

Auditory signals include bellowing (Fig. 9.7), juvenile grunts, and slapping sounds (Garrick et al., 1978). In alligators, males and females bellow, but the duration of bellows and the time between bellows are greater in males than in females. Loud, low-frequency bellows are produced only during the breeding season and after the eggs have been deposited. Coughlike calls are used by males and females during courtship for close range communication. Head slapping is mainly a male signal during male–male interactions. Juveniles usually grunt under conditions of distress. The grunts cause adults to orient to and move toward the young. Adult alligators can also produce grunts, and these cause juveniles to move to the adult.

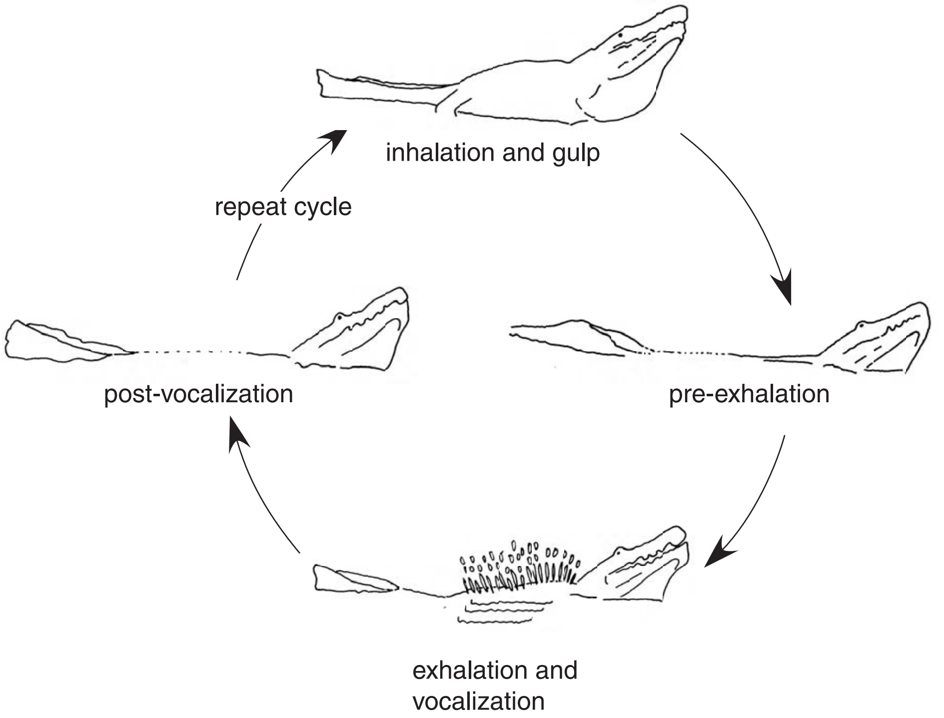


FIGURE 9.7 Sequence of events involved in the production of the bellow of an alligator, *Alligator mississippiensis*. Exhalation causes a fountain of water along the alligator's trunk and also produces a radiating series of ripples at the water surface. Adapted from Garrick and Lang (1977).

Tuataras and Lizards

Tuataras rely on visual cues for male–male and male–female interactions (Gillingham et al., 1995). Males are territorial and defend their territories by first approaching the intruding male, inflating the lungs to increase the apparent size of the gular region and the trunk, elevating the dorsal crest, and darkening the skin above the shoulders and eyes. The intruder performs a similar ritual. Often, the resident performs lateral head shaking; this behavior usually causes the intruder to depart. If the intruder stays, the males approach each other. They face each other but orient their heads in opposite directions while holding their bodies parallel; then they open and rapidly snap their mouths shut. This confrontation is followed by rapid chases initiated by rapid tail whipping. Males commonly croak during the mouth-gaping phase, and during the chase the pursuing male bites the head, body, or tail of the other tuatara. Courtship behavior is similar in the early stages (Fig. 9.8). Females perform a head nod when approached by a male. The courting male responds with what is termed the "stolzer Gang," an ostentatious walk marked by frequent pauses and extremely slow forward progression; limb movements are stiff-legged and exaggerated (Gans et al., 1984).

Male lizards of many species have courting behaviors similar to tuataras. Even though stiff-legged walking can be part of the ritual, it differs by a faster forward progression and the absence of frequent pauses. This behavior is not considered to be a stolzer Gang in lizards.

Within lizards, a dichotomy of signals exists between the Iguania and the Scleroglossa. The former use visual and, to a much lesser extent, chemical and tactile signals in social communication, whereas the latter rely primarily on chemical signals and, to a lesser extent, visual and tactile signals. Most iguanians are territorial and sit-and-wait foragers; in contrast, most scleroglossans are active foragers and likely not to be territorial (see Table 10.1 for a summary of traits associated with this dichotomy). The best known examples of visual communication are in the Iguania, and the best known examples of chemical communication are in the Scleroglossa.

Coloration of dewlaps, heads, and patches on the lateral or ventral surfaces of the body are frequently used in visual communication (Cooper and Greenberg, 1992). Dewlap displays of *Anolis* are combined with signature headbob displays that are species specific (Stamps, 1977; Tokarz, 1995). These displays are categorized as simple, compound, or complex (Echelle et al., 1971). Simple displays involve the extension of

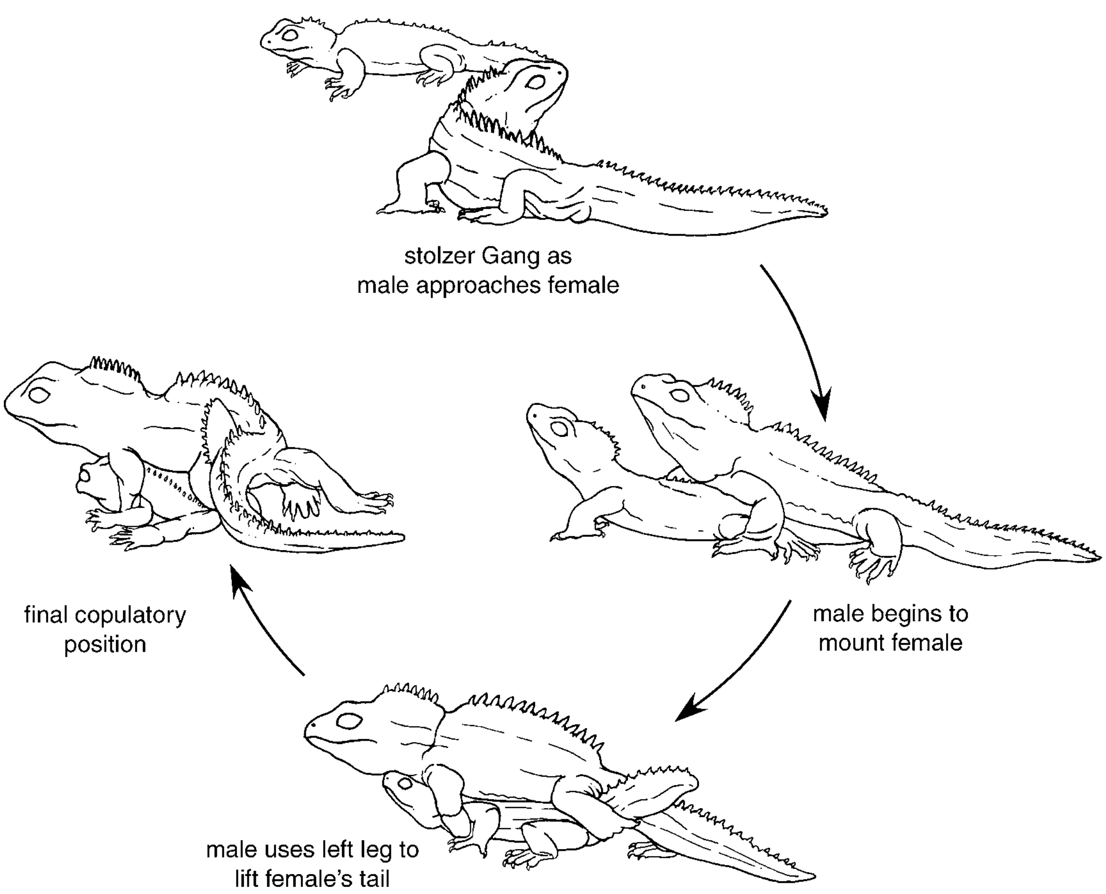


FIGURE 9.8 Mating behavior of the tuatara *Sphenodon punctatus*. Adapted from Gillingham et al. (1995); redrawn by J. P. do Amaral.

a uniformly colored dewlap and a simple headbob pattern (Fig. 9.9). Compound displays occur where the dewlap has a central color surrounded by a second color and a relatively simple headbob pattern. Complex displays result when the dewlap has an intricate pattern of two or more colors, and headbobbing and dewlap extension are relatively independent. The signature headbob display of anoles attracts females and may be the most effective cue for long-distance signaling (Jenssen, 1970a; Martins, 1993). Considerable variation exists among individuals in signature headbob displays, dewlap color, and dewlap extension, supporting the idea that females can discriminate among individual males based on some aspect of the display (Jenssen and Hover, 1976; Fleischman, 1992; Greenberg and Noble, 1944). Female discrimination is confirmed by choice experiments; female anoles select males with "normal" displays over males with even slightly deviant displays (Jenssen, 1970b). The vigor of the male's display appears to be the most important component for the attraction of females. Signature headbob displays occur in many other lizards as well (Fig. 9.10).

A number of studies have demonstrated social responses to color. Female *Anolis carolinensis* prefer males with red dewlaps over males with drab-colored dewlaps. In experiments, male *Sceloporus undulatus* attack females if they are painted with the male's ventral blue coloration; similar male aggression toward females is elicited by painting male coloration on females of *Agama agama*, *Eumeces laticeps*, and species of *Lacerta* (Cooper and Greenberg, 1992).

In some lizards, females are brightly colored. At least seven hypotheses have been suggested to account for bright female coloration; these include sexual recognition, female signaling, aggression avoidance, sexual maturity, courtship rejection or stimulation, and conditional signaling (Cooper and Greenberg, 1992). Conditional signaling appears best supported. Rapid color change in females signals sexual receptivity to the territorial male; additionally the female's long-term retention of the bright colors signals her likely rejection of further courtship. Brightly colored females of keeled earless lizards, *Holbrookia propinqua*, for example, are recognized as females by males (Cooper, 1984). Females

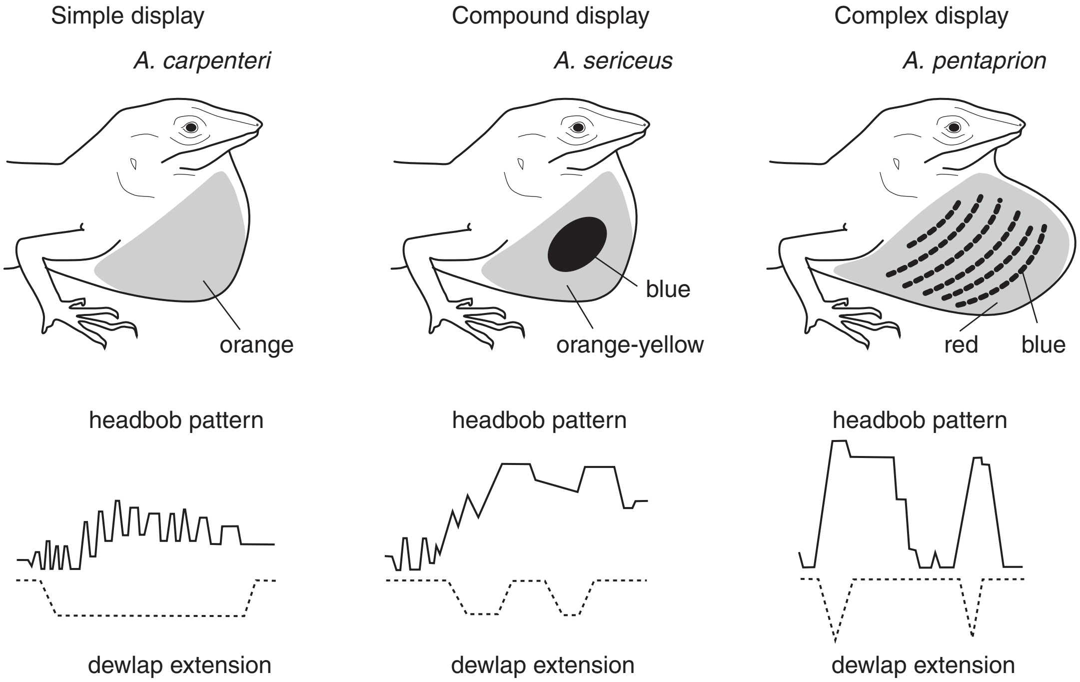


FIGURE 9.9 Three types of visual displays in *Anolis* lizards. Adapted from Echelle et al. (1971).

in the process of undergoing rapid color change are sexually receptive, can store sperm once they mate, and are the females courted by males (Cooper and Crews, 1988; Adams and Cooper, 1988). Females that have completed the transition to the bright color phase aggressively reject courtship attempts by males, and bright coloration is associated with large follicles. The use of bright coloration in females as a social signal to males appears to occur only in species where males are familiar with females, suggesting that territoriality is a prerequisite for this kind of social recognition.

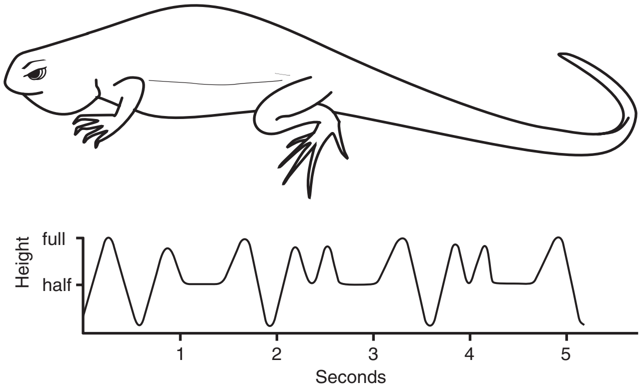


FIGURE 9.10 Display posture and movement-sequence diagram for a male desert iguana, *Dipsosaurus dorsalis.* The line in the diagram denotes the relative height of the head during a push-up defensive display sequence. Adapted from Carpenter (1961).

Among lizards, the chemical communication system is best known in the clade of North American five-lined skinks (*Eumeces laticeps, Eumeces fasciatus*, and *Eumeces inexpectatus*). Early field observations suggested that male *Eumeces* used chemical signals to follow trails of females during the breeding season (Fitch, 1954). Male broad-headed skinks, *E. laticeps*, can discriminate among species of *Eumeces* or sex within their species, and they can determine sexual receptivity of females based on pheromonal cues alone (reviewed by Cooper and Greenberg, 1992). When an adult male first encounters another adult-sized individual, he approaches that individual. If the other skink is a female and does not respond aggressively to the approach, the male begins tongue-flicking the body of the female and ultimately directs the tongue flicks toward the cloaca where a urodeal gland produces the pheromone used for identification of species, gender, and sexual receptivity (Trauth et al., 1987). A series of experiments in which cloacal odors were transferred to other species and sexes of skinks resulted in male *E. laticeps* attempting courtship with other species or other males containing the pheromones of sexually receptive females of *E. laticeps.* Experiments with a diversity of scleroglossan lizards produced similar results in other chemical-signaling species.

Chemical signals seemingly permit individual recognition in some lizards. Desert iguanas discriminate between their own odors and those of other desert iguanas (Alberts, 1992). Similar observations have been made for the skinks *E. laticeps* (Cooper, 1996), *Tiliqua rugosa,* and *Egernia stokesii* (Main and Bull, 1996), and an amphisbaenian (López et al., 1997). In *T. rugosa* and *Eg. stokesii*, mothers discriminate between their own offspring and the offspring of other females.

Monitor lizards use both chemical and tactile signals. Male Komodo dragons (*Varanus komodoensis*) tongue flick females at various positions along the body during the initial stages of courtship. When a male nudges a female with his snout, she will either respond with an assertion display or run away. If the female runs, the male pursues her closely and attempts to court. Males always scratch females on the neck and back during courtship and may even bite the female's neck prior to copulation (Auffenberg, 1981).

Auditory communication is limited in lizards. Many geckos vocalize, although the actual role of vocalization in courtship is not well defined. Some vocalization is associated with aggressive interactions while feeding. The Canary Islands lacertids (*Gallotia*) are also vocalists that may use sound in courtship.

Social communication among juvenile lizards is poorly studied. Juvenile green iguanas, *Iguana iguana*, appear to recognize siblings on the basis of fecal odors (Werner et al., 1987).

Snakes

Initial social communication in snakes is chemical, but tactile interactions are used as close-range signals between the sexes, and, in some cases, between conspecific males. Some skin pheromones are critical for successful reproduction; they are not produced by the cloacal glands (e.g., Halpern, 1992). Snakes have a diversity of glands and secretions, although the paired cloacal scent glands are best known and produce pheromones used by snakes for defense and trailing (Quay, 1972). The glands lie dorsal to hemipenes in males and in the corresponding position in females; often they are very large (Mason, 1992). Of the many explanations of cloacal gland function, defense is the most probable hypothesis because the secretions usually smell bad to humans, and some secretions repel specific snake predators. Observations of snakes returning to den sites and trailing other individuals suggest that glandular secretions are involved in these behaviors (e.g., Noble and Clausen, 1936). In addition to serving as cues for locating aggregation sites, the secretions are used for discrimination during reproductive behavior.

Pheromones that attract males to female during the breeding season occur in the skin on the dorsal surface of the females (Garstka and Crews, 1986; Mason, 1992). Like some scleroglossan lizards, snakes appear able to discriminate among pheromones produced by their own and other species (Halpern, 1992). Garter snakes (*Thamnophis*) are best at discriminating among odors of other sympatric garter snakes (Ford and Schofield, 1984; Ford and O'Bleness, 1986), suggesting local natural selection on chemosensory abilities or the chemicals.

At middle and lower latitudes, garter snakes have an extended breeding season, and males can locate females by following pheromone trails. At northern latitudes, most garter snake breeding occurs when the snakes first emerge from their overwintering sites before they disperse (e.g., Gregory, 1982, 1984). Because they overwinter in aggregations, large numbers of individuals interact. Several pheromones resembling vitellogenin are present in the skin of *Thamnophis sirtalis parietalis,* and whether on the back of a female snake or on the surface of an experimental arena, these chemicals elicit courtship behavior by males (Garstka and Crews, 1981, 1986). Males generally emerge before females; they remain clustered at the den site awaiting the emergence of females. When females emerge, they are mobbed by males responding to the pheromones in their skin. Competition among males for access to the relatively few emerging females is intense, and as a result, most males do not mate.

In most snakes, tactile signals predominate in courtship once a male has determined the gender of a conspecific. Courtship and mating usually involve three discrete phases: tactile–chase, tactile–alignment, and intromission–coitus (Gillingham, 1987). The tactile-chase phase includes the first contact between the snakes, including chemosensory sampling by males to determine sex. This phase usually is followed by chases or attempts to mount the female. During the tactile–chase phase, the male places his body alongside the female (undulation) or with a loop over the female's dorsal surface; segments of his body musculature may contract in a wavelike manner. In addition, the male often rubs his chin on the female's back or even bites her; in snakes with vestigial limbs (e.g., Boidae), the pelvic spurs scratch or titillate the female in the vicinity of her vent (Fig. 9.11). During the tactile–alignment phase, the first attempts to copulate occur. This involves rapid muscle contractions in the male's tail as it is aligned with the female's tail. These caudal vibrating movements are a tail-searching copulatory attempt. Tactile behaviors that occurred during the tactile–chase phase are often continued during the tactile–alignment phase. During the final phase, the female gapes her cloaca to allow the insertion of a single hemipenis, resulting in intromission and coitus.

Several spectacular forms of tactile communication occur in "male combat." Male combat has been observed in viperids, colubrids, boids, and elapids (Gillingham, 1987). Following gender identification by

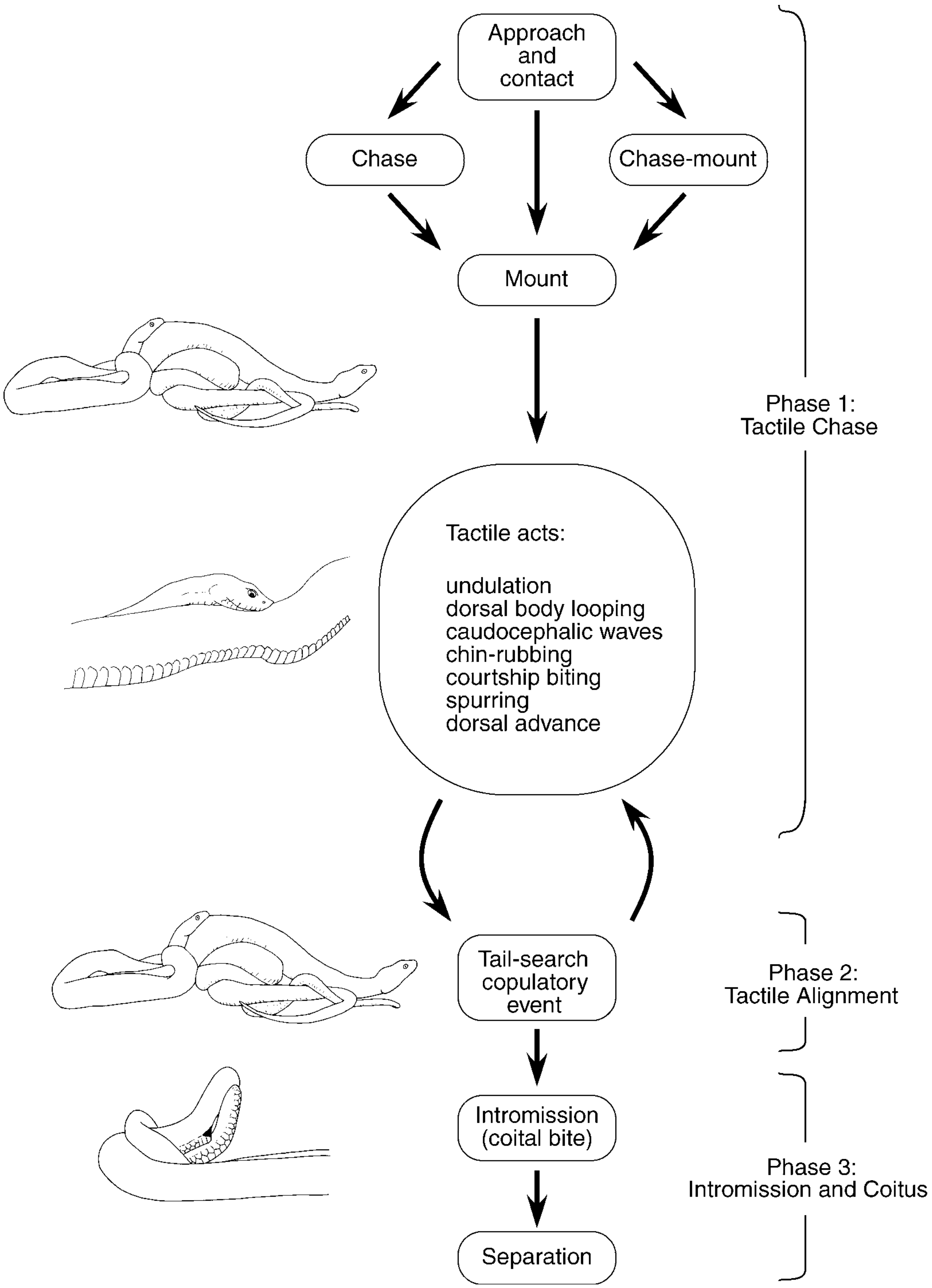


FIGURE 9.11 Three general types of tactile signals are used by snakes during courting and mating. Adapted from Gillingham (1987), with drawings adapted from Carpenter (1977).

chemical cues, two males glide parallel to each other, usually with their heads raised. Although the postures vary among snake clades, male combat is generally a contest in which one male attempts to push down the head of the other male in order to establish dominance. In elapids and colubrids, the interaction is mainly horizontal, but in viperids, males lift their heads and anterior portions of their bodies off the ground, often intertwined, and push each other over, only to initiate the sequence again and again until dominance is established.

REPRODUCTIVE BEHAVIOR

Mating Systems

In general, mating systems are categorized according to the levels of polygamy within a species. Conflicting strategies between the sexes result from the differential investment of the male and female parents in the offspring (Trivers, 1972). From the outset, males invest less in each individual offspring than females. Males produce millions of tiny sperm, few of which will fertilize eggs, whereas females produce relatively few eggs, each of which has a high probability of being fertilized. Each egg contains most of the energy required for development, whereas an individual sperm cell contains only genetic material and a flagellum for propelling itself to the egg. Many factors influence mating systems, including the spatial and temporal availability of reproductively active individuals, the behavioral tactics of males and females, and numerous ecological, phylogenetic, and physiological constraints (Sullivan et al., 1995; Verrell, 1989). In addition, parental care can play a significant role in mating systems (Fig. 9.12.). The study of mating systems of frogs and salamanders presents special challenges because many species are secretive or nocturnal and are thus difficult to observe (Verrell, 1989). Mating systems of caecilians, for example, are largely unknown because these fossorial animals are nearly impossible to observe. The myriad behaviors in which males and females are involved and the choices each makes before and during courtship are oriented specifically toward the goal of mating and the production of offspring (Fig. 9.13).

Many aspects of amphibian and reptilian population and reproductive biology must be detailed to understand the mating system of any species. Population dynamics, mate choice and parental care behaviors, and physiological constraints on reproductive behavior are some of the factors that affect mating systems. The ratio of males and females in a breeding population is a major factor determining the structure of the mating system. If one sex is limited, the reproductive success of the other sex will be affected. Competition will occur among individuals of the abundant sex for access to individuals of the scarce (limited) sex. In most species, males compete for limited females. Determination of the limited sex cannot be made by examining the sex ratio in a large breeding aggregation, because not all individuals appear during any given breeding event. For this reason, the operational sex ratio (OSR) is a critical determinant of the mating system (Emlen and Oring, 1977). The OSR is the ratio of fertilizable females to breeding males at any given time. At any given time, a population's sex ratio tends to be skewed toward males. Determining the OSR for any species presents many difficulties. In pond-breeding salamanders, for example, females may be present that are not ready to breed. In other species, females are present but breed synchronously, in effect making the OSR 1:1 for a brief period of time (Verrell and Halliday, 1985). Terrestrial frogs and salamanders present other problems. If males defend territories, the local OSR may be close to 1:1, depending on the amount of female movement. Among many lizards and snakes, the operational sex ratio continually changes as some females become sexually receptive and others become unavailable after fertilization occurs.

Monogamy and polygamy are the two major mating systems; polygyny and polyandry are two types of polygamy (Table 9.4). To a large extent, the number of mates acquired (mating success) by a particular sex and the number of offspring that result (fecundity) determine the kind of mating system (Arnold and Duvall, 1994). Relative to fecundity, if males increase their fecundity by mating with a large number of females but females have no gains by mating with more than one male, a polygynous mating system should result (Fig. 9.14). Monogamy is the likely outcome when neither males nor females gain by mating with additional individuals of the opposite sex. Monogamy also is expected in mating systems requiring both parents (biparental care) to

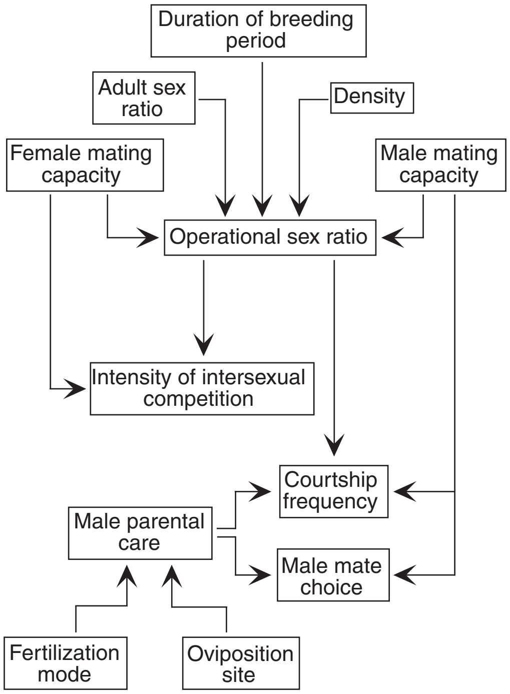


FIGURE 9.12 Determinants of the mating system in salamanders. Adapted from Verrell (1989).

FIGURE 9.13 Social interactions between sexually mature animals culminate in mating as shown for this pair of desert iguanas, *Dipsosaurus dorsalis.* Photograph by J. M. Howland.

ensure the survival of offspring. Most amphibians and reptiles have polygynous mating systems, but there are many interesting exceptions. In addition, the operational sex ratio plays an important role in determining the intensity of sexual selection. Male-biased sex ratios usually result in competition among males for females, and in turn this competition drives the evolution of sexual dimorphism.

Amphibian Mating Systems

The evolutionary framework for mating systems in amphibians considers not only OSR but the type of breeding pattern of a species at any give time (Wells, 1977). At the extremes, some species are explosive breeders that accomplish all reproduction within 2 to 3 days when environmental conditions are suitable. Examples include the spadefoot toads, *Scaphiopus*, which breed during the first summer rains in the Southwest deserts of North America, *Rana sylvatica*, which breeds during the spring thaw in ponds of northern North America, and the salamander *Ambystoma maculatum*, which breeds in vernal ponds for about 1 month in early spring. At the opposite extreme, bullfrogs, many hylids, and many plethodontids are prolonged breeders. Males of these species establish and defend territories for several months, and females arrive gradually over a long period of time. The ratio of females to males can be very different in these contrasting circumstances.

In all species, a critical determinant of the mating system is the mode of sperm transfer (Verrell, 1989). In nearly all frogs, fertilization is external, but the male sequesters the female in amplexus during the actual fertilization of the eggs. Although multiple matings can occur in some species, it is rare; thus, paternity is ensured in most frogs. In contrast, many species of salamanders have internal fertilization by means of a spermatophore that is deposited on the substrate; the sperm packet must be picked up by the female. In most species, the male does not sequester the female in amplexus, but instead he must lead her over the spermatophore; thus, males are particularly vulnerable to interference from rival males at this critical time.

Salamanders Mating systems in salamanders are partly established by whether the lineage is aquatic or terrestrial. In general, aquatic species have shorter breeding periods than terrestrial species (Verrell, 1989), partly because aquatic species depend on rainfall to establish the breeding habitat, which usually is a temporary pond. Prolonged breeding salamanders, exemplified by the plethodontids, are typically terrestrial and usually establish and defend territories. All known species of salamanders are polygynous. Opportunities for mate choice are

TABLE 9.4 Mating System Classification Based on Levels of Polygamy

Mating pattern	Mating system type	Description
Polygyny	Female defense	Males defend groups of females; increased male–male competition
	Resource defense	Males defend resources required by females
	Lek	Males display at a communal site to attract females; both female choice and male–male competition are intense
	Scramble competition	Males locate and mate with as many females as possible; male–male competition intense
Polyandry	Male defense	Females defend male mates in female aggregations
	Resource defense	Females defend resources required by males or by their offspring
Monogamy	Mate-guarding/ assistance	Males mate with single females and defend them against other males; OSR unity
Polygamy	Resource use	Either sex gains by multiple matings

Source: Adapted from Sullivan et al. (1995).

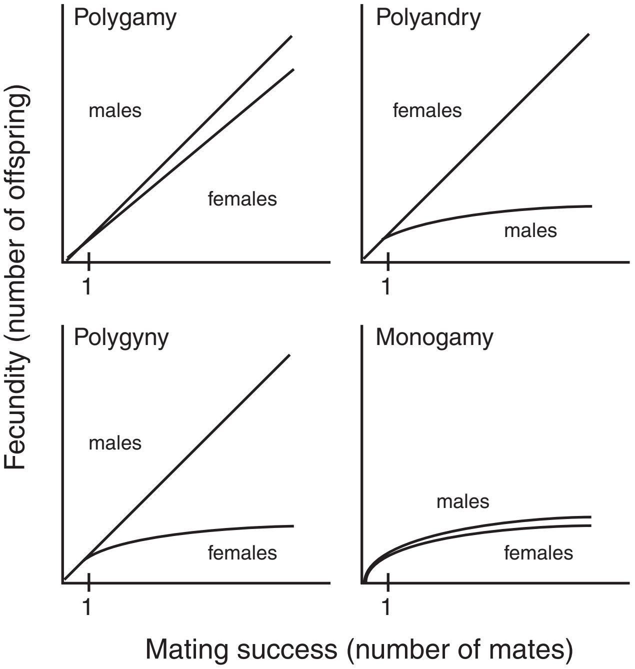


FIGURE 9.14 Mating systems as a function of the relative association between fecundity (number of offspring produced) and mating success for males and females. The line for each sex within a panel represents a sexual selection gradient. For example, in the panel in the lower left (polygyny), potential fecundity of males increases with increased number of mates, resulting in an increase in the intensity of sexual selection in males (line with a high slope), whereas females do not gain in fecundity by mating with additional males and thus there is little sexual selection operating on females (line with no slope). Adapted from Duvall et al. (1993).

limited in explosive breeders but can occur in prolonged breeding species.

Many species of mole salamanders (*Ambystoma*) are typical explosive breeders. Male spotted salamanders (*Ambystoma maculatum*) migrate to temporary ponds in early spring and often deposit spermatophores before the females arrive. Females and males engage in very little courtship; at most, some nudging occurs (Sullivan et al., 1995). Females move around the pond and pick up spermatophores. Competition among males is limited to the deposition of as many spermatophores as possible, and placing a spermatophore on top of another one is common male tactic. Ultimately, a male's reproductive output is related to the number of spermatophores he can deposit.

Another pond-breeding species is the salamandrid *Notophthalmus viridescens*, the red-spotted newt of eastern North America. Even though aquatic, these newts have an extended breeding season and a more complex reproductive behavior than ambystomatids (described above). Females are either ready to lay eggs or become responsive to males during courtship. A male will amplex a female that is not immediately receptive, or he may attempt to induce a nonreceptive female to pick up a spermatophore without amplexus. In either case, courtship interference by other males is intense. In some populations, males mimic female behavior and nudge the cloaca of the courting male, causing him to deposit a spermatophore; later the interfering male deposits his spermatophore to the now more receptive female.

Many studies of courtship behavior have been done under laboratory conditions. These studies have provided much information on interactions and behaviors that are difficult to obtain under natural conditions. However, the results of field studies sometimes conflict with laboratory studies. In red-spotted newts, for example, a laboratory study showed that spermatophore transfer by the courting male was successful in 60% of the amplectant pairs observed (Verrell, 1983), whereas a field study of this newt revealed that spermatophore transfer was successful in only 6% of the observed pairs (Massey, 1988). Natural situations are much more complex than the laboratory, and many more factors impinge on the outcome of individual behaviors.

Terrestrial plethodontid salamanders typically establish territories that contain good food resources and reproductive sites. Their mating system is defined as resource-defense polygyny. Both male and female *Plethodon cinereus* establish territories; male territories do not overlap each other, but female territories often overlap those of several males (Mathis et al., 1995). Whether a female chooses among males is unknown, but females in a laboratory setting have been observed to spend more time around the territories of larger males (Mathis, 1991).

Frogs Many species of anurans exhibit explosive breeding patterns in arid areas, as well as in forest habitats in temperate and tropical areas. The benefits of explosive breeding are obvious in deserts and semiarid areas because breeding can occur only when water is present. The advantages of explosive breeding in wetter areas seems related to the density of predators in aquatic sites, because as the length of the hydroperiod increases in ephemeral ponds, the density of aquatic predators, such as dytiscid and dragonfly larvae, also increases. Explosive breeding at the time of pond formation gives the frog larvae a temporal advantage over their predators.

Explosive-breeding anurans characteristically have a high degree of male–male or scramble competition. Females usually arrive and depart the breeding site quickly; competition for females can be intense. Males may attempt to displace amplectant males, and often the larger male wins the contest. The OSR may not be 1:1 in all cases, and the potential for female choice may exist. Females of some species may approach specific calling males and bypass others (Sullivan, 1989). Explosive breeders include the spadefoot toads (*Scaphiopus*, *Spea)* of North America, *Rana sylvatica* in northern North America, and *Bufo bufo* and *Rana temporaria* in Europe (Fig. 9.5).

Resource defense polygyny occurs or has been implicated in several species of prolonged breeding frogs (Sullivan et al., 1995). In the bullfrog *Rana catesbeiana*, males establish and defend territories that vary in the quality of larval habitats (Howard, 1978a,b). Territories defended by large males have higher larval survivorship because they have lower densities of leeches that feed on the eggs and tadpoles. Whether females choose large males or some aspect of a male's territory is unknown. Relatively little is known about other species of frogs that defend territories and attend the eggs. Centrolenid frogs, for example, call from trees along streams and small rivers, and amplectant pairs deposit their eggs on leaves above the water. In *Hyalinobatrachium fleischmanni*, a species in which males attend eggs, females choose a male and initiate amplexus, but male characteristics on which choice might be based have not been determined (Fig. 9.15). In the sympatric species *Centrolene prosoblepon,* males do not attend clutches, and males initiate amplexus (Jacobson, 1985).

Polyandry, in which a female mates with several males, has the potential advantage of providing the female with a wider range of genetic diversity for her eggs (Backwell and Passmore, 1990). In the rhacophorid *Afrixalus delicatus*, the amplectant pair constructs a small nest by folding a leaf over about 35 eggs. The female does not deposit all her eggs at once, and some females break amplexus after depositing some eggs and seek another male to construct another nest. Males in this system are polygynous; the behavior of females is poorly understood and only 7% (of 100 observed pairs) of the pairs exhibit polyandry. True sex-role reversal in which a female mates with multiple males, each of which then cares for the resulting offspring, is unknown in frogs.

Monogamous mating systems are typically found in birds and a few mammals, but are rare in other vertebrate groups. Monogamy has been widely cited to have evolved in birds because offspring survival is greater when two parents instead of only one are involved in feeding the young. Recent studies using genetic analyses have shown that monogamous relationships are more complex than was previously presumed. In birds, extra-pair fertilizations are common, even though the pair may remain socially monogamous (Birkhead and Moller, 1995). Males may derive increased reproductive success by fertilizing other females, even though they remain with a primary partner. In certain situations, pair-bonded females may mate with another male that may be of higher quality than the social partner but who is not available as a long-term partner. Reproductive parasitism of the other sex may occur if a male or a female can entice an unrelated individual to provide parental care for his or her offspring (Brockmann, 1993).

Monogamy is rare in frogs and has been implicated only in a few species of unrelated dendrobatids and hylids, and like birds, the parents provide biparental care to the tadpoles. Care includes feeding the tadpoles trophic eggs deposited by the female parent. In both groups, the egg and larval habitat is a protected arboreal site, such as a small tree hole or vine hole that holds water. These sites are small, often with reduced or no light, and lack food for the tadpoles. All species of *Dendrobates* deposit terrestrial eggs and then transport their tadpoles to a small tree hole or other type of water-holding plant for development. In the hylids, eggs rather than tadpoles are deposited directly into the water of these habitats. Prolonged parental care is required for tadpole survival.

Dendrobates vanzolinii males and females form pair-bonds, and the pair remains together in a small territory (Caldwell, 1997). Clutch size is very small, about three

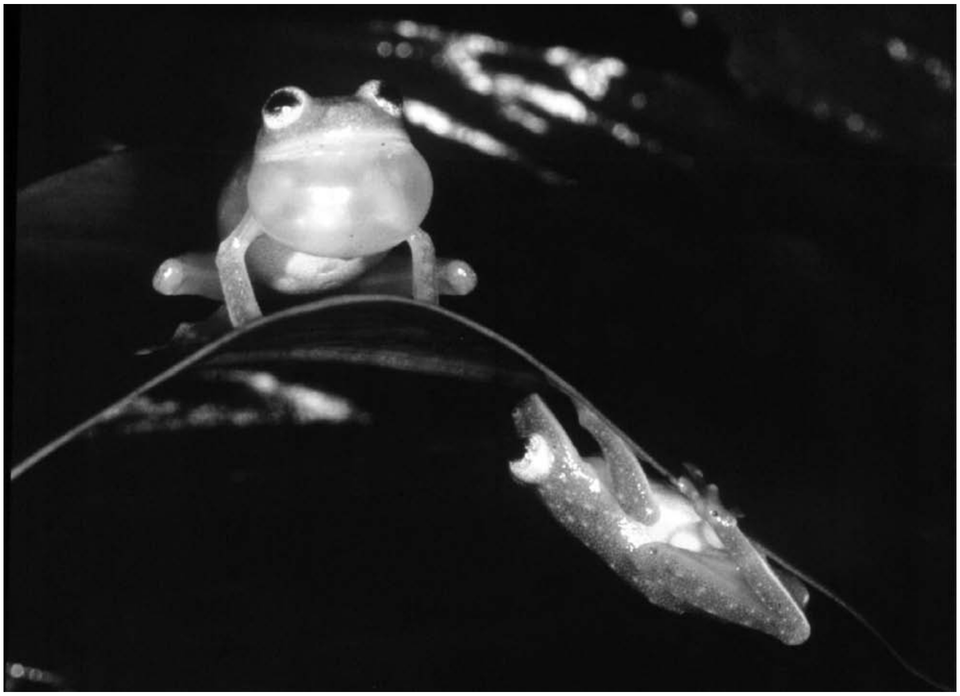


FIGURE 9.15 A male glass frog, *Hyalinobatrachium fleischmanni*, calling from a leaf above a stream; below, a female is attracted to his call. Note that the eggs of the gravid female can be seen through the transparent venter. Photograph by W. Hödl.

eggs that are deposited above the water line on the wall of tiny tree or vine in the Amazonian rain forest (Fig. 9.16). Developing tadpoles are transported singly by the male to another site. Because the tadpoles are cannibalistic, they are not allowed to drop into the water in the same tree hole, where a larger tadpole may be present. No more than one tadpole occupies a small tree hole. The male and female court about every 5 days; the female then ovulates two eggs, one from each ovary (Fig. 9.16). The male guides her to the tree hole containing one of their tadpoles, and the female deposits the trophic eggs for the tadpole to consume (Caldwell and Oliveira, 1999).

In the closely related *Dendrobates ventrimaculatus*, promiscuity is common. In this species, the larval habitat is the small amount of water held in the leaf axils of *Heliconia* plants. Tadpoles are not deposited alone as in *D. vanzolinii*; rather many tadpoles from different clutches are either transported to the same axil or are allowed to slide into the pool as they develop from eggs attached just above the waterline. Cannibalism is common among the tadpoles and may provide a significant source of nutrients for the tadpoles (Summers and Amos, 1999). Indeed, these two closely related frogs may exemplify how natural section has operated in different directions to produce two different types of mating systems. In *D. ventrimaculatus*, reproductive parasitism is high, whereas it appears low in *D. vanzolinii*. The factors driving these two systems appear related to aspects of the larval habitat.

Monogamy and biparental care have also been reported in the hylid *Osteocephalus oophagus* (Jungfer and Schiesari, 1995). In this Amazonian rain forest species, an amplectant pair deposits a clutch of about 250 eggs in a tree hole. As the tadpoles develop, the same male and female return about every 5 days and deposit more fertilized eggs for the developing tadpoles to consume (Fig. 9.17). The mechanism for repeated pairing is not known. After about a month, some tadpoles metamorphose and leave the tree hole. Eggs continue to be delivered but not all of them are consumed by the older tadpoles, and these uneaten eggs hatch into more tadpoles. The result is that tadpoles of different sizes are present in a pool; generally the smaller ones are unable to obtain trophic eggs and die. Oophagy is obligatory in this species; if the parents do not regularly provide trophic eggs, the tadpoles starve (Jungfer and Weygoldt, 1999).

Reptile Mating Systems

Snakes Most snakes have polygynous mating systems, but a few are effectively monogamous (Duvall et al., 1993). In polygynous snakes, males gain in terms of the offspring they sire by mating with more than a single

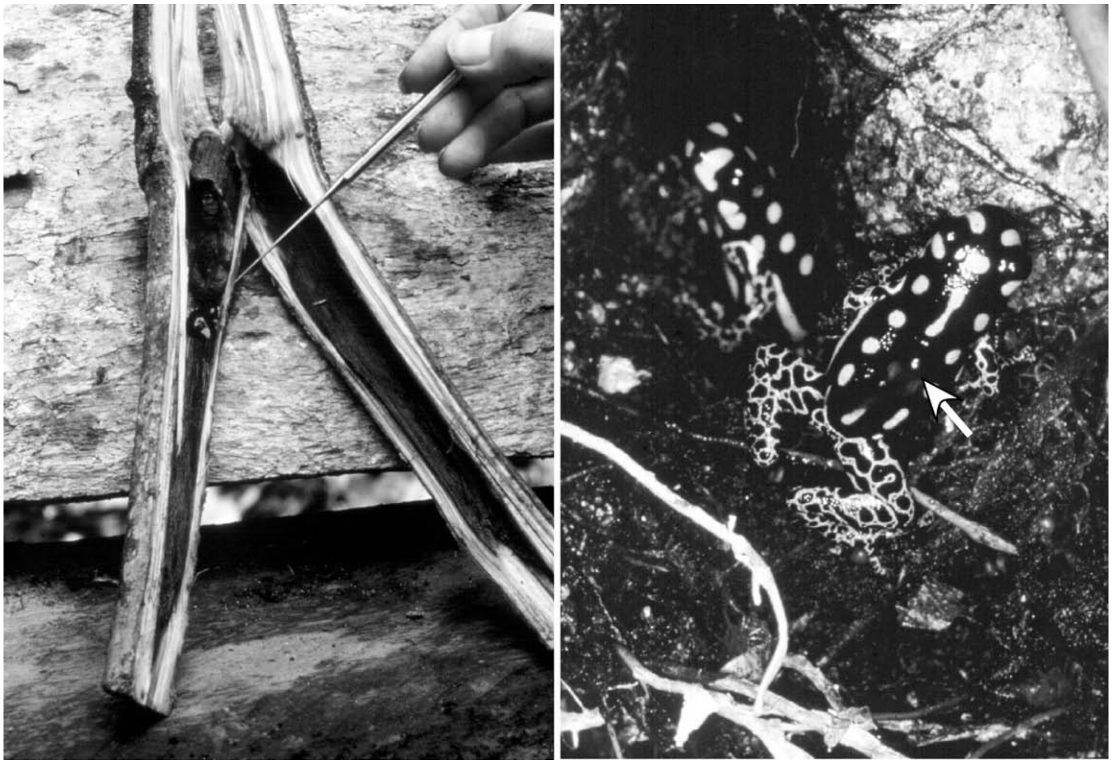


FIGURE 9.16 (Left) Opened vine showing the cavity within used by a pair of spotted poison frogs, *Dendrobates vanzolinii,* as a tadpole nursery. Pointer shows three eggs that have been deposited about the waterline. When opened, a large tadpole was in the water in the cavity. (Right) A pair-bonded male and female emerging from a small tree hole; the male is transporting a tadpole on his back (white arrow). Vine photograph by L. J. Vitt; frogs by J. P. Caldwell.

female. Females maximize production of offspring by mating with a single male and investing time and energy in efficient foraging to gain the benefits associated with increased energy intake, which include a fecundity increase related to body size and condition. Prairie rattlesnakes, *Crotalus viridis viridis*, are polygynous and females are only sexually receptive for short periods of time, partly because they are nonreceptive during the

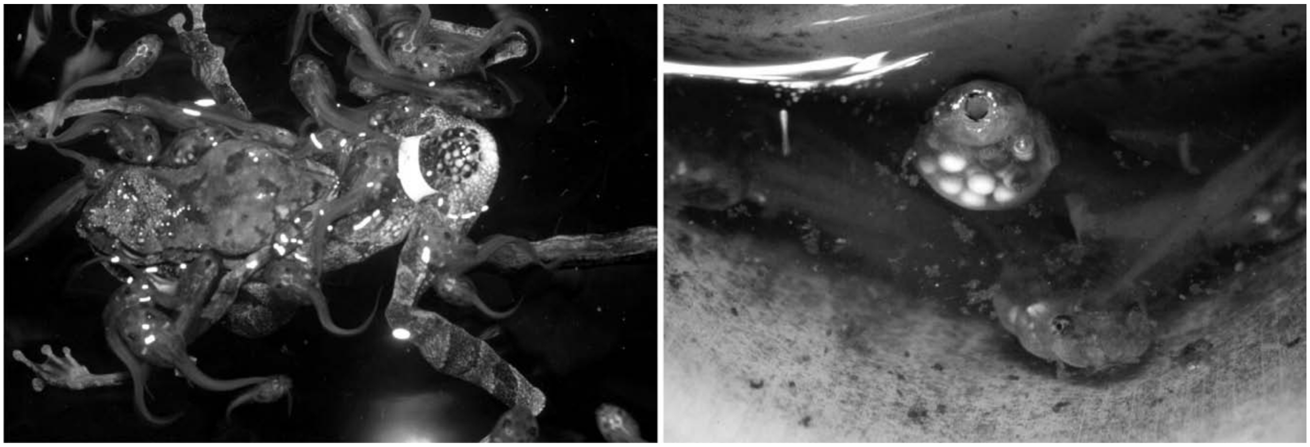


FIGURE 9.17 (Left) A female *Osteocephalus oophagus* returning to a small tree hole to deposit eggs as food for her offspring. Tadpoles nip at her cloaca to stimulate egg deposition. (Right) In a tadpole that has just ingested eggs, the eggs can be seen through its transparent venter. Photographs by K.-H. Jungfer.

extended gestation period. Female body size and the availability of food and heat to females influence the frequency of reproduction. Some females skip several years of breeding. Taken together, these factors result in a variable operational sex ratio—more males available to breed at any one time than females. Thus, the OSR of these snakes depends largely on ecological factors and the peculiarities of viviparous pitviper breeding biology (Fig. 9.18).

As mentioned previously, garter snakes in northern latitudes overwinter in large numbers (Gregory, 1974). Large numbers of small males attempt to copulate with the larger-bodied females as they emerge singly, and female mobbing results in the formation of "mating balls" (Duvall et al., 1993). Male body size appears unimportant for mating success, but some males produce female-mimicking pheromones (Mason and Crews, 1985). These "she-males" apparently cause considerable confusion within the mating balls, and as a result, the she-males gain better positions within the ball and have a higher probability of mating.

Lizards Most lizards have polygynous mating systems, but monogamy or at least extended pair-bonding is more common than previously thought. Among iguanians, males of most species defend at least part of their home range (see Chapter 8), and polygynous mating systems predominate. Male-male interactions commonly lead to sexual dimorphism (Stamps, 1983); however, the degree of polygyny varies greatly. In some species, territorial males mate with only one or two females, whereas in others, individual males may mate with as many as six females. Territories or home ranges of females are often contained within the territory of the male, and male territorial boundaries are defended by males, resulting in low male home range overlap. Most communication is visual in territorial species, and a high diversity of male coloration and ornamentation occurs, perhaps as a result of intrasexual selection. Sexual dimorphism in head size is also common.

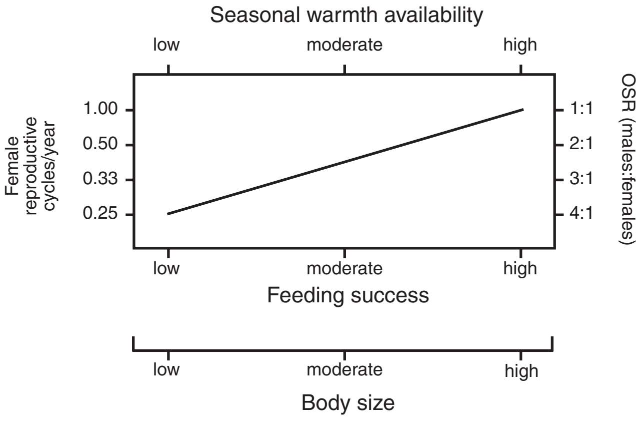


FIGURE 9.18 The operational sex ratios (OSRs) of prairie rattlesnakes are intimately affected by the amount of heat available for thermoregulation and gestation, and by feeding success because it influences energy available for reproduction. Reproductive success is influenced by body size because it determines the number of offspring produced in a given season. Adapted from Duvall et al. (1992).

Among territorial iguanians, males appear to more vigorously pursue nonresident females that enter their territories than resident females. Males of keeled earless lizards, *Holbrookia propinqua*, and brown anoles, *Anolis sagrei*, either more intensely court nonresident females or selectively court nonresident females when offered a choice (Cooper, 1985; Tokarz, 1992). In both of these species, males appear able to recognize familiar and unfamiliar females. Vigorous courting of nonresidents might result in a nonresident female taking up residence in the male's territory or, even if the female leaves, if the male copulates with the female, it provides additional opportunities to sire offspring, thus increasing his individual fitness.

Even though most scleroglossans are nonterritorial, polygynous mating systems predominate. Because males usually search for females, often using a combination of visual and chemical cues, and courtship can be extended as can postcopulatory mate guarding, polygyny is often sequential. When male–male interactions occur, they are contests associated with the acquisition of a female that is being courted by one of the males. Sexual dimorphism in coloration and head size occurs in many species. In some long-lived scleroglossans, extended pair-bonds and near monogamy occur.

In the sand lizard *Lacerta agilis*, females mate with many males even though they produce only one clutch of 4 to 15 eggs each season. The males with which they mate are variously related to the female. Female sand lizards appear to exert mate choice by preferentially using sperm from more distantly related males, likely as a result of intrauterine sperm competition. DNA fingerprinting studies demonstrate that males most closely related to the female sire fewer offspring that those that are more distantly related (Olsson et al., 1996). Because several males can sire the offspring of a single female even though a single clutch is produced, the mating system is effectively polyandrous.

Most teiid lizards have sequential polygyny, in which males guard females when the females are receptive. Males often interact aggressively with other males that attempt to court the female (Anderson and Vitt, 1990). In *Ameiva plei*, large males win in male-male encounters and guard females during their entire sexually receptive period of 1 to 4 days (Censky, 1995). Among 21 mature males in a study site, only 6 mated with females and the 4 largest males accounted for more than 80% of matings and sired nearly 90% (estimated) of the eggs produced. Because male body size determines success in guarding receptive females and guarding determines mating success, selection favors the evolution of large body size in males even though territoriality is not involved. In addition, females reject small males when a large courting male is removed but do not reject proxy large males, indicating that females select larger males (Censky, 1997). Presumably, females are harassed less when guarded by a large male and, as a result, can spend more time foraging.

In Australia, males and females of the long-lived, large-bodied skink *Tiliqua rugosa* form monogamous pairs that remain together up to 8 weeks prior to breeding (Bull and Pamula, 1998). Males are often observed with the same female in consecutive years, suggesting longer-term pair-bonds as well (Bull, 1994). Unlike monogamous frogs, there is no extended parental care so there is no advantage to monogamy for either sex relative to offspring survival. Moreover, the close association of males and females occurs prior to the time when the young are produced and ends after mating. Males and females are easily observed prior to and during the breeding season and, when in pairs, are often feeding. They are omnivores, with a diet dominated by plant material. A similar percentage of unpaired (69.9%) and paired (78.3%) females had food in their mouths when first observed. Thus, females feed similarly regardless of the presence of a male. The same was not true for males. Single males more frequently had food in their mouths (62.2%) than males observed with females (26.1%). A paired male follows closely behind the female while she forages, stopping when the female stops, but often not feeding (Bull, 1988). Although one reason for the male to defer feeding when the female stops is to maintain alertness for the possibility of an approaching male, another is to maintain vigilance to detect approaching predators. Both sexes gain from this behavior. The male gains by having access to a female for reproduction, and the female gains by being able to feed and gain energy for reproduction while the male watches for predators.

Most male *T. rugosa* are monogamous (82%), but some males sequentially pair with different females (Bull et al., 1998). Both females and males are occasionally observed with one or more additional partners even though the apparent long-term bond is with only one partner. Based on microsatellite DNA analysis of females, their offspring, and their male partners, some females were found to produce offspring fathered by a second male, a finding not surprising considering the occasional extrapair associations. Females paired with polygynous males were more likely to have extrapair fertilizations than females paired with high-fidelity males. Females with polygynous partners have opportunities to be courted by other males.

Alternative Mating Strategies

Recently, researchers have closely studied the mating tactics of individual animals. By marking individuals and following them for a long time, it has been discovered that males in the same population use different strategies to obtain mates. It is uncertain whether these alternative strategies are genetically based, or whether individual males switch strategies, depending on current internal or external factors. Future studies will investigate these questions in amphibians and reptiles.

Satellite Males

The satellite male strategy is common in frogs and occurs in some reptiles as well. In frogs, a male can adopt a calling strategy or become a satellite. Satellites do not vocalize but rather they wait near a calling male to intercept females that are attracted to the calling male. Satellite male behavior occurs in numerous species of hylids, ranids, bufonids, and other clades.

Several hypotheses address the evolution of this strategy (Halliday and Tejedo, 1995). (1) Calling sites or suitable territories are limited, and males compete for these sites and defend them by calling. Site holders are more competitive that satellites and may be larger. (2) Some males select a satellite status and become sexual parasites. This strategy includes individuals that switch back and forth between calling and satellite status, although other males are persistent satellites or persistent callers. Satellite behavior must have a payoff for it to have evolved and be maintained. In some cases, the mating success of satellites is equal to that of calling males. (3) The third hypothesis involves the adoption of satellite status because of an energetic constraint. If a male's fat body reserves are low or even if he has a more temporary condition, such as a buildup of anaerobic metabolic byproducts, he adopts a satellite status. To date, experiments have not confirmed this hypothesis.

Experiments with satellite males of various species indicate that these hypotheses are not mutually exclusive. In *Hyla minuta*, for example, some satellites begin calling when the nearby calling male is removed. This behavior supports the hypothesis of limited calling sites; however, in the same population, other satellites do not begin calling but move to another calling male, thereby supporting the switching hypothesis.

For a female, interception by a satellite male may lower her fitness. Females of many species assess a potential mate's fitness based on attributes of his call. Because satellites are silent, females cannot evaluate their fitness (Halliday and Tejedo, 1995). In at least one species, *Bufo calamita*, females struggle to be released when amplexed by a silent male.

Whether satellite males exist in snakes is uncertain. In the European *Vipera berus*, large males generally win male–male combat and gain access to females. Smaller males avoid interactions with large males, yet about 10% of the matings involve smaller males that "shadow" females (Madsen and Shine, 1993, 1994). Even though the breeding season last for only 3 weeks, females mate up to eight times, making it is possible for small males to mate and sire offspring even though the females have already mated (Madsen et al., 1992). Multiple paternity of *V. berus* offspring occurs in many females, so advantages potentially exist for satellite behavior (Höggren and Tegelström, 1995). Moreover, the operational sex ratio varies considerably through time due to seasonal weather, the availability of receptive females, and variation in survivorship. When the operational sex ratio is lowest (i.e., many receptive males compared to few receptive females), combat among males for access to females is most likely to occur, and this, in turn, intensifies sexual selection for large body size in males (Fig. 9.19).

Sexual Interference

In salamanders, males do not use the satellite strategy. Because the mode of sperm transfer requires a male to entice a female to pick up his sperm packet, interference by other males is the main type of intermale competition (Verrell, 1989). The major factor determining whether a male courts or interferes is whether he finds a courted or noncourted female. Males apparently adopt a courtship strategy or an interference strategy based on the circumstances.

Males have evolved at least four types of interference behaviors. These behaviors include interference through female mimicry; spermatophore covering; wrestling with a male already in amplexus to attempt a takeover; and overt fighting (Verrell, 1989).

Some male newts (*Notophthalmus* and *Triturus*) mimic female behavior to avoid detection by a courting male. The rival male can cause the courting male to deposit his spermatophore at the wrong time by nudging his cloacal lips; subsequently, the rival deposits a spermatophore and induces the female to pick it up. In ambystomatids, an interfering male deposits his spermatophore on top of the courting male's spermatophore, thus substituting his sperm for that of the courting male. In salamandrids and ambystomatids, a courting male often amplexes a female if it she is not immediately receptive. A wrestling bout ensues if a rival male attempts to dislodge the amplectant male. Both size and prior ownership determine the outcome of the attempted takeover. Duration of the contest increases with increasing size of the intruder, and displacement occurs only when the amplectant male is smaller than the intruder (Verrell, 1989).

Overt fighting is most common in plethodontid salamanders. Fighting includes biting, chasing, and the adoption of certain postures. One male can affect the future reproductive success of another male by inflicting physical injury. For example, damage to the tail can result in the loss of the tail and its fat reserves, whereas damage to the nasolabial grooves can interfere with a male's ability to obtain food (Jaeger, 1981).

Sexual interference is undoubtedly common in lizards based on numerous anecdotal observations of territory

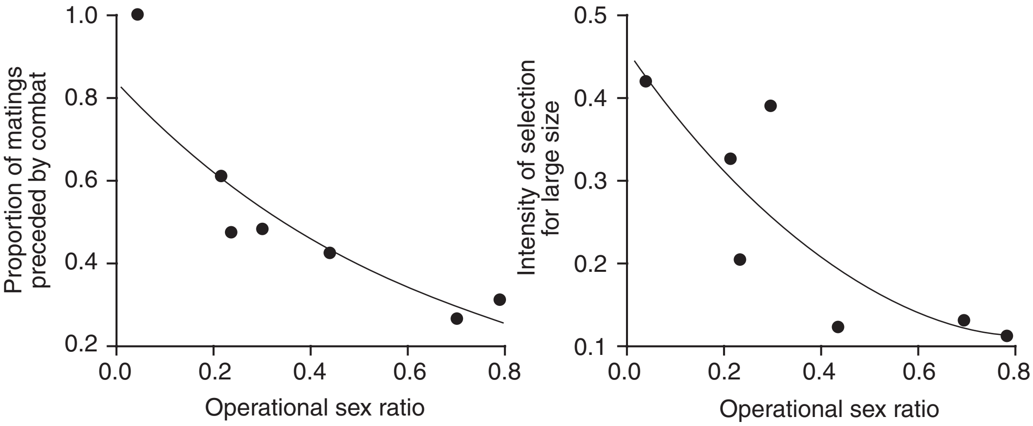


FIGURE 9.19 When the operational sex ratio in adders (*Vipera berus*) is low, male–male combat increases (left), resulting in increased sexual selection for large body size in males (right). Adapted from Madsen and Shine (1993).

holders repeatedly chasing off smaller males and smaller males trailing courting pairs of nonterritorial lizards. In the large-bodied *Ameiva ameiva* and in the broad-headed skink *Eumeces laticeps*, females are frequently pursued by more than one male. The courting male chases the trailing male when the latter approaches too closely. If the males are similarly sized, the chase is prolonged and either delays or diverts the courting male's ability to mate.

Among the most fascinating example of sexual interference in reptiles is the presence of "she-males" in garter snakes (Mason and Crews, 1985, 1986). Some male *Thamnophis sirtalis parietalis* elicit courtship behavior of other males in large mating aggregations. These she-males apparently produce an estrogen as a result of high testosterone levels; this chemical cue either causes other males to misidentify them as females or prevents their identification as males (Mason, 1992). In experiments testing the mating success of she-males and normal males, she-males were more than twice as successful as normal males, so she-males have a strong mating advantage. Behaviorally, interference works in two ways. A she-male gains because other males do not interfere during courting, or by courting a she-male, a normal male's reproductive effort is misdirected and potentially lost. While she-males may have a mating advantage, they may not have a fitness advantage because the production of estrogen potentially can result in fewer or less viable sperm.

Sexual Dimorphism and Sexual Selection

Sexual dimorphism in body size, coloration, and a variety of morphological characteristics is well known in amphibians and reptiles. Male bullfrogs, *Rana catesbeiana*, and green frogs, *Rana clamitans*, for example, have larger tympana than females because male calls are critical for territory maintenance (Fig. 9.20). In many instances, competition among individuals of the same sex (usually males) for access to individuals of the other sex is the driving force behind the evolution of sexual dimorphism. These interactions between individuals of the same sex determine reproductive success and result in intrasexual selection. Male competitive ability is at a selective advantage. Because size often dictates a male's success in contests with other males, intrasexual selection can drive the evolution of increased body size in males and result in sexual dimorphism in which males are larger than females. In other instances, females may choose males for mates based on either size or some other overt male trait. This female choice can result also in males being the larger sex. Sexual selection, however, is not the only factor that determines body size within each sex. For example, large female body size can be selected because size and fecundity are linked in many species (Berry and Shine, 1980). Sexual size differences can arise from differing growth trajectories, age at sexual maturity, and patterns of energy use (Anderson and Vitt, 1990; Stamps and Krishnan, 1997; Stamps et al., 1994, 1998).

FIGURE 9.20 Sexual dimorphism in the tympanum of the green frog, *Rana clamitans*: female left, and male right. Photographs by R. W. Van Devender.

Differences in size between males and females more often represent a combination of the effects of sexual selection and natural selection (Lande, 1980; Price, 1984).

In frogs, females are larger than males in about 90% of the species studied (Shine, 1979). Although sexual selection is the usual explanation for male and female size differences, other factors also are involved in anurans (Woolbright, 1983). For example, many species of frogs are explosive breeders, and male–male competition for mates is the rule in these species. Among prolonged breeders that maintain territories, larger males most often win in bouts with smaller intruders. In species with female choice, females choose males based on their calls, and they often prefer calls with a lower fundamental frequency, that is, those produced by larger males. All of these factors typically drive selection for large size in males. Thus, sexual selection does not explain why females are larger than males (Woolbright, 1983).

In many species increased fecundity is correlated with large size in females. But why males do not achieve the same size as females is unclear. One explanation is that males have energetic demands associated with breeding (Woolbright, 1983). Males must call to attract mates, maintain territories, and compete with other males. Recent studies show that females prefer males with high calling rates or with longer or more complex calls, both of which are energetically expensive. Calling requires more energy than any other male activity (Runkle et al., 1994). Males may have less time to forage, resulting in slower growth and ultimately in smaller size.

In turtles, sexual dimorphism in body size and coloration is common. In some species, males are the larger sex, but in others, females are larger (Berry and Shine, 1980). Males are larger than females in most terrestrial taxa, and male combat is common in these species, suggesting that intrasexual selection drives the evolution of large body size in males. Males are smaller than females in most aquatic species. In these, male mobility determines reproductive success; males must locate females and court them in a high-density, three-dimensional environment—water. Increased body size in males would likely reduce their ability to gain access to females. Selection on female body size is not relaxed because the number of eggs, and in some cases, the size of individual eggs, increases with body size (Congdon and Gibbons, 1987). Females reach large sizes even though the size of males is constrained. When life history traits are considered, the evolution of sexual size dimorphism becomes more complex (Gibbons and Lovich, 1990). Body size and age at maturity are critical variables; they result in size differences largely because growth rates at sexual maturity decrease. If males reach sexual maturity at a younger age and growth rates are identical, males remain small relative to females even if they continue to grow. For many turtles, natural selection favors the rapid attainment of large size to deter predation, and sexual selection favors rapid maturation, particularly in males, so they can mate sooner.

In snakes, male combat is closely linked to the evolution of sexual dimorphism (Shine 1978). In the 15% of the snakes using male combat, most taxa are sexually dimorphic, and males are larger. Intrasexual selection in which relatively larger males win in male–male social interactions appears to be the ultimate cause of sexual size dimorphism in these snakes. The proximal cause appears to be the continuation of male growth after sexual maturity (Shine, 1994). In most cases where females are the larger sex, male combat does not occur.

In lizards, aggressive interactions among males appear to result in sexual dimorphism, and males are larger than females regardless of whether the lizards are territorial. In addition to males attaining larger size due to intrasexual selection, males often have larger heads or ornamentation (Fig. 9.21; see also Fig. 20.22). In territorial species such as *Anolis* and *Sceloporus*, a male's reproductive success usually correlates with the number of females within his territory or his number of copulations (e.g., Blair, 1960; Trivers, 1976; Ruby, 1981, 1984; Stamps, 1983). In nonterritorial species such as *Ameiva*, most *Cnemidophorus*, and *Eumeces*, home ranges of males are large and overlap those of several females (Anderson and Vitt, 1990). Males not only court females for extended periods, but guard females from advances of other males, often interacting aggressively for access to females that are receptive (Censky, 1996, 1997; Vitt and Cooper, 1985). In both territorial and nonterritorial species, reproductive success of males is determined by size; larger males are successful territory holders in territorial species or are successful at guarding females in nonterritorial species (Fig. 9.22). In both cases, larger males win aggressive encounters. In some nonterritorial species, such as *Ameiva pleei*, females reject small males even in the absence of a larger male. This preference for large males allows females to continue foraging during the breeding period because the presence of a large male reduces the harassment of a female by smaller males (Censky, 1997). In *Eumeces laticeps*, small males avoid encounters with larger males because there is a low probability of winning (Cooper and Vitt, 1987a). Small males only court females when large males are absent, thus deferring agonistic behavior until they are larger and the probability of success is increased.

A variety of ecological factors also can influence sexual size dimorphism. In pond turtles, for example, the annual frequency of clutch production is associated

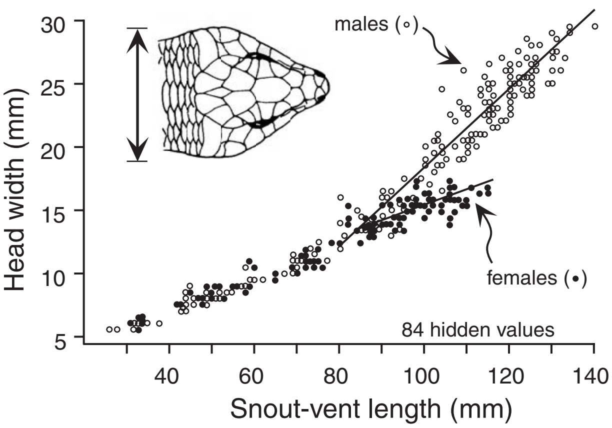


FIGURE 9.21 Sexual dimorphism in relative head size in the broad-headed skink, *Eumeces laticeps* (see also Fig. 20.22). Note that the divergence between sexes in relative head size occurs after sexual maturity is attained (about 84 mm SVL). Adapted from Vitt and Cooper (1985).

with sexual dimorphism. Sexual dimorphism increases with increasing number of clutches produced per season (Forsman and Shine, 1995).

Snakes offer several examples of how ecology can influence body size. Because snakes swallow their prey whole, a strong association exists between the head size and maximum prey size (Savitsky, 1983). Furthermore, unlike lizards, snakes rarely use their heads in mating behavior, so there is no sexual selection on relative head size. Males and females in many snake taxa have evolved differences in body size, relative size of the head, or ecology (Shine, 1991a). Divergence in body size is related to reproductive differences, but the divergence in head size reflects independent adaptations of feeding behaviors in females and males. Neither sexual selection (at least directly on head size) nor resource partitioning causes sexual dimorphism in snakes. Rather, independently evolved differences in size and trophic structures account for the dietary differences between females and males.

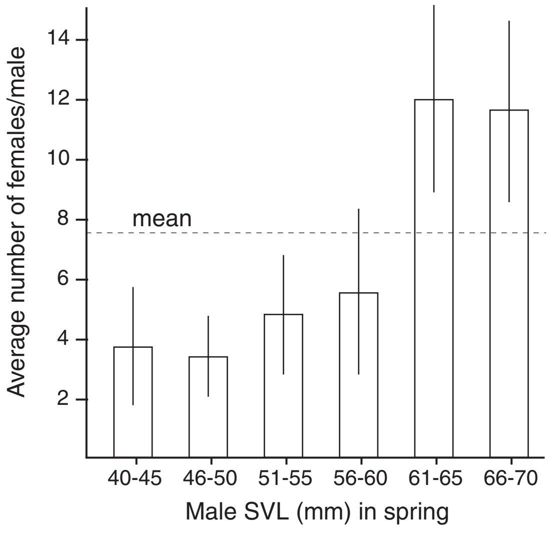


FIGURE 9.22 The number of mating opportunities (females/male) increases with body size for males of *Anolis carolinensis*. Adapted from Ruby (1984).

ADDITIONAL READING

Arnold, S. J., and Duvall, D. (1994). Animal mating systems: A synthesis based on selection theory. *Am. Nat.* **143:** 317–348.

Cooper, W. E., Jr., and Greenberg, N. (1992). Reptilian coloration and behavior. *In* "Biology of the Reptilia, Vol. 18, Physiology. Hormones, Brain, and Behavior" (C. Gans and D. Crews, Eds.), pp. 298–422. University of Chicago Press, Chicago.

Duvall, D., Schuett, G. W., and Arnold, S. J. (1993). Ecology and evolution of snake mating systems. In "Snakes—Ecology and Behavior" (R. A. Seigel and J. T. Collins, Eds.), pp. 165–200. McGraw-Hill, Inc., New York.

Halpern, M. (1992). Nasal chemical senses in reptiles: Structure and function. *In* "Biology of the Reptilia, Vol. 18, Physiology. Hormones, Brain, and Behavior" (C. Gans and D. Crews, Eds.), pp. 422–523. University of Chicago Press, Chicago.

Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. *In* "Lizard Ecology. Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 169–204. Harvard University Press, Cambridge, MA.

Heatwole, H., and Sullivan, B. K., Eds. (1995). "Amphibian Biology, Vol. 2, Social Behaviour." Surrey Beaty & Sons, Chipping Norton, NSW.

Wells, K. D. (1977). The social behaviour of anuran amphibians. *Anim. Behav.* **15:** 666–693.

REFERENCES

Communication and Social Behavior: General: Halliday and Tejedo, 1995; Ryan et al., 1981.

Communication: Alcock, 1998; Ruby and Niblick, 1994.

Caecilians: Billo and Wake, 1987.

Salamanders: Halliday, 1977; Houck and Sever, 1994; Verrell, 1982, 1989.

Frogs: Brenowitz and Rose, 1999; Haddad and Giaretta, 1999; Kluge, 1981; Lindquist and Hetherington, 1996; Pombal et al., 1994; Ryan, 1985; Ryan et al., 1982; Wells, 1980, 1988; Wevers, 1988.

Turtles: Auffenberg, 1965; Boiko, 1984; Halpern, 1992; Jackson and Davis, 1972; Mason, 1992.

Crocodylians: Garrick and Lang, 1977; Garrick et al., 1978.

Tuataras and Lizards: Adams and Cooper, 1988; Alberts, 1992; Auffenberg, 1981; Cooper, 1984, 1996; Cooper and Crews, 1988; Cooper and Greenberg, 1992; Echelle et al., 1971; Fitch, 1954; Fleishman, 1992; Gans et al., 1984; Gillingham et al., 1995;

Greenberg and Noble, 1944; Jenssen, 1970a,b; Jenssen and Hover, 1976; López et al., 1997; Main and Bull, 1996; Martins, 1993; Stamps, 1977; Tokarz, 1995; Trauth et al., 1987; Werner et al., 1987. Snakes: Ford and O'Bleness, 1986; Ford and Schofield, 1984; Garstka and Crews, 1981, 1986; Gillingham, 1987; Gregory, 1982, 1984; Halpern, 1992; Mason, 1992; Noble and Clausen, 1936; Quay, 1972.

Reproductive Behavior: Mating Systems: Arnold and Duvall, 1994; Emlen and Oring, 1977; Sullivan et al., 1995; Trivers, 1972; Verrell, 1989; Verrell and Halliday, 1985.

Amphibian Mating Systems: Backwell and Passmore, 1990; Birkhead and Møller, 1995; Brockmann, 1993; Caldwell, 1997; Caldwell and Oliviera, 1999; Howard, 1978a,b; Jacobson, 1985; Jungfer and Schiesari, 1995; Jungfer and Weygoldt, 1999; Massey, 1988; Mathis, 1991; Mathis et al., 1995; Sullivan, 1989; Sullivan et al., 1995; Summers and Amos, 1999; Verrell, 1983, 1989; Wells, 1977.

Reptile Mating Systems: Anderson and Vitt, 1990; Bull, 1988, 1994; Bull and Pamula, 1998; Bull et al., 1998; Censky, 1995, 1997; Cooper, 1985; Duvall et al., 1993; Gregory, 1974; Mason and Crews, 1985; Olsson et al., 1996; Stamps, 1983; Tokarz, 1992.

Alternative Mating Strategies: Halliday and Tejedo, 1995; Höggren and Tegelström, 1995; Jaeger, 1981; Madsen and Shine, 1993, 1994; Madsen et al., 1992; Mason, 1992; Mason and Crews, 1985, 1986; Verrell, 1989.

Sexual Dimorphism and Sexual Selection: Anderson and Vitt, 1990; Berry and Shine, 1980; Blair, 1960; Censky, 1996, 1997; Congdon and Gibbons, 1987; Cooper and Vitt, 1987a; Forsman and Shine, 1995; Gibbons and Lovich, 1990; Lande, 1980; Price, 1984; Ruby, 1981, 1984; Runkle et al., 1994; Savitsky, 1983; Shine 1978, 1979, 1991a, 1994; Stamps, 1983; Stamps and Krishnan, 1997; Stamps et al., 1994, 1998; Trivers, 1976; Vitt and Cooper, 1985; Woolbright, 1983.

Chapter

10

Foraging Ecology and Diets

Amphibians and reptiles are often the most abundant vertebrates at any locality in the warmer parts of the world and, like other animals, they must eat other organisms to survive. Given their high species diversity and abundance, their impact on other animal species, and in some instances plants, is not trivial. Although some particularly interesting exceptions exist, caecilians generally feed on earthworms and other invertebrates, frogs and salamanders feed almost exclusively on insects (at least as adults), crocodylians feed largely on other vertebrates, turtles feed on a combination of plants and animals, and squamates feed largely on invertebrates or vertebrates, although one lizard taxon (Iguaninae) and a few members of several other taxa are herbivorous.

In nature, amphibians and reptiles have numerous food items available, yet no amphibian or reptile eats all available items. Instead, an individual eats a particular subset of prey, which is species specific. The preferred food can range from a variety of appropriate-sized arthropods or insects to just one prey type, such as termites. Even among species living in the same area, diets differ. Are these differences the result of competition? The type and origin of such interactions are examined in Chapter 13. The emphasis here is how amphibians and reptiles detect, pursue, and capture their prey, the relative sizes of prey, and the evolution of sensory systems relative to prey choice. These aspects of foraging behavior directly influence many aspects of the feeding ecology of amphibians and reptiles.

FORAGING MODES

Two well-publicized foraging modes are recognized: sit-and-wait foraging (also referred to as "ambush foraging") and active foraging (also referred to as "wide foraging"). These foraging modes were originally defined on the basis of behaviors used to locate and capture prey (MacArthur and Pianka, 1966; Pianka, 1966; Schoener, 1974b). Theoretically, sit-and-wait foragers invest little time and energy searching for prey. They typically remain stationary and attack mobile prey that move within their field of vision (Gerritsen and Strickler, 1977). Most foraging energy is spent in the capturing and handling of prey. Active foragers move about through the environment in search of prey, expending considerable energy in the search phase but little energy in the capture phase of foraging. Although many species of amphibians and reptiles can easily be placed into one of these two categories, some are herbivorous, and as a consequence they do not pursue prey in the classical sense. In addition, there is likely a continuum of foraging modes from the two extremes described above (Huey and Pianka, 1981a).

Our theory on foraging is based heavily on the notion that foraging behavior is evolutionarily plastic and responds to differences in prey abundance and behavior. A decade ago, discussions of foraging mode were strictly selection based. Foraging behavior was assumed to be driven in each species by a combination of competition and energetic aspects impinging upon a particular species. This interpretation was made and widely accepted in spite of the observation that specific foraging modes were shared by closely related species and groups of species. The introduction of the modern comparative method applying cladistic analysis to behavioral and ecological phenomena provides a different perspective. For example, phrynosomatine lizards are sit-and-wait foragers, whereas teiid lizards are active foragers. Mapping foraging modes on a phylogenetic dendrogram reveals that sit-and-wait foraging is shared among the earliest branching lizard clades and the other lepidosaurian clade, the sphenodontidans or tuataras. This observation argues for the evolution of sit-and-wait foraging in the distant past and the origin of active foraging much later or more recently in the evolution of lizards (Cooper, 1995). The observation further suggests that active foraging in lizards likely arose as a single evolutionary event.

The bimodality of sit-and-wait versus active foraging that appears so obvious within single assemblages of species (e.g., lizards in the deserts of the southwestern United States) breaks down when the confounding effects of phylogeny are removed (Fig. 10.1). Phylogenetic analyses of other behaviors related to foraging also indicate that much of the variation has its origins deep within phylogeny rather than representing repeated adaptive responses to prey types, distribution, or abundance (Cooper, 1994a,b, 1995; Schwenk, 1993, 1995).

Nevertheless, extremes in foraging behavior are apparent regardless of the number of evolutionary events causing them. Foraging behavior does not evolve in a vacuum; consequently, numerous ecological, behavioral, physiological, and life history correlates of foraging mode can be identified. Similar to time spent moving and the number of moves per unit time (behaviors associated with search behavior; Fig. 10.1), the so-called "correlates" of foraging mode likely also have an historical basis. Many correlates are intuitively obvious based on behaviors associated with prey search and capture (Table 10.1). Species that are sit-and-wait foragers typically do not move while waiting for potential prey to pass through their field of vision. They would be expected to be visually oriented or even use thermal cues (as in pit vipers), have cryptic morphology or coloration (so that neither the prey nor predators detect them), and have a physiology that results in optimal function under conditions in which little movement, other than prey attack, occurs. Actively foraging species search throughout a habitat for prey and are expected to use a combination of visual and chemical cues for prey detection. Because they move while foraging and possess well-developed chemical senses, they can find nonmoving, clustered, or hidden prey that might not be detected by sit-and-wait foragers. Movement alone offsets crypsis to at least some degree, so active foragers would be expected to be wary because potential predators would have little problem detecting them. Rapid response would be at an advantage for these species, reducing the probability that predators could capture them. Also, because of their seemingly continual motion while foraging, their physiology should cause them to function optimally while actively searching. Support for this view of the influence of foraging ecology on other aspects of an animal's biology of amphibians stems mainly from studies comparing two or a few species that differed not only in foraging behavior but also in evolutionary histories. Such analyses cannot distinguish whether the evolution of active foraging from sit-and-wait foraging caused the behavioral, physiological, and ecological differences or is just part of a complex set of coevolved traits. As compelling as foraging behavior appears to be as the driving force behind

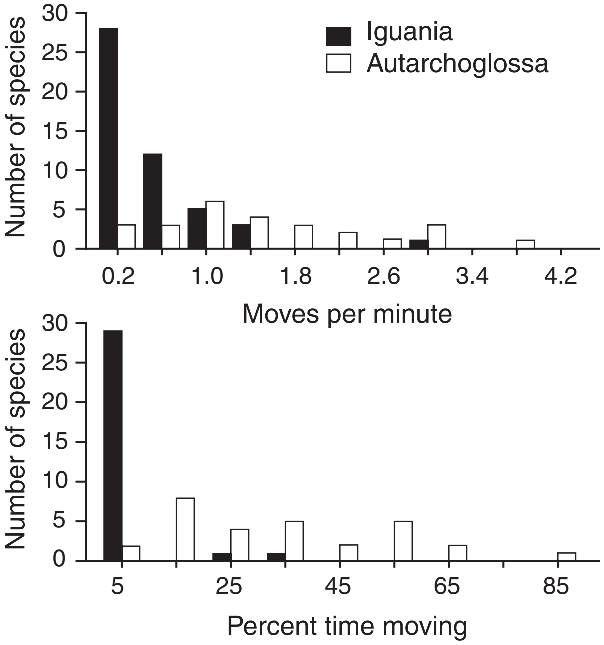


FIGURE 10.1 Two important behavioral attributes of lizard foraging, the number of moves per unit time and the percentage of time spent moving, vary considerably across lizard species. Most lizard species in the Iguania, a group typically considered sit-and-wait foragers, make fewer moves and move shorted distances than lizards in the Autarchoglossa (Lacertiformes + Diploglossa), a group typically considered to be active foragers. Phylogenetic analyses of percent time moving and number of moves per unit time confirm that the apparent bimodality in behavioral attributes of foraging mode has an historical basis (i.e., they reflect phylogenetic patterns rather than easily identifiable ecological patterns). Adapted from Perry (1999).

TABLE 10.1 Correlates of Foraging Mode

Character	Sit-and-wait foraging	Active foraging
Escape behavior	Crypsis, venoms (viperids)	Flight, skin or blood toxins (*Phrynosoma* and many frogs), and venoms (elapids, helodermatids)
Foraging behavior		
Movements/time	Few	Many
Movement rate	Low	High
Sensory mode	Vision	Vision and olfactory
Exploratory behavior	Low (social)	High (food)
Prey types	Mobile	Sedentary
Morphology	Associated with microhabitat	Streamlined
Physiological characteristics		
Endurance	Limited	High
Sprint speed	High	Intermediate to low
Aerobic metabolic capacity	Low	High
Anaerobic metabolic capacity	High	Low
Heart mass	Small	Large
Hematocrit	Low	High
Activity body temperatures	Moderate (25–37°C)	High (32–41°C)
Energetics		
Daily energy expenditure	Low	Higher
Daily energy intake	Low	Higher
Social behavior		
Home range size	Variable, but smaller	Variable, but larger
Territoriality	Common	Rare
Mating system	Resource defense polygyny	Sequential mate defense polygyny
Social signals	Visual	Visual and chemosensory
Reproduction		
Relative clutch mass	If clutch size is variable, relatively high; if clutch size is fixed, low	Relatively low and consistent across species regardless of clutch size

Sources: Bennett and Gleeson (1979); Cooper (1994a, 1995); Garland and Losos (1994); Huey and Pianka (1981a); Huey et al. (1984); Nagy et al. (1984); Perry et al. (1990); Perry and Pianka (1997); Pianka (1966); Pough and Taigen (1990); Schwenk (1993, 1995); Secor and Nagy (1994); Seigel et al. (1986); Vitt and Congdon (1978); Vitt and Price (1982); Werner (1997); and Werner et al. (1997).

the traits listed in Table 10.1, an analysis of complete physiological, behavioral, and ecological data testing this hypothesis has not been performed. The analysis by Perry (1999) is a bold step toward solving this complex puzzle and should be taken as a challenge to assemble the data set allowing such an analysis. Phylogenetic analyses by others (Schwenk, 1993; Cooper, 1995) suggest that chemosensory behavior, lingual-vomeronasal morphology, and foraging mode compose an adaptive complex driving the evolution of lizards.

Optimal foraging theory is a popular explanation for the evolution of foraging modes. This theory dictates that animals best able to harvest resources should be at a selective advantage when competition among individuals exists. Thus natural selection should favor the fine-tuning of resource acquisition (“optimal foraging”). Because growth, maintenance, and reproduction require energy (Chapter 7), the payoff for foraging “optimally” is presumably increased reproductive success. Although heuristically appealing, optimal foraging theory is overly simplistic and most empirical studies fail to support most of its predictions (see Perry and Pianka, 1997). One prediction, however, is supported; when food is scarce, animals tend to eat a greater variety of prey types than they do when food is abundant (Gray, 1987). In natural environments, foraging is extremely complex. External, internal, and historical factors influence the ability of individual organisms to acquire food, and these factors are difficult if not impossible to model (Table 10.2).

TABLE 10.2 Factors Influencing Foraging Behavior

External factors
Prey availability
Predation risk
Social interactions (e.g., competition)
Habitat structure (e.g., perch availability)
Opportunities for thermoregulation
Internal factors
Hunger
Learned experiences
Age (e.g., ontogenetic diet shifts)
Sex and reproductive state (e.g., energetic trade-offs)
Epigenetic inheritance (e.g., maternal effects)
Dietary preferences (as influenced by nutrient requirements, toxins, distasteful compounds)
Historical (phylogenetic) factors
Sensory limitations
Morphological characteristics (e.g., mouth shape, head size)
Physiological constraints (e.g., sprint speed)
Behavioral set (e.g., conservative foraging mode)

Source: Adapted from Perry and Pianka (1997).

DETECTING, CAPTURING, AND EATING PREY

Prey Detection

Prey of amphibians and reptiles can be detected by visual (usually moving prey), chemical (usually nonmoving prey), tactile (moving and nonmoving), or thermal (moving and nonmoving) cues. Many species rely on a single type of cue but others use combinations of cues to detect prey. Caecilians appear to use their tentacles as chemosensory samplers (Badenhorst, 1978). Salamanders and frogs primarily use visual cues to detect moving prey and in many instances responses to movement are so stereotypical that inanimate nonfood items can be rolled in front of some species (e.g., *Bufo marinus*) and they will be ingested. In other species (e.g., *Salamandra salamandra*) prey must meet a specific set of criteria to elicit attack (Luthardt and Roth, 1979). Certain frogs and salamanders, such as *Bufo boreas* and *Plethodon cinereus,* are quite good at locating some prey items on the basis of olfactory clues alone (Dole et al., 1981; David and Jaeger, 1981). Prey detection in crocodylians appears to be mostly based on visual cues. Tactile cues, based on water movement, and chemical cues may also play a role in prey detection. For most turtles, the primary cues are visual, but chemical and tactile cues may also be involved. Among squamates, the entire spectrum of cues for prey detection are used. In most iguanian and gekkotan lizards, visual cues associated with prey movement result in prey attack. In most other lizards (including snakes), chemical cues are important in prey detection and discrimination.

Visual Prey Detection

Visual prey detection is used by most amphibians and reptiles that are sit-and-wait predators, and to a lesser degree by many active foraging species. Neurophysiological studies of the anuran eye show that prey recognition derives from four aspects of a visual image: perception of sharp edges, movement of the edges, dimming of images, and curvature of the edges of dark images (Roth, 1986). Perception is greatest when the object image is smaller than the visual field. Under these conditions, anurans can determine the speed, direction of movement, and relative distance of the prey. Success in capture by visual predators depends on binocular perception in many species; most align their head or entire body axis with the prey before beginning capture behavior. Chameleons are an exception. The eyes of chameleons are independently movable, and when one eye sights a prey item, the head turns to allow both eyes to focus on the prey prior to aiming the projectile tongue. These movements give the impression that binocular vision is being used to determine the distance of the prey item (Fig. 10.2). However, accommodation (focus) is most important in coordinating prey detection and prey capture in chameleons. They can accurately orient on and capture a prey item at substantial distances with only one functioning eye.

The extensive use of vision in prey capture is also apparent from the number of diurnal and nocturnal species with large, well-developed eyes. Nocturnal predators locate prey under low-light conditions and require maximum light entry into the eye for perception. Horizontal or vertical elliptical pupils allow the maximum movement of the iris and the greatest dilation of the pupil (Fig. 10.3).

Nevertheless, even in species that appear to use visual cues, more than simple detection of movement is involved. For example, most phrynosomatine lizards eat a wide diversity of insects, but lizards in one genus, *Phrynosoma*, specialize on ants (Pianka and Parker, 1975). Arguably *Phrynosoma* do not specialize on ants because ants are usually the most abundant insects; however, by the same reasoning, other synoptic lizards are selectively not eating ants (see Toft, 1980, for a similar discussion with respect to frogs). Regardless of which

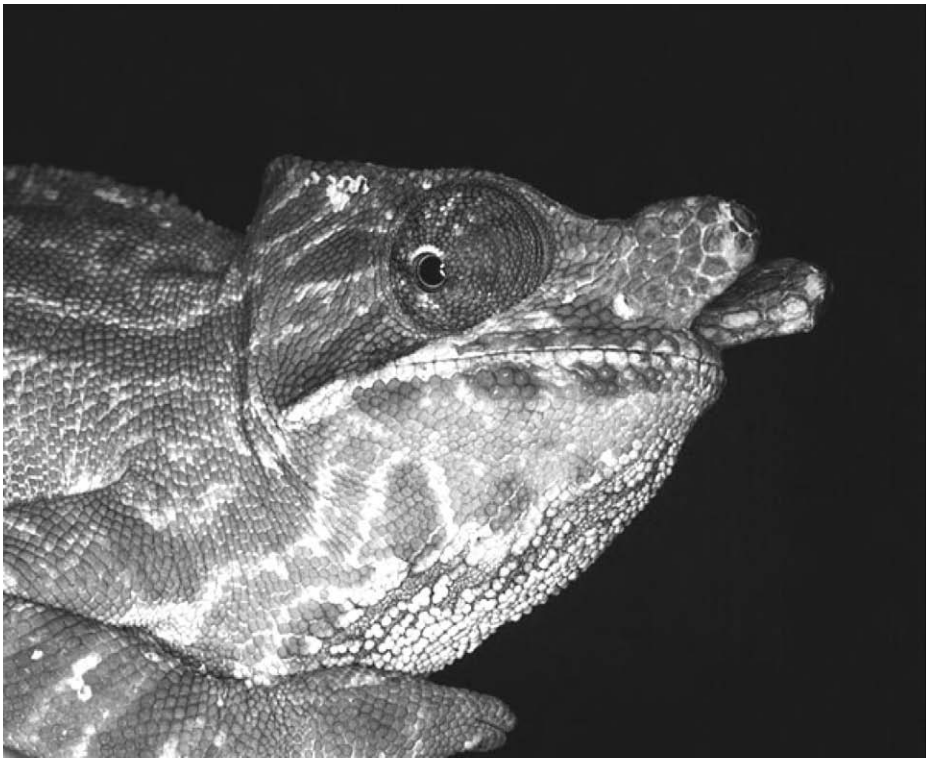


FIGURE 10.2 The eyes of chameleons move independently until a prey item is sighted. Photograph by L. J. Vitt.

species actually are the specialists, amphibians and reptiles relying on visual cues do not randomly capture all available moving prey. Prey selection demonstrates a high level of visual acuity sufficient to discriminate based on size and shape.

Chemosensory Prey Detection

The use of chemical cues in prey detection by amphibians and reptiles is just beginning to be appreciated (Cooper, 1995; Schwenk, 1995). Chemosensory-oriented amphibians and reptiles possess three chemical senses: olfaction, vomerolfaction, and taste (gustation). The first two are used in prey location and identification; olfaction uses airborne odors and vomerolfaction uses airborne or surface odors. The olfactory epithelium in the nasal chamber is sensitive to volatile compounds carried by the air and inspired with respiratory air or "sniffing" by rapid buccal or gular pumping. The vomeronasal (Jacobson's) organ is especially sensitive to high-molecular-weight compounds that are transported into the oral or nasal cavity by the snout or tongue. Olfaction acts mainly in long-distance detection, for example, the presence of food and its general location, and triggers tongue-flicking and the vomeronasal system. Vomerolfaction operates as a short-range identifier and appears more important than olfaction or gustation in feeding. The vomeronasal system requires that chemicals be brought in, usually by the tongue, which can pick up volatile chemicals from the air or nonvolatile chemicals by lingual contact with surfaces (Fig. 10.4). Gustation functions during feeding as the final discriminator.

Olfaction and vomerolfaction have long been recognized as feeding senses in salamanders and scleroglossan lizards (including snakes), and are often used in conjunction with vision. Actively foraging predators, such as skinks, use vision while moving across open-surface microhabitats but depend on olfaction to locate prey in dark crevices or buried in leaf litter or soil. Likewise, many salamanders probably alternate between visual and vomerolfactory searching, depending upon the availability of light and crypsis of the prey. Some salamanders, such as *Hydromantes italicus*, locate, orient on, and capture prey in total darkness based on chemical cues alone (Roth, 1987). Iguanian lizards (except the Iguaninae) and most anurans are highly visual predators and most lack well-developed olfactory–vomerolfaction systems. However, observations on *Bufo marinus* and a few other anurans responding to chemical cues in food suggest that the role of chemoreception in prey detection by anurans may be underappreciated (Rossi, 1983). At least some iguanine lizards (e.g., *Dipsosaurus dorsalis*) are

FIGURE 10.3 Elliptical pupils are found in some nocturnal frogs, lizards, and snakes, and in all crocodylians. The pupils, closed here, open in low light to facilitate vision at night. Clockwise from upper left: *Phyllomedusa vaillanti, Phyllopezus pollicaris, Caiman crocodilus,* and *Corallus hortulanus.* Photographs by L. J. Vitt and J. P. Caldwell.

sensitive to chemical cues in food (Cooper and Alberts, 1990). Historically, turtles and crocodilians were considered to be visual foragers; however, both groups produce pheromones for individual and species recognition and would seem capable of locating prey via odor and/or vomerodor. Experiments have shown that the American alligator can locate visually hidden food both in the water and on land, suggesting chemoreception in prey identification (Coulson and Hernandez, 1983). Snakes are perhaps best known for their chemosensory abilities because of the often rapid sampling of the air and surfaces with their long, flexible, forked tongues (Fig. 10.5). Not only does the tongue transmit particles to the vomeronasal organs, but because it is forked and thus samples two points, directional information is also conveyed (Schwenk, 1994a). In some garter snakes (*Thamnophis sirtalis similis*), visual cues alone do not elicit foraging even though they are important for prey capture (Teather, 1991). Foraging commences when the snakes detect chemical signals with their vomeronasal system.

Taste is a chemosensory sense but it is not used to locate prey. When combined with the tactile sense organs of the oral epithelium, taste can serve to identify food items once in the mouth and permit rapid acceptance or rejection. Items may be rejected because of taste or because of mechanical stimulation of the tactile sense based on the presence of spines or urticating hairs.

Similar to differences among species in foraging behavior, much of the variation in use of chemical cues has a historical basis in squamates (Fig. 10.6). When scleroglossans diverged from the Iguania, chemosensory acuity for prey detection appeared and was carried into most of the taxa derived from them, including snakes. From a historical perspective, the evolution of chemosensory prey detection made a large set of prey available to scleroglossines that was not available to the visually oriented Iguania—nonmoving prey and hidden prey, many of which are larvae of insects eaten by visually oriented amphibians and reptiles. The development of the chemosensory mechanism for prey discrimination certainly played a major role in the subsequent

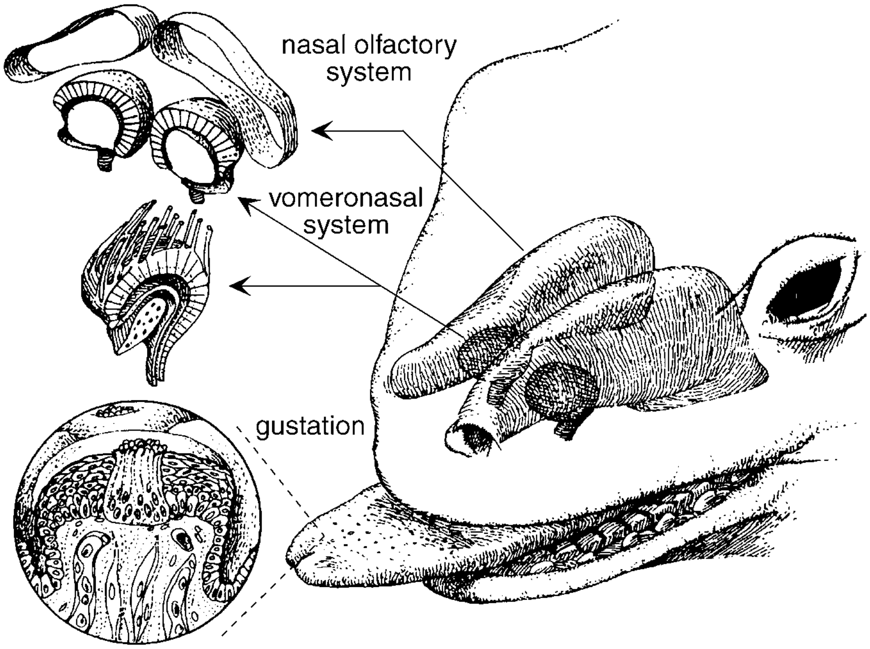


FIGURE 10.4 Squamate reptiles have three kinds of chemical senses: (1) olfaction, which involves the nasal olfactory system and is mediated by sensory epithelia within the nasal cavities; (2) vomerolfaction, which involves the vomeronasal system and is mediated by vomeronasal epithelia within the paired vomeronasal organs; and (3) gustation (taste), which is mediated by taste buds on the lingual and oral surfaces. Adapted from Schwenk (1995).

diversification and success of scleroglossan lizards (including snakes).

Although the development of chemosensory cues for prey detection occurred in scleroglossans or their immediate ancestor, the chemosensory structures (vomeronasal organs, taste buds) were present in squamate ancestors, and many iguanians use chemical cues for social communication (Schwenk, 1986). Only in the

FIGURE 10.5 The long, flexible tongue of *Xenoxybelis boulengeri* picks up particles from the air, surfaces, and potential prey. The odors are transmitted to the vomeronasal organs and allow identification and discrimination. The same sensing system is used in chemosensory-based social communication. Photograph by L. J. Vitt.

iguanines, which are herbivorous, are chemical cues used for discrimination among food types. Thus, even though the basic morphological structures for prey discrimination were in place when squamates began diversifying, they were not used for prey detection and discrimination by members of the arthropod-eating iguanians.

Auditory Prey Detection

Use of airborne sound to locate prey may occur widely in amphibians and reptiles, but it remains largely undocumented. The observations are mostly anecdotal, such as *Bufo marinus* orienting and moving toward a calling *Physalaemus pustulosus* (Jaeger, 1976), although a recent field experiment showed that the gecko *Hemidactylus turcicus* locates male crickets based on their calls and preys on female crickets coming to the male (Sakaluk and Belwood, 1984).

For some amphibians and reptiles, sensitivity to substrate vibrations or seismic sounds is likely a major prey detection mechanism. Seismic sensitivity may be particularly important for fossorial (burrowing) species or those with fossorial ancestors, both for the avoidance of predators and for the location of prey. Snakes, salamanders, and caecilians have no external ears, so they probably possess a high sensitivity to seismic vibration, although actual tests are lacking for most species. Uniquely, both frogs and salamanders possess a special pathway (opercularis system) for the transmission of vibrations from the substrate to the inner ear (Hetherington, 1985), and the limited data indicate that salamanders are two times more sensitive to these sounds than frogs. The opercularis system links the forelimb to the inner ear through the opercularis muscle that extends from the scapula to the opercular bone lying in the fenestra ovalis of the otic capsule. The muscle acts like a lever arm; vibrations received by the forelimb rock the tensed muscle, thereby pushing-pulling the operculum and creating fluid movement in the otic capsule. These seismic vibrations are of low frequency, typically less than 200 Hz, and stimulate the neuroreceptors in the sacculus and lagena rather than those of either the basilar or amphibian papilla, although the latter may be stimulated by frequencies as low as 100 Hz. These low frequencies are made by such activities as the digging of insect prey or mammalian predators. In snakes, seismic vibrations appear to be transmitted via the lower jaw through the quadrate–columella to the inner ear. Snakes also detect seismic vibrations through mechanoreceptors in the skin, although not with the same fine-scaled resolution as with the ear. Other fossorial groups (e.g., caecilians, amphisbaenians) likely use mechanoreceptors for detection of seismic vibrations.

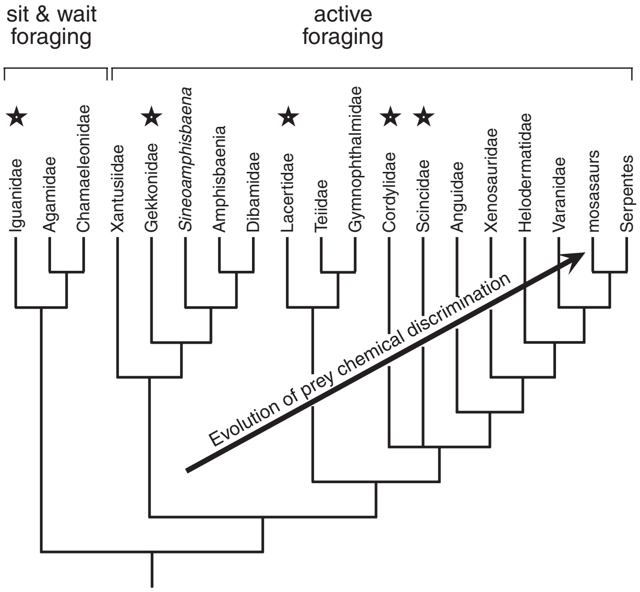


FIGURE 10.6 The evolution of prey chemical discrimination and of foraging mode appear linked in squamates. The Iguania contains only a single taxon that cannot be characterized as sit-and-wait foragers, the Iguaninae; the remainder of iguanid taxa are sit-and-wait foragers as are the Agamidae and Chamaeleonidae. Several evolutionary reversals have occurred within taxa (marked with stars). In instances where reversals have occurred, such as the evolution of sit-and-wait foragers within the Lacertidae, chemical cues are not used for prey discrimination even though the sensing systems are developed. Adapted from Cooper (1995).

Thermal Prey Detection

Thermal cues are used by some snakes for locating and orienting on prey (Cock Buning, 1985; Shine, 1991b; Greene, 1997). Infrared light (long-wavelength light) is sensed by trigeminal-innervated blind nerve endings in the skin of the head. Many boas and pythons (e.g., *Corallus, Morelia*) and all viperid snakes in the Crotalinae (e.g., *Crotalus, Agkistrodon, Lachesis, Bothrops*) have infrared-sensitive pits either along the jawline in the labial scales (boids) or in the loreal scales (crotalines) at the front of the jaw (Fig. 10.7). The pits open (face) anteriorly and provide a binocular perception field. These receptors are capable of detecting thermal objects moving within the snake's sensory thermal landscape. Temperature changes lower than 0.05°C elicit a response from some snakes. Experiments have demonstrated that snakes can accurately orient on and strike objects based on thermal cues alone. Infrared cues are putatively most effective for nocturnal snakes that feed on mammals and birds because of the large temperature differential between the background thermal landscape and the moving prey, but these cues are likely to be equally effective for a pitviper hidden in a crevice, for example, when a lizard with an elevated body temperature enters the crevice.

FIGURE 10.7 Facial heat-sensing pits along the jaw of *Morelia viridis* (left) and between the nares and the eye on *Bothriopsis bilineata* (right) allow these snakes to detect moving prey on the basis of their contrast with the background thermal landscape. Photographs by L. J. Vitt.

Tactile Prey Detection

Tactile prey detection is poorly understood in amphibians and reptiles. Mechanoreceptors in the skin presumably facilitate prey location and identification. Aquatic amphibians use the lateral line, a string of mechanoreceptors along the body, to sense changes in water pressure reflecting from stationary or motile objects in the near vicinity of the predator to identify and locate prey. Such recognition would certainly be enhanced by a weak electric field (see the discussion of sense organs in Chapter 2). Preliminary evidence from aquatic salamanders indicates that prey identification and size determination occur solely by the lateral line system.

Alligator snapping turtles (*Macrochelys temminckii*) certainly use tactile cues when making the decision to close their mouths on an unsuspecting fish that tries to sample their wormlike tongue (Fig. 10.8). Tactile cues may also be important for turtles, such as *Chelus fimbriata*, that expand their throats rapidly to vacuum in fish or tadpoles moving in front of them. Flaps of skin are highly innervated and undoubtedly are involved in detection of tactile cues (Hartline, 1967).

Prey Capture and Ingestion

Once detected, prey must be subdued and ingested in order for the amphibian or reptile to appreciate a net gain in energy from the pursuit of prey. A vast majority of amphibians and reptiles swallow their prey whole, and in most species, prey are very small relative to the size of the predator (see below). Toads (*Bufo*), for example, flick the tongue in and out at such a rapid rate that the entire event cannot be detected easily by the human eye (Fig. 10.9). At the opposite extreme are crocodylians such as *Crocodylus moreletii* in Veracruz, Mexico, that drown large prey and hold them in their mouths for as long as 3 days until they began to decompose, and then dismember and eat them (Perez-Higareda et al., 1989). Komodo dragon lizards fatally wound moderate-sized mammals by slicing through the musculature of the prey's body or legs with their serrated teeth. The mammals die, and monitors are attracted to the putrefying corpse, which they are able to dismember, swallowing large pieces (Auffenberg, 1981). Herbivorous lizards feed on clumped, stationary plant parts, so prey "capture" is a trivial problem. Many species of snakes kill their prey by constriction, or envenomation, but some simply swallow their prey alive (Greene, 1997).

Numerous behavioral and morphological adaptations are associated with capturing and subduing prey. In catching mobile prey, motor and sensory units are finely coordinated to intercept the moving prey, and usually the strike/capture mechanism aims at the center of mass/gravity of the prey. The center of gravity is the most stable part of the target and has the least amount of movement.

Biting and Grasping

Prey capture by most amphibians and reptiles involves biting and grasping. Prey are attacked, either as the result of a rapid sprint by the predator followed by biting the prey, or by a rapid movement (e.g., strike) of the head and neck from a stationary position. Reptiles or amphibians with long, flexible necks (turtles, varanid lizards) and limbless ones (amphiumas, pygopods, snakes) can and regularly do use the strike mechanism, often from ambush but also following a slow stalk of the prey. In both strikes and bites, the mouth commonly does not open until

FIGURE 10.8 The alligator snapping turtle, *Macrochelys temminckii*, lures fish into its mouth by waving its fleshy tongue. The cryptic morphology of this nonmoving turtle combined with the resemblance of the tongue to a small earthworm facilitates prey capture. Photograph by R. W. Barbour.

the head moves toward contact with the prey, and the bite/strike is an integrated behaviour of motor and sensory units. When the open mouth encompasses the food, the tactile pressure on teeth and oral epithelium triggers rapid closure of the mouth. A few animals use lures to attract the prey to the predator. Juvenile viperids use caudal luring enhanced by bright coloration on the tail and cryptic coloration of the body (Fig. 10.10), pedal luring occurs in a few *Ceratophrys* frogs, and lingual-appendage luring occurs in alligator snapping turtles (*Macrochelys*).

Only minimal food processing occurs in the mouth of amphibians and reptiles. Teeth may crush or perforate food items, which are commonly swallowed whole. Some evidence suggests that most lizards, for example, do not swallow arthropod prey items until they have crunched the exoskeleton. If hard-bodied prey fail to crush when bitten, the broad-headed skink, *Eumeces laticeps*, repositions the prey repeatedly and attempts to crush it. If the hard-bodied prey happens to be a female mutilid wasp (velvet ''ant''), repeated biting allows the insect to use all of its defense mechanisms (Vitt and Cooper, 1988). The powerful sting, injected deep into the tongue, causes the lizard to release the wasp. When approached by a xenodontine snake, some species of *Bufo* inflate their body by filling their lungs and tilt their back toward the snake. In response, some snakes, such as *Waglerophis merremii*, puncture the inflated lungs of *Bufo* with their razor-sharp and enlarged maxillary teeth. In these species, the maxillary is reduced in length and rotates forward during biting. Once deflated, the toads can be swallowed by the snake.

Fragmentation of food is limited to herbivores that bite off pieces of foliage, and large lizards, turtles, and crocodilians may use a combination of sharp jaw sheaths or teeth and limb/body movements to break up large items. Turtles have continuously growing keratinous sheaths on their upper and lower jaws; each sheath provides a uniform bladelike labial surface that is effective in cutting food (Fig. 10.11). Tooth structure in amphibians and diapsid reptiles is highly variable, ranging from simple conelike teeth to molarlike teeth or bladelike teeth with serrated edges. Specialized diets usually are associated with specialized teeth: broad and sturdy teeth for crushing mollusks are found in *Dracaena*; bladelike teeth for cutting vegetation or fragmenting large prey are found in *Iguana* and *Varanus*, respectively; long recurved teeth for feathered prey occur in *Corallus hortulanus*; and hinged teeth for capturing skinks occur in *Scaphiodontophis.*

Once captured, prey must be moved through the oral cavity into the esophagus. Three main ''swallowing'' mechanisms are recognized in amphibians and reptiles. Inertial feeding is mechanically the simplest and most widespread in reptiles. In its simplest form, inertial feeding involves moving the head and body over the food

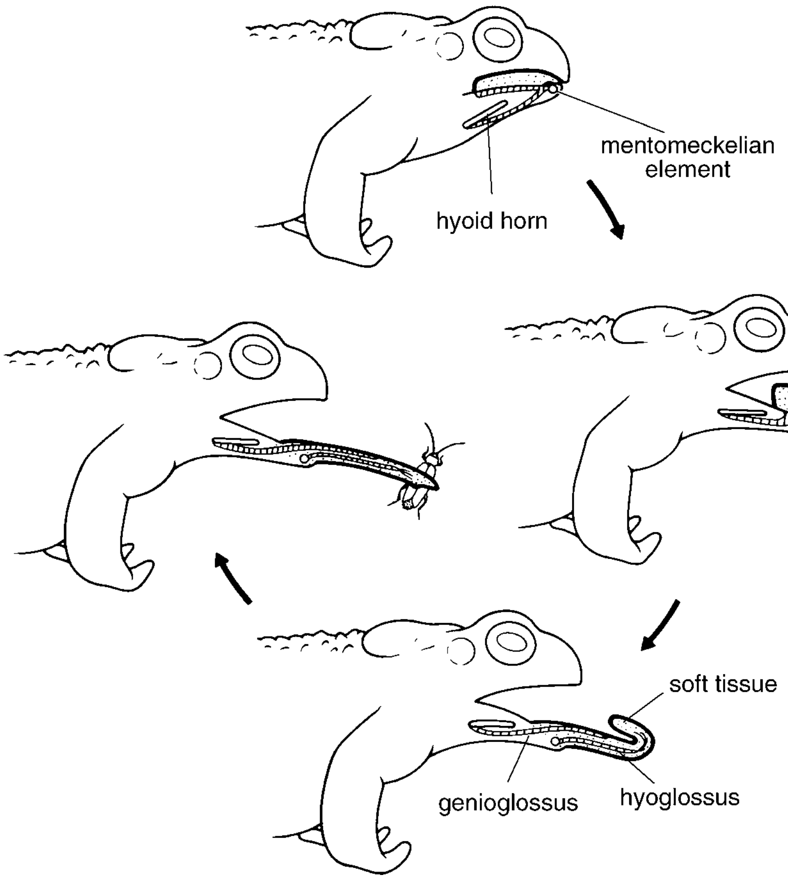


FIGURE 10.9 The anatomical mechanics of an anuran projectile tongue (*Bufo marinus*). The four schematic stages show the projection sequence from tongue at rest on the floor of the oral cavity (top) to its full extension and capture of an insect (left). Five anatomical features are labeled: soft tissue of tongue (stippled); two muscles, the genioglossus from the hyoid to the base of tongue, and the hyoglossus from the mentomeckelian (mm) element to the base of tongue; and two skeletal elements, the hyoid horn lying below the tongue, and the mm element at tip of jaw. Projection begins (right) with the mouth opening; the mm element snaps downward by the contraction of a transverse mandibular muscle (not shown) and the genioglossus contracts to stiffen the tongue. The tongue flips forward (bottom) from the momentum generated by the downward snap of the mm element and the genioglossus contraction; the two tongue muscles then relax and are stretched. The tongue is fully extended and turned upside down (left) and the dorsal surface of the tongue tip encircles the prey. The genioglossus and hyoglossus muscles contract, drawing the tongue with the adhering insect back through the mouth as it closes. Adapted from Gans and Gorniak (1982).

based on inertia alone. The food is held stationary in the mouth. Each time the mouth is slightly opened, the head is thrust forward, thereby shifting the head forward over the food (Fig. 10.12). Snakes swallow large prey in this manner by alternately advancing the left and right sides of the head over the prey using the movement of the palatoquadrate–mandibular skeletal complex. Prey are held secure by this complex on one side of the head, while the bite–grasp on the opposite side of the head is relaxed, the jaws shifting forward and then contracting to gain a grip. The alternate forward movement of the left and right sides moves the head and body over the prey.

Manipulation of the tongue and hyoid appears to be the principal swallowing mechanism in amphibians. Some salamanders use hyoid–tongue retraction to swallow prey. After capturing a prey item and with the mouth

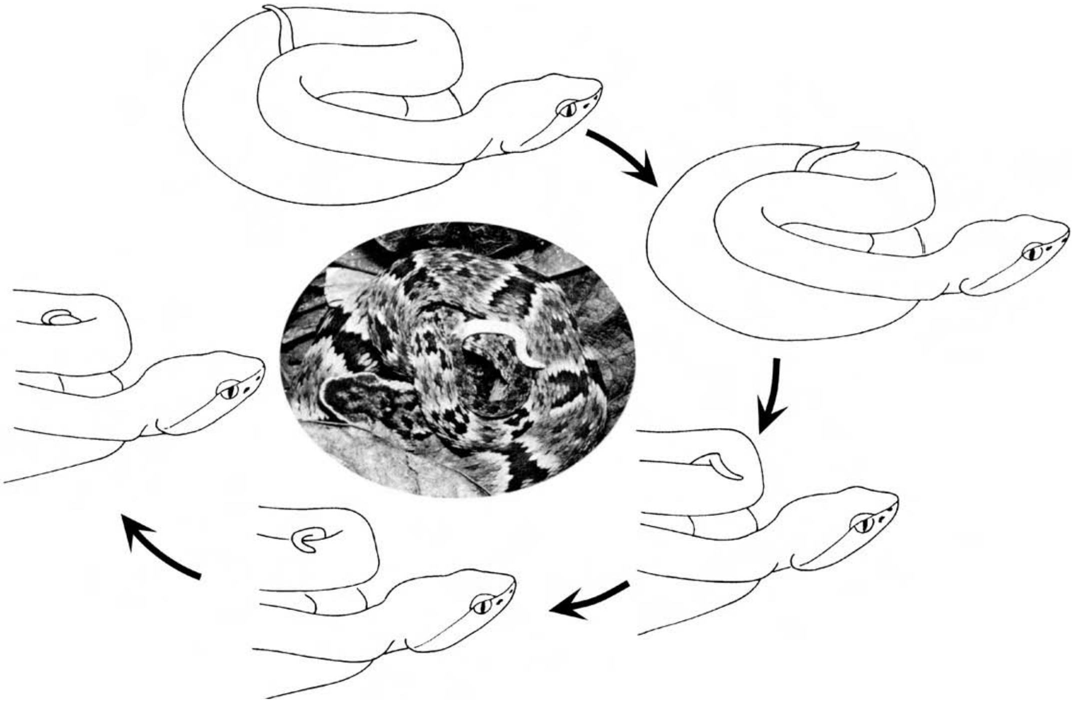


FIGURE 10.10 By waving its brightly colored tail, *Bothrops jararaca* attracts frogs and other small insectivorous animals within strike range. The insert shows the contrast between the tail color (yellow in life) and the cryptic coloration of the snake. Adapted from Sazima (1991). Insert photograph by I. Sazima.

FIGURE 10.11 Juvenile Aldabran tortoises (*Geochelone gigantea*) eating a leaf from their shade tree. Photograph by G. R. Zug.

FIGURE 10.12 The mollusk-eating snake *Dipsas indica* uses inertial feeding behavior to swallow a large slug. Photograph by I. Sazima.

closed, the tongue presses the prey tightly against the roof of the mouth and vomerine–palatine teeth. The mouth opens quickly and the tongue, still firmly holding the prey, retracts and draws the prey inward as the mouth slowly closes. This cycle is repeated until the prey moves through the buccopharyngeal cavity. Swallowing in frogs also involves tongue–hyoid movement, although the actual mechanics are known in less detail. Frogs have voluminous oral cavities and captured prey are usually completely engulfed. Apparently a similar hyoid–tongue retraction cycle without opening the mouth moves the prey inward. This movement is assisted by the compression of the palate, visible externally by the retraction of the eyes.

Constriction

Constriction is a specialized bite-and-grasp technique used by numerous snakes to hold or kill prey. A constricting snake strikes its prey, and if its bite–grip is secure, a loop of the body is thrown on and around the prey. Additional loops (coils) of the body encircle the prey with continual adjustment to reduce overlapping loops. As the prey struggles and then relaxes portions of its body, the snake tightens its grip. The tightening continues and ultimately circulatory failure causes death—increasing compression of the thorax stops the flow of blood to the heart (Hardy, 1994). When struggling ceases and the prey is dead or unconscious, the snake relaxes its coils, locates the head of the prey, and begins to swallow it. Constriction is best known in boas and pythons, but it is common in other snakes as well (Fig. 10.13). Even some highly venomous snakes constrict their prey after biting and injecting venom (Shine and Schwaner, 1985). It is easy to visualize constriction in boids where the prey typically are birds or mammals. However, the effectiveness of constriction as a means of subduing and killing prey is best exemplified by snakes that constrict fish. The filesnake (*Acrochordus*) can attach its tail to underwater roots of mangroves as an anchor, strike a large fish, and rapidly subdue it by constriction (Shine, 1991b). The rough scales on the filesnake facilitate holding the fish and the elastic body apparently serves to buffer the thrashing movements of the struggling fish. Some limbless amphibians (*Amphiuma*) may use constriction to subdue prey.

Injected Venoms

Venom delivery systems have evolved independently a number of times within the Squamata. Considerable variation in morphology, derivation, and effectiveness of

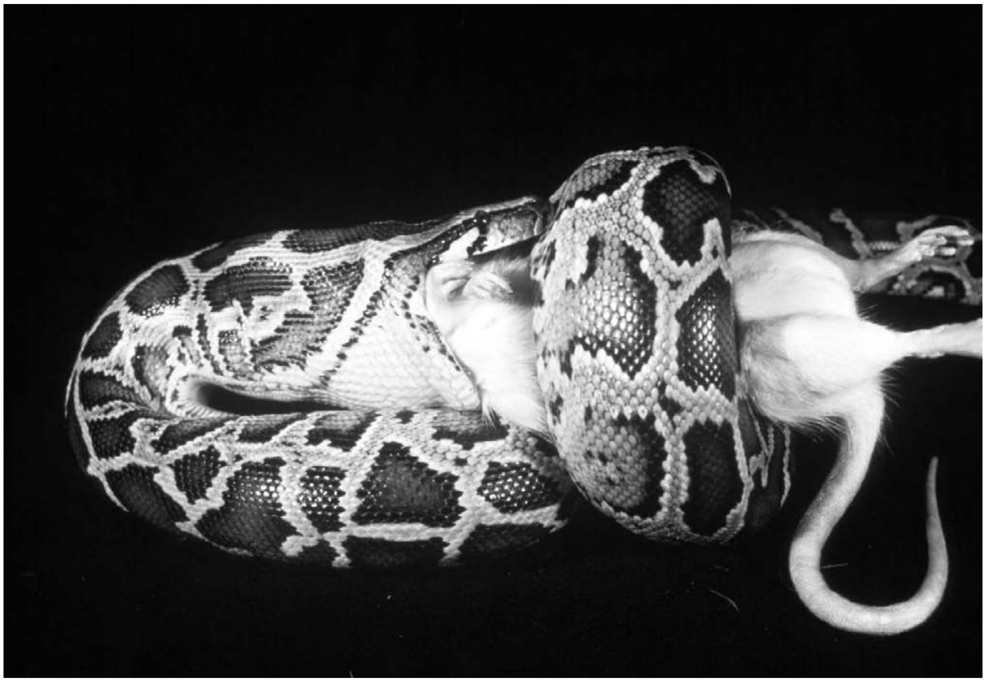


FIGURE 10.13 Following prey detection and strike and grasp, many snakes, like this Burmese python, coil around their vertebrate prey. Not only does constriction subdue the prey, but it also causes circulatory failure, which kills the prey. Photograph by S. C. Secor.

venom delivery systems exists. All members of the Helodermatidae, Elapidae, and Viperidae are venomous, as are several groups of colubrids. Venom subdues the prey either by anesthetizing or killing it. A nonstruggling prey is much safer and less energetically demanding to capture and swallow than a struggling one. Also a predator can eat larger prey if they do not resist capture and consumption. Many of the viperids add a third benefit to the injection of venom by injecting proteolytic enzymes that aid in digestion.

A venom delivery system contains four items: glands to produce the venom; muscles to force venom from the glands; ducts to transport venom from the gland to the injection system; and fangs (modified teeth with open or closed canals) to inject the venom into the prey (Fig. 10.14). The fangs of helodermatids and most venomous colubrids bear a single groove on one side of each enlarged tooth, whereas the fangs of elapids and viperids have closed canals. The venom is produced continuously in the venom glands and stored in venom-gland chambers. When elapids or viperids bite a prey animal, muscles over (adductor superficialis in the elapids) or around (compressor glandulas in viperids) the glands contract and squeeze a portion of the venom through the venom ducts and into the fang canals. The snake can regulate the venom dose depending upon the size of the prey and possibly how much venom is available (Hayes et al., 1992). Viperids and some elapids strike, bite, inject venom, and release the prey, whereas most elapids, colubrids, and *Heloderma* maintain their bite–grasp and chew the wound to ensure the deep penetration of the venom. Elapids and most rear-fanged colubrids have relatively small fangs. With few exceptions, these fangs are fixed in an erect position. The greatest deviation from fixed fangs in elapids occurs in the death adder (*Acanthophis antarcticus*) of Australia, which has morphology and foraging behavior strikingly convergent with that of

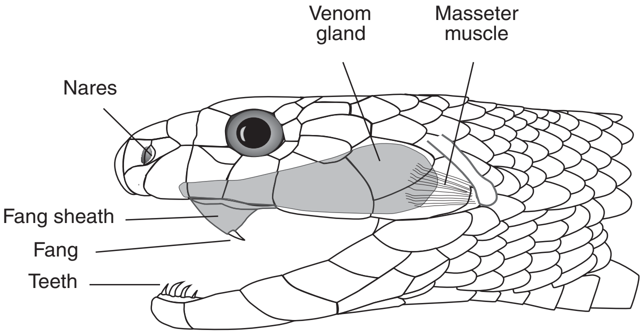


FIGURE 10.14 Venomous snakes have movable (Viperidae) or fixed (Elapidae, some Colubridae) fangs to inject venom. Venom is delivered to the fangs from the venom glands via venom ducts. Modeled after a drawing of a taipan, *Oxyuranus scutellatus,* in Shine (1991).

terrestrial viperids (Shine, 1980a). The front fangs are fixed on a highly movable quadrate bone.

The venom of each species is a composite of several compounds that work synergistically to subdue the prey (Table 10.3). Typically, the venom of a species causes either tissue destruction or neurological collapse. The tissue-destruction venoms subdue the prey because the prey goes into shock, and neurological-collapse venoms prevent nerve impulse transmission and interrupt all motor activity, including respiration. The immobile prey can then be eaten safely.

TABLE 10.3 Major Types of Reptilian Venoms and Some Examples of the Function of Each Type

Enzymes. All venoms contain several different enzymes; more than 25 enzymes occur in reptilian venoms.	
Proteolytic enzymes	Digest tissue protein and peptides causing hemorrhagic necrosis and muscle lysis; also known as endopeptidases. (Common in crotalines, less in viperines, absent in elapids)
Thrombinlike enzymes	Interfere with normal blood clotting, by acting as either an anticoagulant or a procoagulant. (Common in viperids, rare in elapids)
Hyaluronidase	Breaks down mucopolysaccharide links in connective tissue and enhances diffusion of venom. (In all venomous snakes)
Phospholipase	Modifies muscle contractability and makes structural changes in central nervous system; also interferes with the prey's motor functions. (Common in colubrids, elapids, viperids)
Acetylcholinase	Interrupts ganglionic and neuromuscular transmission and eventually affects cardiac function and respiration. (Common in elapids, absent in viperids)
Polypetides. The polypetides are toxic nonenzymatic proteins of venoms. These toxins commonly act at or near the synaptic junctions and retard, modify, or stop nerve impulse transmission.	
Crotactin	Produces paralysis and respiratory distress. (In rattlesnakes, crotalines)
Cobrotoxin	Acts directly on heart muscle to cause paralysis. (In cobras, *Naja*)
Viperatoxin	Acts on medullary center in brain, resulting in vasodilation and cardiac failure. (In *Vipera*)
Miscellanea. Various ions and compounds that are found in venoms, but as yet have no recognizable prey-type or taxonomic group association.	
Inorganic ions	Sodium, calcium, potassium, iron, zinc, and others; some enhance the activity of specific enzymes.
Glycoproteins	Anticomplementary reactions that suppress normal immunological tissue response.
Amino acids and biogenic amines	

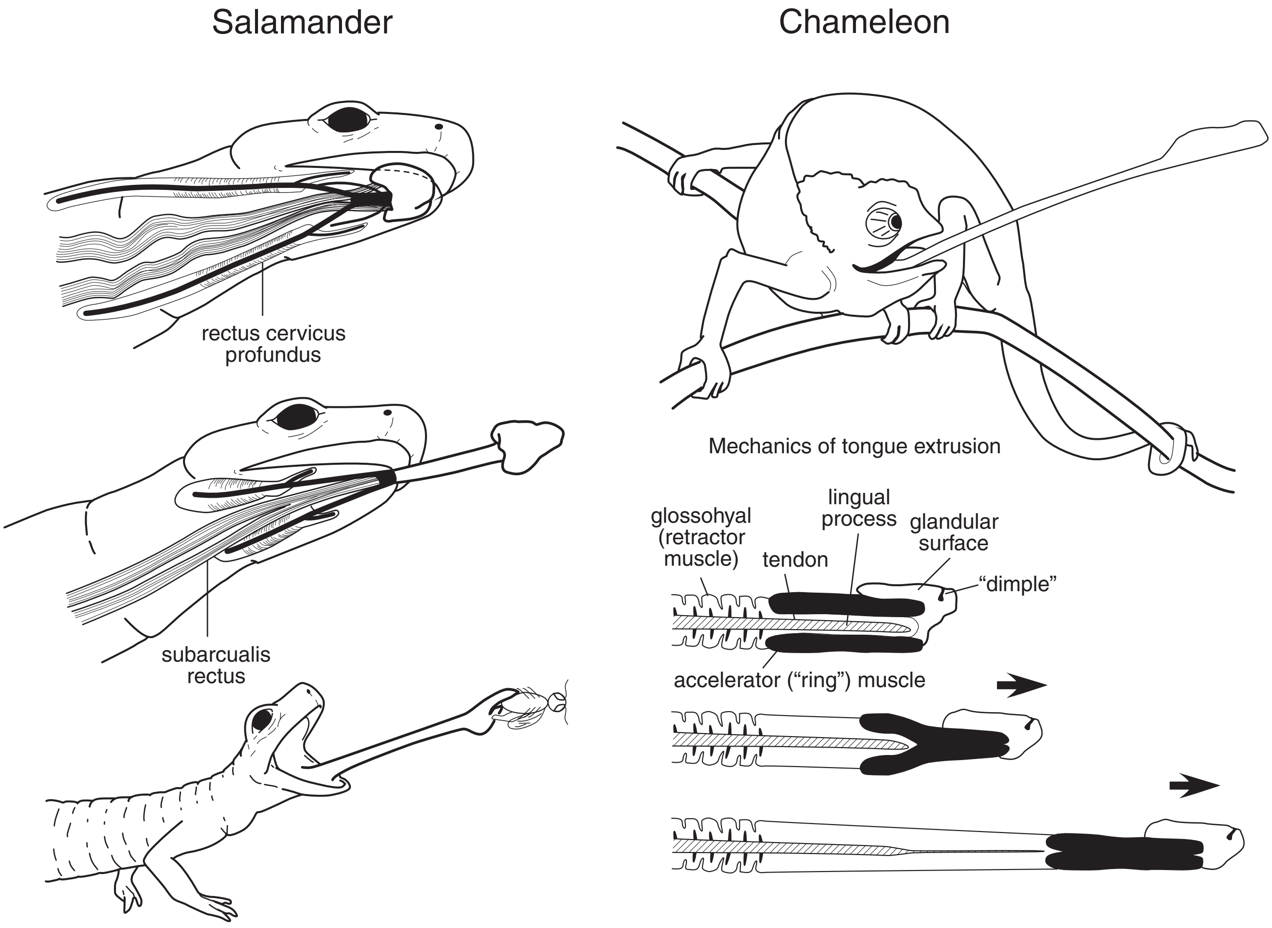
Note: Reptilian venoms are an admixture, consisting mainly of enzymatic and nonenzymatic proteins.

Projectile Tongues

Tongues are small and usually have limited or no mobility in aquatic amphibians and reptiles. Tongues became important in terrestrial animals when water was no longer present to carry food through the oral cavity into the esophagus. A protrusible tongue for sampling the environment and gathering food probably evolved early in terrestrial tetrapods, because protrusion is widespread in amphibians and reptiles. Many bite-and-grasp feeders (herbivores and carnivores) use their tongues to retrieve small items. The tongue is simply extended through the mouth and the item is touched by the tip or dorsal surface of the tongue. The item is held by sticky saliva and the tongue is retracted. The most dramatic tongue protrusions are the projectile tongues, which have evolved independently several times in amphibians and reptiles.

Most frogs capture prey by projecting the tongue (Figure 10.9), but the mechanism is different than that found in salamanders (Fig. 10.15). The frog's tongue is attached at the front of mouth, and has a direct attachment to the cartilaginous sympyhsis joining the right and left sides of the mandible. When a prey item is identified, the frog orients its body perpendicular to the prey. The mouth opens and the lower jaw drops downward. The genioglossus muscle, which lies within the tongue, contracts, stiffening the tongue. The submentalis muscle (linking left and right mandibles beneath the middle of the tongue) contracts to form a pivot point that yanks the symphyseal cartilage downward. This movement pulls the anterior end of the tongue downward and the momentum imparted to the tongue flicks the posterior end outward, in much the same fashion as a catapult (Gans and Gorniak, 1982). The weight of the tongue's posterior half stretches the tongue to twice its length, and as the upper surface of the tongue hits the prey, the tip wraps over the prey. The tongue is retracted by a quick contraction of the hyoglossus muscle in the posterior region of the mouth, with the prey stuck to the tip of the tongue.

Terrestrial salamanders orient on prey and rapidly extrude the tongue, which, in many species, has a large pad on the tip. Mucous on the tongue tip adheres to the prey item, and longitudinal muscles retract the tongue and prey. The mechanics of tongue extrusion vary among salamander taxa. A large fleshy tongue is simply flopped out on a prey item in *Ambystoma*, whereas highly


Salamander

Chameleon

FIGURE 10.15 The anatomical mechanics of a salamander and a chameleon tongue. Salamanders redrawn from Duellman and Trueb (1986); chameleon redrawn from Kardong (1998).

derived elongate tongues with fleshy tips are projected for considerably longer distance in various plethodontids (Larson and Gutherie, 1985; Lombard and Wake, 1977). Projectile tongues appear to have evolved independently several times in salamanders, including three times within the Plethodontidae. The projectile mechanisms in salamanders derive from modifications of the hyoid apparatus, a structure that usually functions to move the floor of the buccal cavity during respiration. Salamanders with projectile tongues (plethodontids and the salamandrids *Chioglossa* and *Salamandrina*) are lungless and, as a result, the hyoid apparatus is not involved in respiration. The general mechanism of tongue extension includes the projection from the mouth of the pedestal-like tongue tip by the hyoid apparatus (Lombard and Wake, 1976). The posterior, bilaterally paired hyoid arms lie in the floor of mouth like a partially opened fan with the hinge-tip pointed anteriorly. When the hyoid muscles contract, the fan closes and drives the tip outward. The movement is rapid and the momentum, as in frogs, assists in stretching the tongue as much as 40–80% of the salamander's body length. The structure of the hyoid apparatus varies considerably among salamander species. Tongue movement in *Bolitoglossa* is so rapid that a sensory feedback system is not involved. The extensor and retractor muscles fire simultaneously but the retractor muscle contains enough slack that it does not begin to retract the tongue until it is fully extended.

Chameleons have one of the most spectacular tongue projection systems known in vertebrates. They can project their tongues at high speed for as much as 200 percent of their snout–vent length and accurately hit and capture an insect. Precise integration between the ocular system and the tongue projection system is critical. The projectile tongue of chameleons shoots forward by a hyoid mechanism. Once a chameleon has oriented on an insect after detecting it visually, the head is extended toward the prey, the lower jaw opens, and the tongue slowly extends a short distance out of the mouth.

The tongue then shoots out toward the prey, the sticky tip captures the insect, and the tongue is drawn back into the mouth with the insect (Fig. 10.16). The mechanism includes a precision system of depth perception based on accommodation, a highly modified hyoid apparatus including a powerful accelerator muscle, and exceptionally contractile hyoid muscles (Wainwright et al., 1991; Wainwright and Bennett, 1992a,b).

Filter Feeding

The diets of most tadpoles consist mainly of algae and protists (e.g., Inger, 1986), and hence tadpoles are microphagous ("small eating"). Comblike tooth rows on the oral disc scrape detritus from surfaces. Tadpoles use the movement of water in through the mouth, buccal, and pharyngeal cavity, and out through the gills (branchial arches) for both respiration and food entrapment. Microphagy requires a filter or straining mechanism to capture tiny items and direct them into the gut. A system that includes branchial food traps and gill filters in the pharynx captures smaller particles (Fig. 10.17). Buccal papillae extract large particles and funnel them directly into the esophagus (Wassersug, 1972, 1980).

The buccopharyngeal cavity of tadpoles is large—more than half the volume of the head of most tadpoles. The upward and downward movement of the buccal floor in association with the opening and closing of the mouth and gill filter valves (vela) moves water through this large cavity. As the mouth opens, the floor drops and draws water into the cavity; the vela prevent a major backflow through the gill openings. The mouth then closes and the floor rises, forcing the water outward through the gill slits. The flow of water brings the food particles to the rear of the cavity and in contact with the gill filter surface. The large particles cannot pass through the filter and are picked up by the papillae, which move them into the esophagus. The smaller particles touching the surface are snared by strings of mucus. A combination of water movement and ciliary activity move the strings and trapped food rearward. The strings aggregate into larger clumps before passing into the esophagus with the larger food particles. This filtering mechanism is regulated by the volume of food entering the mouth cavity. When particle suspension density is high, the buccal pump works more slowly to prevent the gill filters and mucus traps from clogging, and, conversely, if particles are sparse, the system works more rapidly.

FIGURE 10.16 The tongue of a chameleon can be projected as much as twice the lizard's snout–vent length. A combination of visual acuity and a highly developed tongue projectile system results in prey capture. Photograph by J. P. Jones.

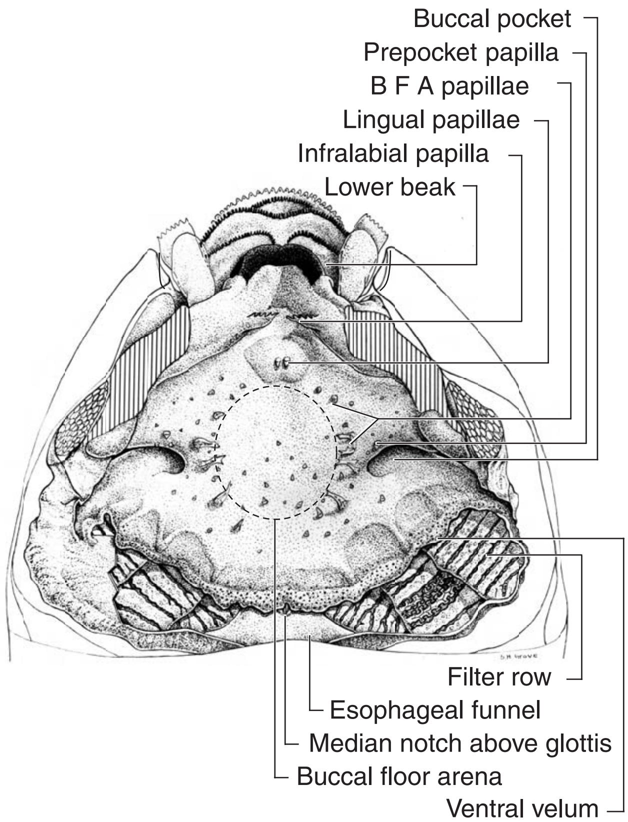


FIGURE 10.17 Floor of the mouth of the tadpole of *Pseudacris regilla*. Tadpoles have several mechanisms for filtering food particles from the water taken into their mouths. Large food particles are channeled into the esophagus by rows of papillae on the floor and roof of the mouth. Smaller particles are strained out of the water as it passes through elaborately folded filters located on the gill bars. Even smaller particles are trapped in mucous strands secreted from glands located in the mouth. Adapted from Wassersug (1976).

Suction Feeding

Aquatic salamanders, pipid frogs, and some turtles capture prey by opening their mouths simultaneously with the enlargement of their buccal (mouth) cavity. The prey is literally vacuumed into the mouth by the rush of water flowing into the reduced-pressure cavity created by the enlarged buccal cavity. The matamata turtle, *Chelus fimbriata*, offers the most vivid demonstration of suction feeding. Either from ambush or by slowly stalking or even herding prey (Holmstrom, 1978), the matamata moves its head so that it is aligned with the prey, usually a fish or a tadpole. The head shoots forward while the hyoid musculature simultaneously contracts, dropping the floor of the buccal cavity. With the valvular nostrils closed, a tremendous suction vacuum results; the buccal cavity may increase by three to four times its normal size. Just prior to reaching the prey, the mouth opens and prey and water surge into the buccal cavity. The mouth is shut, but not tightly; the buccal floor rises, expelling the excess water without losing the prey (Mahmoud and Klicka, 1979). The success of this prey capture technique depends upon accurate alignment of the head to the prey, good timing, and rapid enlargement of the buccal cavity. Matamatas respond to increased prey density by moving less in search of prey (Formanowicz et al., 1989).

The hellbender, *Cryptobranchus alleganiensis*, can capture prey alongside its head in addition to prey situated in front of it. This primitive salamander is capable of asymmetrical movements of its lower jaw and hyoid apparatus, which allow it to open its mouth on only one side (Cundall et al., 1987). The key feature is the ligamentous attachment of the left and right dentaries at the front of the mouth. The flexible attachment permits one side of the jaw to remain in place while the opposite side swings downward, accompanied by a unilateral depression of the hyoid apparatus; this series of movements results in asymmetrical suction.

Prey Types and Sizes

The kinds of prey eaten by amphibians and reptiles have already been introduced in a very general way. A multitude of factors determine the kinds of prey a particular species will eat. The spectrum of prey available in a particular habitat is certainly a major limiting factor. For example, seaturtles would not be expected to eat insects simply because there are no truly pelagic insects. Species that ingest a random sample of the prey available in a particular habitat are considered generalists, whereas species that select specific portions of the prey-availability spectrum are specialists. Measuring prey availability independent of the predators, however, has proven difficult. Different sampling regimes produce different results, and often the sample does not contain all prey captured by the amphibians and reptiles living in the sampled habitat.

A statement by Winemiller and Pianka (1990) exemplifies the problem:

> *Considerable effort has been expended in grappling with the difficult problem of resource availability. Resource availabilities are not easily measured in the field. For example, when insects are sampled with sweep nets, D-vac, Tanglefoot sticky traps, and/or pitfall traps, results differ dramatically. In a study of the herpetofaunas of several sites in the high Andes, Pefaur and Duellman (1980) fenced study plots and conducted exhaustive collections of all herps and insects encountered within the plots with the intention of using the insects as intact whole specimens for comparison standards with the stomach contents of the herps. Yet fewer than*

10% of the insect species actually eaten by the herps were collected by diligent humans. . . .

Winemiller and Pianka recommended using all prey from the pooled set of consumers as a measure of resource availability. Even though the sample is not independent from the consumers (e.g., Toft, 1980), it contains only the prey eaten by the consumers and thus may better represent the actual prey-availability spectrum.

Most species of amphibians and reptiles eat a variety of prey types and sizes. In leaf litter habitats of the Brazilian Amazon, the frog *Leptodactylus mystaceus* relies heavily on beetles, termites, and grasshoppers. In the same microhabitat, the lizard *Anolis nitens* feeds primarily on insect larvae, roaches, and spiders (Fig. 10.18). In both species, many other prey items are eaten, but to a lesser extent. Prey data based on volumetric data differ somewhat from prey data based on numeric data, largely because taxonomic groups of invertebrates vary greatly in size. Ants, for example, rank second numerically for *L. mystaceus* and third numerically for *A. nitens,* yet volumetrically, they are relatively unimportant. Because the diets of these two species are strikingly different even though they live in the same microhabitat (leaf litter), it is clear that frogs and lizards do not randomly sample available prey.

Seaturtles, seasnakes, and the marine iguana provide a different perspective on feeding in reptiles because all of their foraging occurs in seawater. Green seaturtles feed on a wide variety of red, green, and brown algae, sea grasses, jellyfish, mollusk eggs, and sponges (Bjorndal, 1996). At some localities, such as near the coast of Peru, invertebrates are much more common in green seaturtle diets, and some fish are taken. Loggerhead seaturtles feed mostly on marine invertebrates, including horseshoe crabs. Hawksbills appear to feed largely on sponges but also take other invertebrates. The diets of other species include combinations of algae and invertebrates. The leatherback seaturtle, however, feeds mostly on gelatinous organisms, usually scyphozoans, pelagic coelenterates, and their parasites and commensals.

Seasnakes feed on a diversity of fishes and marine invertebrates, but they mostly eat fish that are sedentary, bottom-dwelling species with fine scales or no scales at all (Fig. 10.19). Different feeding modes translate into different prey types (Glodek and Voris, 1982; Voris, 1983). Marine iguanas feed exclusively on algae that they scrape off of submerged rock surfaces. No foraging occurs in the terrestrial environment, but high temperatures associated with the rocks make it possible for these lizards to bask and raise their body temperatures, which aids in processing their plant diet.

Taken together, seaturtles, seasnakes, and the marine iguana sample a broad taxonomic diversity of food items available in the oceans. The overall lack of amphibians in seawater does not seem surprising since water and electrolyte balance present major challenges to animals with permeable skin in saltwater. Nevertheless, it seems surprising that such a vast and resource-rich habitat has not been exploited by more reptiles, given their ability to regulate water loss in hyperosmotic environments (Chapter 6).

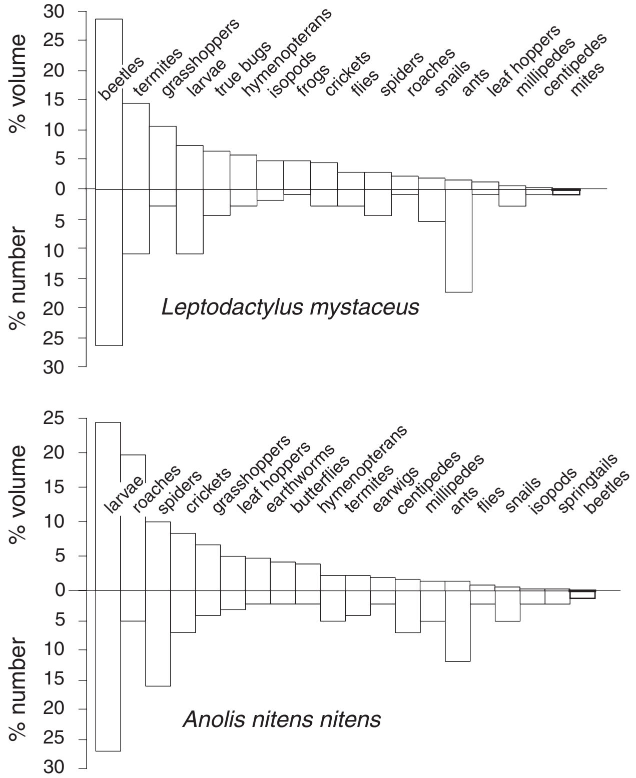


FIGURE 10.18 Representative diets of a frog, *Leptodactylus mystaceus,* and a lizard, *Anolis nitens,* that occur in the same microhabitat (leaf litter) in Amazonian rain forest. Both species feed on a variety of arthropods and other invertebrates but the diets are considerably different. In both species, a few prey categories dominate the diet. Volumetric data, which indicate energy gain, are not always reflected in numerical data, which indicate the cost of acquiring prey. Unpublished data from Vitt and Caldwell.

Body size of amphibians and reptiles also plays an important role in prey selection. Small species cannot eat the same size prey that large species can. A summary of data for eight frog and seven lizard species from the northern Amazon rain forest, all living in leaf litter, shows that body size and prey size are related (Fig. 10.20). Careful examination of the data shows also that the relationship between prey size and frog or lizard body size differs among species (Caldwell and Vitt, 1999). Frogs that are ant specialists tend to eat relatively smaller prey than species that are not ant specialists and the same is true for lizards (Toft, 1980; Caldwell, 1996a;

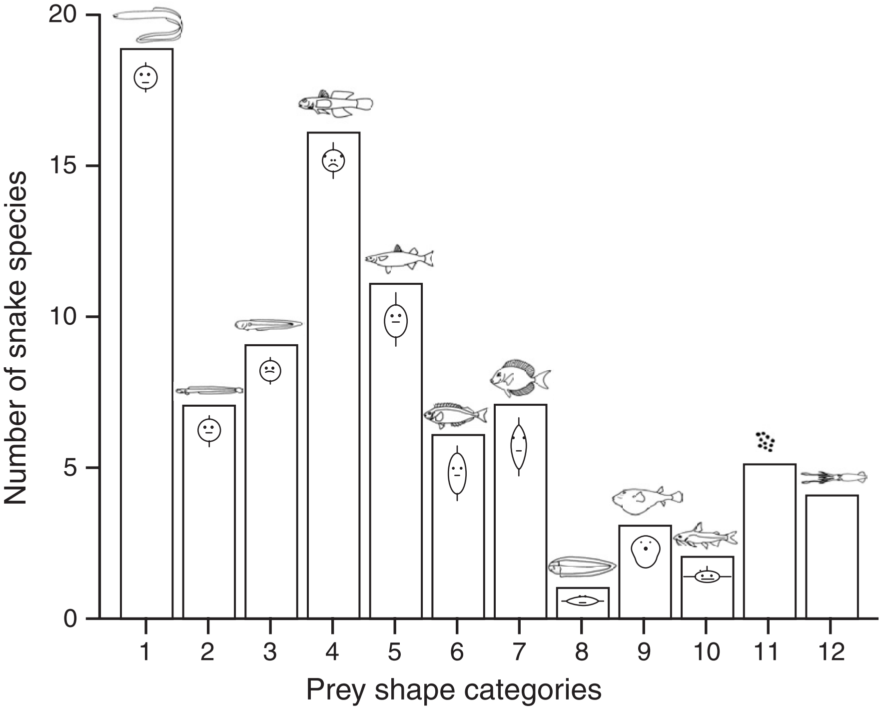


FIGURE 10.19 An examination of the shapes of prey fed on by species of sea snakes reveals that the majority of species feed primarily on fish that are elongate and nearly circular in cross section. The last two columns represent fish eggs and squids. Adapted from Voris and Voris (1983).

Vitt and Zani, 1996a). Not only do ant specialists eat relatively smaller prey than similar-sized nonant specialists, they eat more prey items.

Small species of reptiles and amphibians often feed on some of the smallest arthropods available. Mites and tiny ants are among the smallest arthropods available in tropical rain forest leaf litter. Although many frog species eat some mites, most eat very few (Simon and Toft, 1991). However, several small species of frogs, such as the dendrobatid *Minyobates*, specialize on mites.

All blind snakes (Leptotyphlopidae, Typhlopidae, and Anomalepididae) eat small prey, usually social insects in their nests. Even though most of these snakes are small themselves, they are large compared with their prey. Consequently skull kinesis is not necessary to successfully prey on social insect castes. A majority of snakes eat very large prey and are capable of doing so because of their feeding apparatus. The upper and lower jaws are highly kinetic and the right and left portions of each move independently. Moreover, unlike other reptiles and amphibians, the lower jaws are not fused in snakes, which allows even more freedom of movement. Taken together, these characteristics allow a large expansion of the feeding apparatus, leading to the accommodation of large prey. Based on variation in relative size and shape of prey, four distinct feeding types are recognized in snakes (Table 10.4).

Ontogeny of Diets

Adult amphibians and reptiles do not necessarily eat the same prey as larvae or juveniles. The most obvious example of a dietary shift is in amphibians with aquatic larvae and terrestrial adults. Most anurans shift from detritivores as larvae to insectivores as adults. Among frogs with predaceous tadpoles (e.g., *Dendrobates castaneoticus*), the dietary shift is from aquatic insect larvae as tadpoles to ants as adults (Caldwell, 1993, 1996a). Among amphibians and reptiles in which juveniles have the same morphology as adults, a large component of dietary shifts is associated with size. Ontogenetic dietary shifts are probably common in amphibians and reptiles but are not well studied. Four species of water snakes in Florida shift their diets with age (Mushinsky et al., 1982). *Nerodia erythrogaster* and *Nerodia fasciata* feed primarily on fish as juveniles but switch to mostly frogs when they reach about 50 cm in snout–vent length (Fig. 10.21). Even though *Nerodia rhombifera* and *Nerodia cyclopion* feed on fish throughout their lives, the kinds of fish they eat change with snake age and size. Several factors contribute to ontogenetic diet shifts in these snakes, including the effect of snake body size on the size of prey that can be taken, differences in microhabitat use between juveniles and adults; and sexual differences (size-based) in prey types taken.

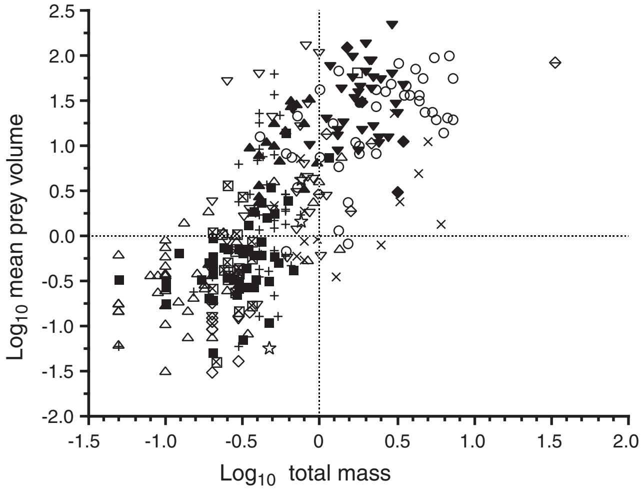


FIGURE 10.20 Both the mean size of prey eaten and the maximum prey size (not shown here) are correlated with body size of frogs and lizards. Even though a strong correlation exists with all species included, species differences in the relationship also exist. In general, species that feed on the smallest prey, mites and ants, tend to eat smaller prey and more of them than species eating other prey types. Frog species are *Elachistocleis ovalis*, ×; *Adenomera andreae*, open triangle; *Leptodactylus bolivianus*, parallelogram with cross; *Le. fuscus*, solid parallelogram; *Le. mystaceus*, solid upside down triangle; *Lithodytes lineatus*, open star; *Physalaemus ephippifer*, solid square; and *Pseudopaludicola boliviana*, open square with cross. Lizard species are *Anolis nitens*, open circle; *Coleodactylus amazonicus*, open parallelogram; *C. septentrionalis*, cross; *Arthrosaura reticulata*, open square; *Gymnophthalmus underwoodi*, solid triangle; *Leposoma percarinatum*, upside down open triangle; and *Tretioscincus oriximinensis*, solid circle. Adapted from Caldwell and Vitt (1999).

Potential ontogenetic shifts in diet can be offset by morphological variation among age groups. Juveniles and adults of the salamander *Plethodon cinereus* feed on the same prey types; small mites are among the most common prey (Maglia, 1996). Prey size does not vary with head size in adults but the size of the largest prey items does vary with head size in juveniles. Consequently, size does constrain the diet of juveniles in that they cannot eat the larger items that adults eat. Nevertheless, juveniles have relatively broader heads than adults, which allows them to eat all but the largest prey taken by adults (Fig. 10.22).

TABLE 10.4 Among Snakes, Four Distinct Feeding Types Have Been Described

Type I	Extremely small prey that require no immobilization
Type II	Heavy, elongate prey that because of their shape do not require large gapes, but because of their size require constriction or envenomation for subduction
Type III	Heavy bulky prey that require specializations for both subduction and swallowing
Type IV	Prey that are lightweight relative to diameter (e.g., fishes, birds) that require gape specializations but not subduction specializations (venom or constriction)

Source: Adapted from Greene (1997).

Note: The categories are based on two measures of prey size: relative mass and relative girth.

Evolution of Diets

Recognition that diets of amphibians and reptiles might evolve just as morphological or physiological traits is just gaining acceptance. Surprisingly, it has long been known that within some clades, a group of species share a diet preference unlike that of other closely related species. For example, horned lizards (*Phrynosoma*) as a group eat primarily ants (Pianka and Parker, 1975; but see Greene, 1982); all of the Iguaninae are herbivorous, at least as adults; frogs in the genus *Dendrobates* eat ants primarily (Toft, 1995; Caldwell, 1996a); and snakes in the closely related families Typhlopidae, Leptotyphlopidae, and Anomalepididae eat eggs, larvae, and pupae of ants and termites (Shine, 1991b; Greene, 1997). Indeed, insectivory in these snakes (the Scolecophidia) is one of the pieces of evidence suggesting that they are the most primitive snake clade. Species in the Sonorini clade of colubrine snakes feed on arthropods (Savitzky, 1983), and the xenodontine colubrids feed on frogs (Cadle and Greene, 1993). Many other examples suggest that diets within particular clades reflect the evolutionary trajectories of the clade, a topic we examine in Chapter 11.

Ant specialization has evolved independently in a number of families of frogs and lizards. Within the Phrynosomatinae, species in the genus *Phrynosoma* feed primarily on ants. These tanklike lizards are cryptic in morphology and coloration, move very little, and eat literally hundreds of ants each day. Most other genera of phrynosomatine lizards eat a diversity of insects, including some ants. From a strictly energetic perspective, eating ants seems to be inefficient because ants are generally small and contain a large amount of exoskeleton compared to larger insects such as caterpillars. If a lizard had to move to find each ant, the energy gain would be less than the energy required to capture the ant. Ants also often contain noxious chemicals. Consequently there are energetic costs to eating ants as well as potential metabolic processing costs to handle ingested chemicals. Several benefits of ant-eating offset the potential costs. First, ants often occur in clusters, and as a consequence, the energy involved to find a thousand ants may be the same or less than the energy to find a single large grasshopper. More importantly, the same chemicals that ants use for defense may be metabolized by *Phrynosoma* and contribute to the bad taste of their

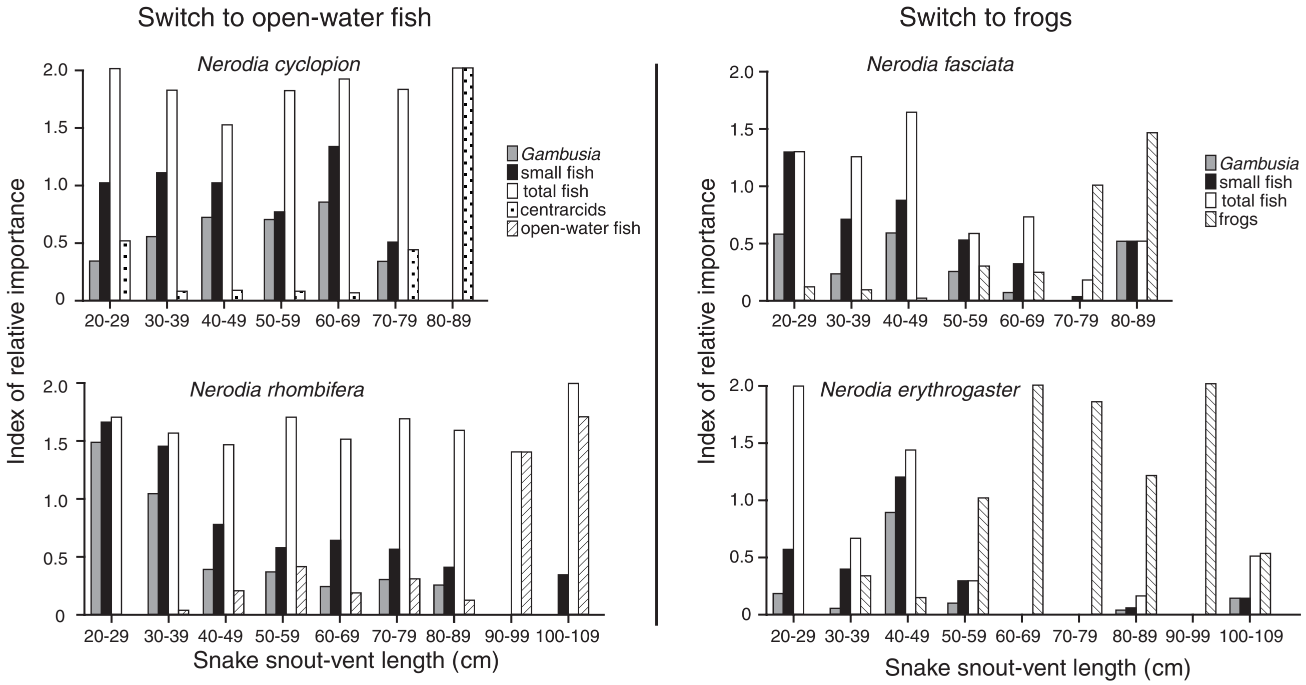


FIGURE 10.21 The diets of four species of water snakes change with age and size. Adapted from Mushinsky et al. (1982).

blood that appears to repel canid predators (see Chapter 11). Likewise, in the frog genus *Dendrobates*, ants compose most of the prey eaten. Other genera of dendrobatid frogs feed on relatively fewer ants (Caldwell, 1996a; Toft, 1980, 1995). However, in the family Dendrobatidae, not only do some species eat large proportions of ants, ant specialization appears to be related to a behavioral defense complex involving toxic or bad-tasting skin secretions and aposematic coloration (Fig. 10.23). Among other things, bright coloration of *Dendrobates* warns predators that the frogs have bad tasting or toxic skin, likely resulting from the ingestion of ant chemicals (see Chapter 11). In both frogs and lizards that eat ants, the benefits in defense accruing from mobilizing chemicals from their ant prey may offset the potential risks associated with eating many small prey. Likewise, even though many frogs eat some small ants, larger insects compose most of their diets.

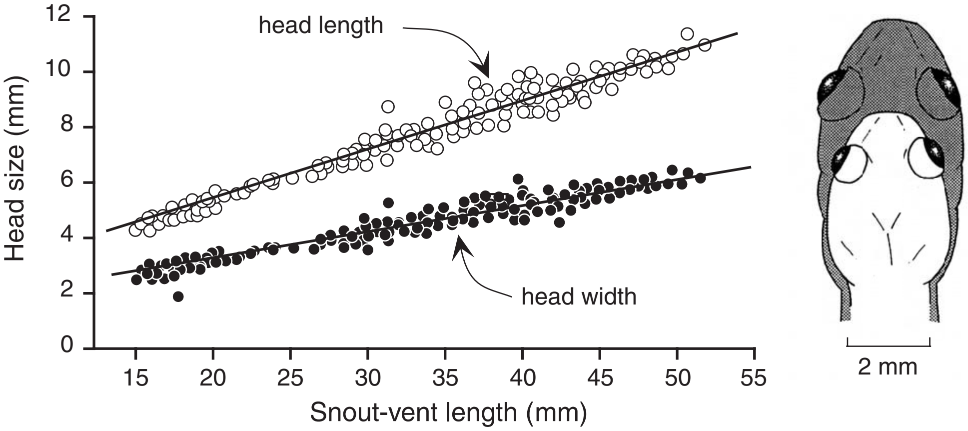


FIGURE 10.22 Although both head width and length increase with body size (snout–vent length) in *Plethodon cinereus*, head width is proportionately greater in juveniles, which allows them to feed on relatively large prey. Adapted from Maglia (1996).

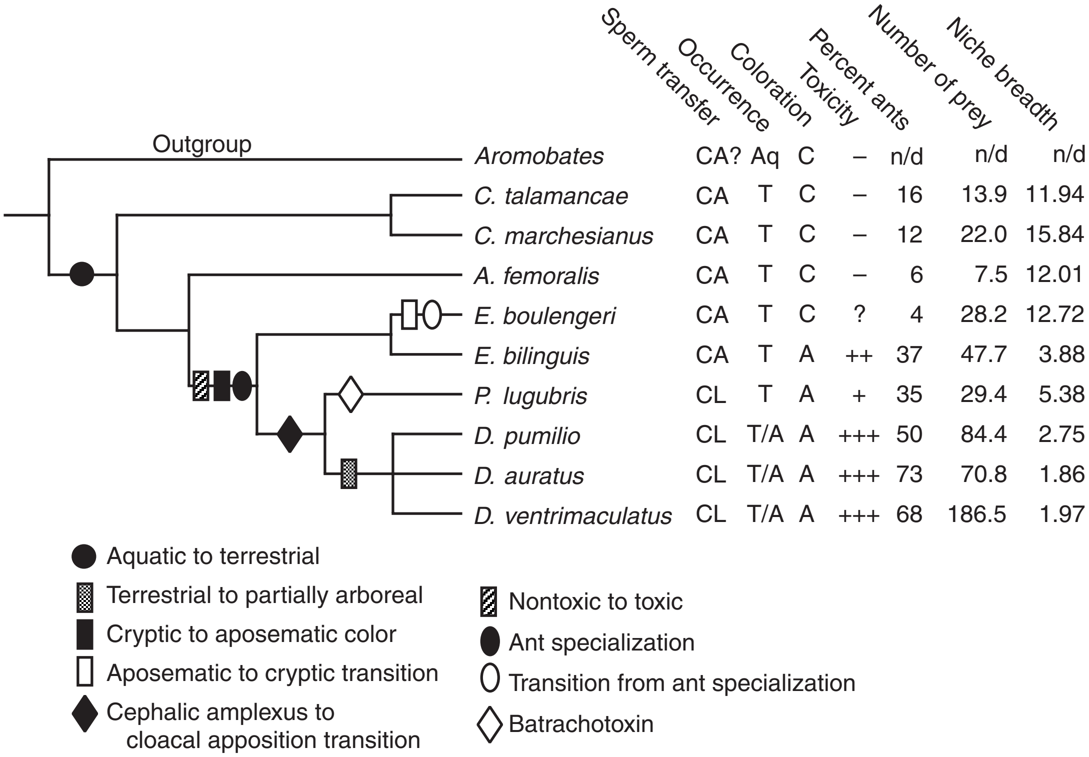


FIGURE 10.23 In dendrobatid frogs, the evolution of specialization on eating ants is linked with the evolution of skin toxins and aposematic coloration. Frogs that specialize on ants produce toxic skin compounds that are used in predator defense. Frog genera are *Aromobates, Colostethus, Allobates, Epipedobates, Phyllobates,* and *Dendrobates.* Adapted from Caldwell (1996a).

Herbivory Among amphibians, herbivory is almost totally limited to anuran tadpoles. Ingestion of plant materials has been reported in a few frogs (e.g., Das, 1996). This limitation is due to the difficulties of digesting fiber (see below). Tadpoles avoid the herbivory conundrum by consuming mainly the algal and bacterial scum (aufwachs) in the water. Herbivory in tadpoles appears widespread but is poorly verified owing to few studies on tadpoles that examine which cells in the gut contents are digested and which are voided whole. Tadpoles gather their food from all levels of the water column—grazing on bottom sediments, filtering midwater phytoplankton, and skimming the surface scum. Most species specialize on a particular portion of water column and use a certain style of harvesting.

Obligate herbivory is absent in adult amphibians and rare in adults of reptiles even though many typically insectivorous reptiles occasionally feed on at least some plant material (Table 10.5). For example, *Tropidurus* lizards on two isolated rock outcrops in the western Amazon rain forest of Brazil eat as much as 17.6 and 14.0% plant materials (flowers). A population on the Rio Xingu in the eastern Amazon eats 26.5% plant materials (mostly fruits; Vitt, 1993). Insects, spiders, and other invertebrates make up the remainder of the diet.

Herbivory poses a digestive problem for vertebrates. Vascular plants contain cellulose in the support structure of their cells. No vertebrates produce cellulase to breakdown cellulose. Thus, vertebrate herbivores must depend upon the presence of a gut microflora of cellulolytic bacteria to digest plant food. Without such a microflora, it is doubtful that an amphibian or reptile could eat and process enough plant matter to survive on a strictly herbivorous diet. To maintain an efficient gut microflora, a constant and elevated body temperature appears necessary. Other requirements are a constant food supply, slow passage of food items to permit adequate time for bacterial degradation, anaerobic gut environment, regulation of gut pH, and removal of fermentation waste by-products (Troyer, 1984a). Lowland tropical reptiles feed year around and maintain fairly high and constant body temperatures. Once a cellulolytic microflora is obtained, it is improbable that the microflora would need to be renewed. Such microflora stability is less certain for temperate-zone reptiles owing to the low temperatures of the body core and possible

TABLE 10.5 Examples of Reptilian Herbivores, Whose Diets Are Predominantly Plant Matter as Adults

Taxon	Food items
Turtles	
Batagur baska	Foliage, fruit, animal
Chelonia mydas	Sea grasses, algae
Melanochelys trijuga	Foliage, animal
Pseudemys nelsoni	Foliage, animal
Most Testudinidae	Foliage, fruit, flowers
Geochelone carbonaria	Fruit, flowers, foliage, animal
Geochelone gigantea	Foliage
Gopherus polyphemus	Foliage, fruit
Lizards	
Angolosaurus skoogi	Foliage, animal
Meroles anchietae	Seeds, animal
Corucia zebrata	Foliage, fruit, flowers
Dicrodon guttulatum	Fruits
Hoplodactylus pacificus	Nectar, fruit, animal
Lepidophyma smithii	Fruit, animal
All Iguaninae	Foliage, fruit, flowers
Cyclura carinata	Foliage, fruit, flowers, animal
Dipsosaurus dorsalis	Flowers, foliage, animal
Iguana iguana	Foliage, fruit, flowers
Sauromalus hispidus	Foliage, flowers, fruit

Sources: Turtles are Bb (Moll, 1980), Cm (Bjorndal, 1980), Mt (Wirot, 1979), Pn and mT (Ernst and Barbour, 1989a), Gc (Moskovits and M. Bjorndal, 1990), Gg (Hamilton and Coe, 1982), and Gp (MacDonald and Mushinsky, 1988). Lizards are As (Steyne, 1963), Aa (Robinson and Cunningham, 1978), Cz (Parker *in* Greer, 1976), Dg (Holmberg, 1957), Hp (Whitaker, 1968), Ls (Mautz and Lopez-Forment, 1978), aI (Iverson, 1982), Cc (Auffenberg, 1982), Dd (Mautz and Nagy, 1987), Ii (Rand et al., 1990), and Sh (Sylber, 1988).

Note: Some possess a cellulolytic microflora in the digestive tract and/or colic modifications of the hindgut. The list does not include all well-documented cases of herbivory. Plant matter is arranged in order of decreasing volume in the taxon's diet.

absence of a food bolus during dormancy. Low temperature and/or the purging of the digestive tract prior to hibernation or estivation might well eliminate a specialized microflora. Only a single temperate species, the gopher tortoise (*Gopherus polyphemus*), has been closely examined, and it efficiently digests a high fiber diet and effectively absorbs the nutrients generated by the bacterial fermentation in the hindgut. It either retains a microflora bolus or restores its microflora each spring.

The how and when of gut microflora acquisitions remains unknown for all but *Iguana iguana*. For *Iguana iguana*, a complex behavioral mechanism has evolved to ensure the acquisition of plant-digesting microbes (Troyer, 1984b). The hatchlings eat soil before emerging from the nest cavity and continue to do so after emergence as they begin to feed regularly on plants. After a few days, the young iguanas move from the low shrubbery around the nesting area upward into the canopy and join the older juveniles and/or adults; here they consume the feces of their seniors, and this inoculation ensures the presence of the correct microflora in their guts. Inoculation of gut microflora in hatchlings of other species resulting from ingestion of adult feces likely occurs in other reptilian herbivores, but direct observations have not been made. *Gopherus polyphemus* defecates within its burrows and presumably eats some of its feces prior to emerging in the spring (Bjorndal, 1987). But where do the juvenile gopher tortoises and, for that matter, the young of all other reptilian herbivores obtain their fiber-digesting microfauna? In mammalian herbivores, gut microflora acquisition poses no problem, because the young and the parents are closely associated from birth through weaning. The mammalian mother regularly licks the young and the young feeds from the mother's mammary glands, so young mammals acquire the microflora early from the ingestion of the mother's saliva or fecal material. This close association of mother and offspring does not exist for any reptilian herbivore. In herbivorous Aldabran tortoises, the absence of a gut microflora led to a low digestive efficiency (30%), in contrast to digestive efficiencies of about 65% for the red-footed tortoises and 85% for the green iguana, both of which have gut microfloras (Bjorndal, 1989; Hamilton and Coe, 1982).

ADDITIONAL READING

Cooper, W. E., Jr. (1995). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* **50:** 971–985.

Greene, H. W. (1997). "Snakes: The Evolution of Mystery in Nature." University of California Press, Berkeley.

Huey, R. B., and Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology* **62:** 991–999.

MacArthur, R. H., and Pianka, E. R. (1966). On optimal use of a patchy environment. *Am. Nat.* **100:** 603–609.

Perry, G., and Pianka, E. R. (1997). Animal foraging: Past, present, and future. *TREE* **12:** 360–364.

Schoener, T. W. (1974). Theory of feeding strategies. *Ann. Rev. Syst. Ecol.* **2:** 369–404.

Schwenk, K. (1995). Of tongues and noses: Chemoreception in lizards and snakes. *TREE* **10:** 7–12.

REFERENCES

Foraging Ecology and Diets: Foraging Modes: Cooper, 1994a,b, 1995; Gerritsen and Strickler, 1977; Gray, 1987; Huey and Pianka, 1981a; MacArthur and Pianka, 1966; Perry, 1999; Perry and Pianka, 1997; Pianka, 1966; Schoener, 1974b; Schwenk, 1993, 1995.

Prey Detection: Badenhorst, 1978; David and Jaeger, 1981; Dole et al., 1981; Luthardt and Roth, 1979.

Visual Prey Detection: Pianka and Parker, 1975; Roth, 1986; Toft, 1980.

Chemosensory Prey Detection: Cooper, 1995; Cooper and Alberts, 1990; Coulson and Hernandez, 1983; Rossi, 1983; Roth, 1987; Schwenk, 1986, 1994a, 1995; Teather, 1991.

Auditory Prey Detection: Hetherington, 1985; Jaeger, 1976; Sakaluk and Belwood, 1984.

Thermal Prey Detection: Cock Buning, 1985; Greene, 1997; Shine, 1991b.

Tactile Prey Detection: Hartline, 1967.

Prey Capture and Ingestion: Auffenberg, 1981; Greene, 1997; Perez-Higareda et al., 1989.

Biting and Grasping: Vitt and Cooper, 1988.

Constriction: Hardy, 1994; Shine, 1991b; Shine and Schwaner, 1985.

Injected Venoms: Hayes et al., 1992; Shine, 1980a, 1991b.

Projectile Tongues: Gans and Gorniak, 1982; Larson and Gutherie, 1985; Lombard and Wake, 1976, 1977; Wainwright and Bennett, 1992a,b; Wainwright et al., 1991.

Filter Feeding: Inger, 1986; Wassersug, 1972, 1980.

Suction Feeding: Cundall et al., 1987; Formanowicz et al., 1989; Holmstrom, 1978; Mahmoud and Klicka, 1979.

Prey Types and Sizes: Bjorndal, 199; Caldwell, 1996a; Caldwell and Vitt, 1999; Glodek and Voris, 1982; Pefaur and Duellman, 1980; Simon and Toft, 1991; Toft, 1980; Vitt and Zani, 1996a; Voris, 1983; Winemiller and Pianka, 1990.

Ontogeny of Diets: Caldwell, 1993, 1996a; Maglia, 1996; Mushinsky et al., 1982.

Evolution of Diets: Cadle and Greene, 1993; Caldwell, 1996a; Greene, 1982, 1997; Pianka and Parker, 1975; Savitzky, 1983; Shine, 1991b; Toft, 1980, 1995.

Herbivory: Bjorndal, 1987, 1989; Das, 1996; Hamilton and Coe, 1982; Troyer, 1984a,b; Vitt, 1993.

Chapter

11

Defense and Escape

A large majority of amphibians and reptiles do not survive to reach sexual maturity, and once adults, many do not survive long enough to produce offspring. Predation is the greatest cause of mortality in natural populations and can occur in any life history stage (Fig. 11.1). Eggs of amphibians are eaten by insects, leeches, fishes, other amphibians, and many reptiles. Fungus and bacteria also cause significant mortality in amphibian eggs (Stebbins and Cohen, 1995). Eggs of reptiles are eaten by a variety of mammals, including foxes and raccoons. Many reptiles eat the eggs of amphibians and reptiles, and even ants prey on reptile eggs. Juvenile amphibians and reptiles are prey for numerous arthropods, including insects, spiders, centipedes, and amblypygids, and nearly all vertebrate groups from fishes to mammals and birds prey on juvenile amphibians and reptiles. Although a few invertebrates and numerous vertebrates prey on adult amphibians and reptiles, the increased body size of adults relative to juveniles and relative to the body size of predators reduces the diversity of predators that can effectively capture them. Body size of some species, such as the saltwater crocodile, Komodo monitor, anaconda, and Galapagos tortoise, renders adults virtually immune to predation by all animal species except humans.

During the evolutionary history of amphibians and reptiles, any morphological, physiological, behavioral, or ecological trait that reduced predation increased in frequency as individuals not exhibiting those traits were removed from the breeding population. The selective pressures driving the evolution of predator-escape mechanisms were and continue to be strong because as prey respond evolutionarily to predictable predation events, predators respond by evolving new or more effective ways to find and capture prey. The diversity of predator-escape mechanisms in amphibians and reptiles continues to surprise herpetologists; new defenses are being continually discovered. Many mechanisms are obvious, such as alert responses followed by rapid flight or the loss of tails by salamanders and lizards that allow the "prey" a second chance at escape. Many are much more subtle and include rapid development of amphibian eggs and tadpoles to offset predation by aquatic insect larvae or the evolution of large clutches of small eggs to offset heavy and predictable predation on early life history stages. Some involve the use of chemicals to deter or even poison predators. In the ant-eating frog genus *Dendrobates,* chemicals obtained from the diet can be mobilized and used in defense. In viperid and elapid snakes, injected venoms used to acquire prey serve to fend off or even kill potentially lethal predators. Taken together, predator-escape mechanisms provide some of the most fascinating questions for biological research and lie at the center of Charles Darwin's "struggle for existence."

Escape from predation requires interference with a predator's ability to detect or identify an individual as prey or the successful escape of a potential prey once

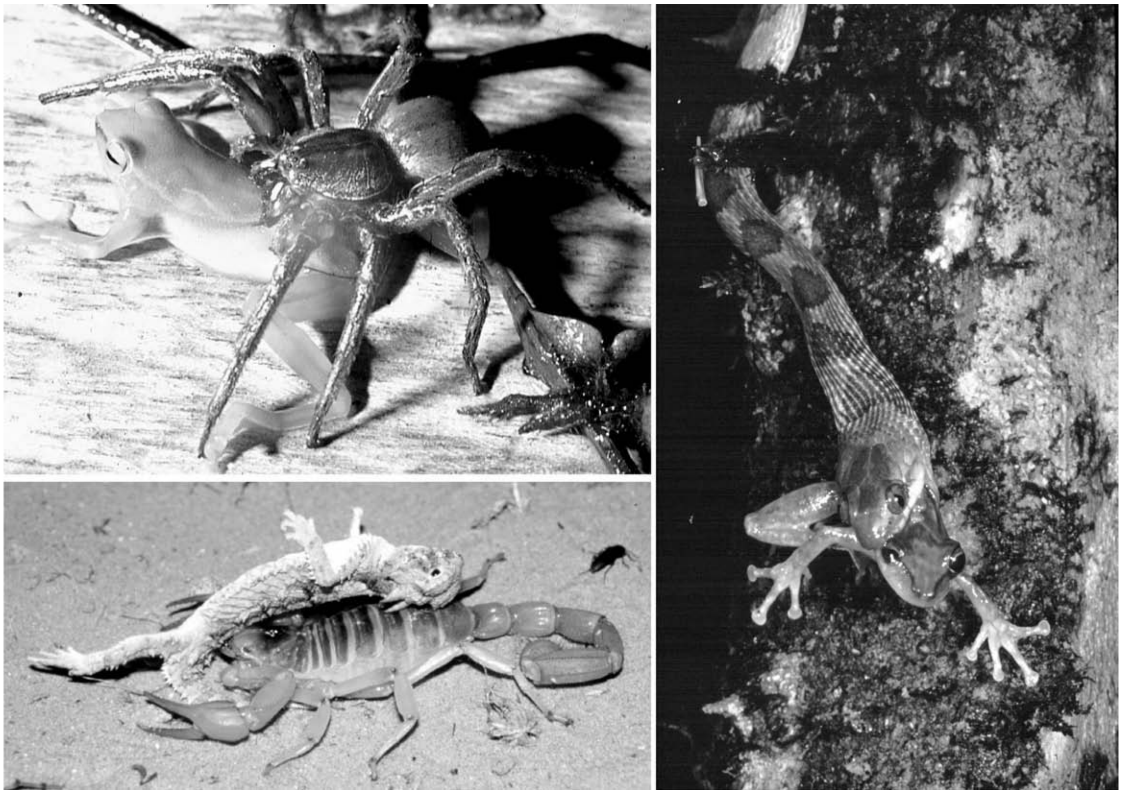


FIGURE 11.1 Predation on amphibians and reptiles. Clockwise from top left: a spider eating a small hylid frog (photograph by W. Hödl); a *Leptodeira* eating a *Hyla* (K. Miyata); and a desert hairy scorpion eating a *Phrynosoma* (J. Rorabaugh).

detected. In a heuristic sense, the evolution of escape mechanisms seems obvious. In nature, predator escape is much more complex because the diversity and abundance of predators is not constant in space or time and the complement of potential predators changes depending on the life history stage of the prey and numerous other factors (e.g., Schall and Pianka, 1980). Trade-offs associated with reproduction, social behavior, and activity can influence both the evolution of escape mechanisms and the manner in which predator escape might take place. Most amphibians and reptiles employ several different predator-escape mechanisms, often using different ones during different life history stages.

PREDATOR AVOIDANCE

Escaping Detection

Predators detect prey by vision, heat, and auditory, tactile, and olfactory cues. Escaping detection requires (1) interference with a predator's ability to use cues, or (2) not being present when a predator might be searching for prey. Limiting activity to time periods when predators are unlikely to be active affords some relief from predation. The most obvious example is nocturnal activity by many amphibians and reptiles, which effectively removes them from predation by diurnal bird species. Other animals, including nocturnal snakes and bats, might be effective predators on a given species at night. Altering activity patterns involves a multitude of trade-offs. Limiting activity to night, for example, might also limit energy acquisition rates in environments where many arthropods, the primary food, are diurnal. Nighttime activity and the associated lower body temperatures of ectotherms might result in reduced performance while active, affecting both prey acquisition and escape from whatever predators might be active at night.

Crypsis and Immobility

Cryptic coloration, morphology, or both, particularly when coupled with immobility, the lack of movement, appear to be highly effective in deterring detection by visually oriented predators (Fig. 11.2). A species is cryptic if its coloration or morphology resembles a random

FIGURE 11.2 Cryptic coloration and morphology render amphibians and reptiles nearly invisible against the appropriate background. Clockwise from the upper left: the salamander *Cryptobranchus alleganiensis* on stream bottom (Photograph by L. J. Vitt); the frog *Theloderma corticale* assuming a balled posture on moss (D. Fenolio); the eyelash viper *Bothriechis schlegelii* on a log (L. J. Vitt); and the Amazonian polychrotine lizard *Enyalius leechii* in leaf litter (L. J. Vitt).

sample of relevant aspects of the environment in which it lives (Endler, 1978; Greene, 1988). Exactly what comprises ‘‘relevant aspects’’ may not always be clear, but most observers have no difficulty determining that a cryptically colored species, such as a rough green snake, *Opheodrys aestivus*, matches its green leafy vegetation background. Movement offsets crypsis, and as a result, effective use of crypsis usually includes nearly total immobility (Brodie et al., 1974). Color and pattern can vary geographically in amphibians and reptiles, and individuals in local populations may match the corresponding microhabitat. *Crotalus lepidus* is light gray in the limestone rock outcrops near the small village of Boquillas but orange in the orange-colored rocks and hardpan of the Grapevine Hills of Big Bend National Park in Texas. Similarly, individuals of *Uta stansburiana* are various shades of gray in flatland desert habitats of Southwest deserts but nearly black on black basaltic lava flows in the eastern Mojave Desert.

Disruptive coloration can be an important component of crypsis. Patterns of blotches, stripes, bands, or spots break up the general outline of an individual and make it difficult to detect the whole animal, especially against a background containing a mixture of patterns and colors. In some species, such as the frog *Proceratophrys*, not only is coloration disruptive, but different individuals have different patterns (Fig. 11.3). Polymorphism in coloration and pattern presumably makes it difficult for predators to form a reliable search image. It would seem particularly advantageous in species with polymorphic color patterns for individuals to select microhabitats matching their pattern. One study suggests that they do. Green and brown morphs of *Pseudacris regilla* more frequently select matching than nonmatching backgrounds (Morey, 1990). Moreover, the natural predator, *Thamnophis elegans*, has higher success at detecting the frogs when they are against nonmatching backgrounds.

Often color patterns that appear brilliant are cryptic against some backgrounds. The bright contrasting bands of the coral snake patterns (black and white or yellow; black, yellow, and red) effectively conceal snakes in forest-floor litter, particularly when patches of light filter through the canopy and reach the forest floor.

FIGURE 11.3 A variety of color patterns occur among individuals of the Amazonian frog *Proceratophrys*. Each is cryptic against leaf litter, and the polymorphism makes it difficult for predators to form a search image. Photograph by J. P. Caldwell.

Modifications of body shape enhance the effects of color camouflage by making it difficult to find edges or by causing the animal to resemble a structural aspect of the environment. *Pipa, Phrynosoma,* trionychid turtles, viperid snakes, and many other amphibians and reptiles are dorsoventrally compressed. Flattening of the body makes it difficult to detect edges when these animals rest on a flat substrate (Fig. 11.2). Adding spines and other appendages to body edges further disrupts body shape and prevents a match with a predator's search image. Many frogs have modifications of the skin that enhance crypsis. Supraciliary processes, scalloped fringes along the outer margins of the limbs, and a variety of warts and tubercles aid in disrupting the outline of the animal. The long, thin vine snakes, *Oxybelis* and *Xenoxybelis*, resemble the thin branches of their habitat while they are stationary and are nearly impossible to detect. Unlike most snakes that frequently extrude their tongues, making them detectable by the movement, *Oxybelis* and *Xenoxybelis* even hold the tongue out for extended periods without moving it (see Fig. 10.5).

Other forms of crypsis may aid in escape from predators that use other senses to detect their prey. A small mammal might be cryptic from the perspective of infrared heat sensors of rattlesnakes that are tuned to the thermal landscape as long as it remains perfectly still. As with visually oriented predators, immobility is critical. Any movement by the small mammal would be perceived by the rattlesnake as a moving, and therefore alive, thermal signal. Relatively little is known about nonvisual cues but it would not be surprising to discover chemicals in amphibians and reptiles that render them "cryptic" from the perspective of chemosensory-oriented predators. Some blind snakes (*Leptotyphlops*) are known to produce chemicals that protect them from attacks by the ants they prey on (see Chemical Defense below), but whether these or other chemicals render them "cryptic" in the chemical landscape of a social insect nest remains poorly known.

Escaping or Misdirecting Identification

Once a predator has detected a potential prey item, the predator must identify it prior to attacking or attempting to eat it. The cost to a predator of misidentification potentially can be high, particularly if the prey is toxic or has other effective defenses. Prey identification can be visual, olfactory, tactile, or a combination of these cues. Prey have evolved many fascinating mechanisms to deceive predators into misidentifying them and consequently leaving them alone, the most striking of which is aposematic coloration of potentially harmful prey and mimicry by palatable prey.

Aposematic Coloration and Postural Warning

Many frogs and salamanders are brightly colored and produce noxious or lethal chemicals from granular glands in their skin (see Chemical Defense). The bright

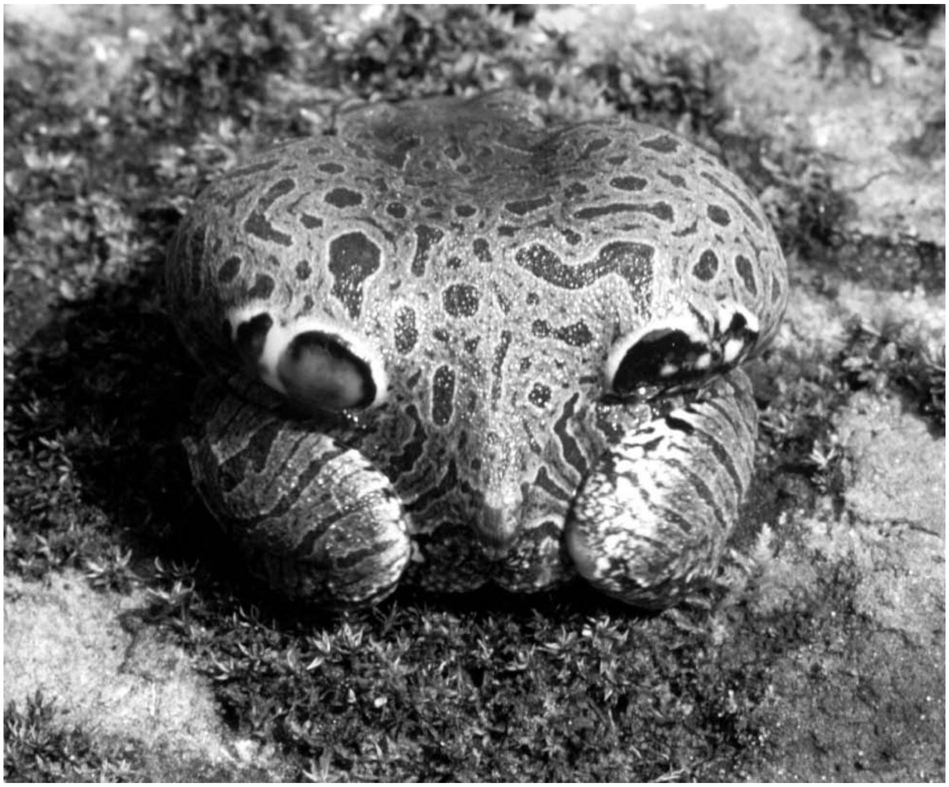


FIGURE 11.4 Defense posture of *Physalaemus nattereri* from Brazil. The frog raises the posterior part of the body and exposes large eyespots that begin secreting noxious chemicals. Photograph by J. P. Caldwell.

coloration, or in some instances, specific postures, warn predators of the high cost to attempted predation, causing them to discontinue approach and thus end the predation sequence. When bright coloration is associated with potentially life-threatening defense mechanisms (e.g., toxins), the coloration is considered a warning or aposematic coloration. Predators either learn or evolve recognition of these warning colors and avoid those potential prey. In this case, proper identification by the predator results in escape by the prey.

Some frogs, such as *Physalaemus nattereri*, assume a defensive posture with the posterior part of the body elevated to expose large eyespots that produce noxious chemicals (Fig. 11.4). Another posture, known as the unken reflex, occurs in both salamanders and frogs. First described in *Bombina*, ‘‘Unken’’ is the German word for this toad. The back is arched and the head and limbs of the body are elevated to expose bright ventral or lateral coloration while the animal remains perfectly immobile. Examples include the frog *Bombina variegata* and the eft stage of the salamander *Notophthalmus viridescens*, both of which are red or orange on the ventral surfaces. In addition, *Bombina variegata* roll their feet over to expose their brilliantly colored undersides (Fig. 11.5). Other salamanders hide their head while lashing with their tails. Because the tail contains mucous and granular glands, this behavior presumably further deters a predator that may come in contact with the noxious secretions.

Mimicry

Although the term ‘‘mimicry’’ has been widely applied to nearly every situation in which one species of animal resembles another, its definition with respect to predatory escape behavior is much more explicit. Mimicry occurs when one species of animal (the mimic) resembles another species that has easily recognizable characteristics (the model) and as a result deceives a potential predator (the dupe) that might otherwise capture and eat it (e.g., Greene, 1988; Pough, 1988). The model is usually poisonous, noxious, aggressive, or otherwise protected from predation and its colors, odors, or behaviors signal to a potential predator that it is dangerous and therefore not worth pursuing. A mimic takes advantage of an aposematically colored species that is truthfully advertising its high cost of capture. Batesian mimicry occurs when a nontoxic or otherwise nonprotected

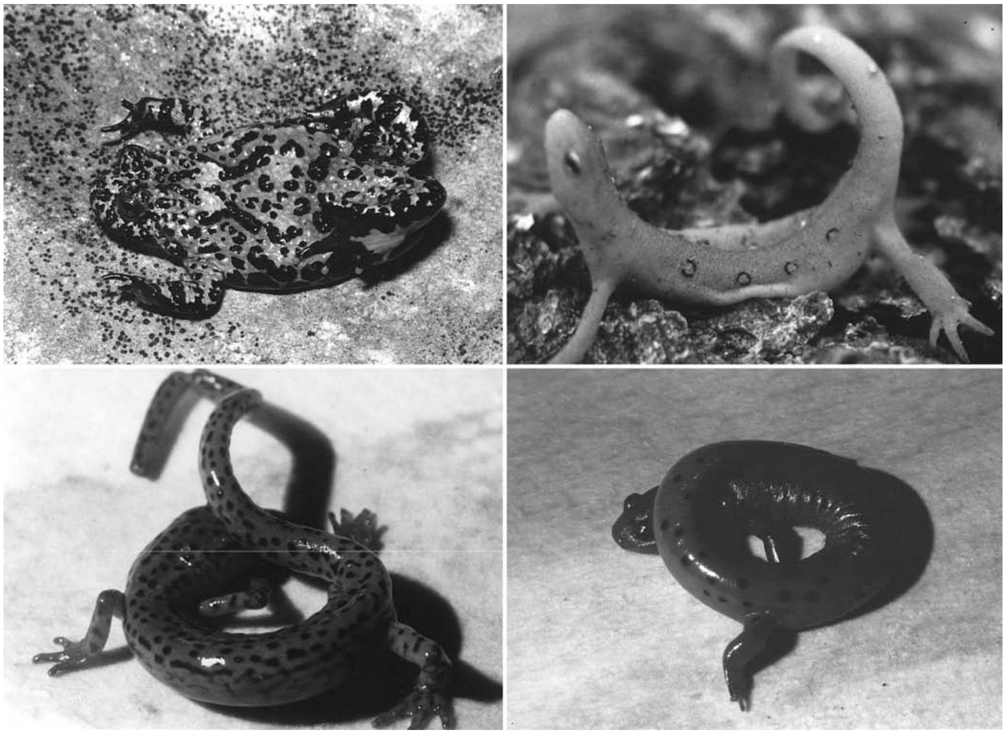


FIGURE 11.5 Some amphibian defense postures. Clockwise from top left: unken reflex, *Bombina orientalis* (Chinese fire-bellied toad); unken reflex, *Notophthalmus viridescens* (red-spotted newt); head hiding and tail lashing, *Pseudotriton montanus* (mud salamander); and tail lashing, *Eurycea lucifuga* (cave salamander). Photograph of frog, R. W. Van Devender; salamanders, C. K. Dodd, Jr.

species mimics a toxic or protected species, whereas Mullerian mimicry occurs when one or more potentially dangerous species resemble each other and each is both the model and the mimic. In both types of mimicry, the assumption is that similarities in coloration, pattern, or behaviors between the mimic and the model converge. In instances where two sister taxa have the same color or pattern, mimicry probably did not evolve independently in each taxon even though each may gain some advantage with respect to escaping predators by having similar patterns. In those species, a single evolutionary event produced the matching colors or patterns, and it occurred in their common ancestor or even farther back in the evolutionary history of the group.

Many descriptive studies have identified possible mimicry systems in amphibians and reptiles, and a few experimental studies have shown that some predators are duped by mimics of known models. Verifying that the models themselves are protected from predation has been much more challenging and often the evidence is indirect, partially because observation of natural predation events is uncommon. The most widely publicized and debated example of mimicry in amphibians and reptiles is coral snake mimicry, in which a number of harmless or mildly venomous snakes with various combinations of banding patterns resemble highly venomous New World coral snakes (*Micrurus* and *Micruroides*).

All species of coral snakes are highly venomous and capable of inflicting potentially lethal bites to predators. Most coral snakes have patterns of alternating, high-contrast bands, usually red, yellow, and black or at least a combination of either red and black or yellow and black. Laboratory experiments have shown that birds avoid cylindrical pieces of wood doweling with high-contrast bands, suggesting that coral snakes are models in a mimicry system (Smith, 1975, 1977). Their putative mimics (mostly colubrid snakes) have similar patterns and usually are about the same size as coral snakes. The most convincing comparative evidence that colubrid snakes mimic coral snakes is the concordant change in coloration and pattern by some colubrid snakes as coral snake patterns change geographically (Greene and McDiarmid, 1981; Sazima and Abe, 1991). Five species of coral snakes, *M. fulvius, M. limbatus, M. diastema, M. mipartitus,* and *M. elegans*, have distinctly different color and banding patterns through Mexico and Central America. One, *M. diastema*, has at least three distinct color patterns depending on locality. At each locality containing a specific species or color morph of coral snake, a species or color morph of the mildly venomous

FIGURE 11.6 The highly venomous coral snake *Micrurus albicintus* (above) and the nonvenomous snake *Atractus latifrons* (bottom) occur together in the Brazilian Amazon. This example of a nonvenomous snake with a pattern and color that matches a highly venomous coral snake represents Batesian mimicry. Photographs by L. J. Vitt.

snake *Pliocercus* matches the local coral snake. Mimics not only have high-contrast banding patterns similar to coral snakes in general, but the banding patterns of the mimics vary with the banding patterns of coral snakes as they change geographically. Similar geographic matches occur between coral snakes and nonvenomous snakes throughout much of the New World (Fig. 11.6).

Experimental evidence also suggests that coral snake patterns provide some protection from predation in natural situations (Brodie, 1993; Brodie and Janzen, 1995). Both plain-colored and tricolored snakelike models were placed on the forest floor in Costa Rica to determine if natural predators would disproportionately attack the plain-colored models. Because the models were made of soft plastic, predation attempts could be scored based on bite marks left by the predator. A similar experiment was conducted on a plain background to determine whether crypsis was also involved. Bird attacks (based on beak marks) were much more frequent on plain-colored models regardless of whether they were on the forest floor or on a plain background, suggesting that birds avoided the coral snake banding pattern. Further studies on models with a variety of coral snake patterns showed that attack frequency varied among models, indicating that birds can distinguish quite well among different patterns and that some patterns are more effective at deterring predation attacks. These studies differ from those performed by Smith (e.g., 1975) in that the models were more realistic and were presented to potential predators in natural habitats.

Numerous other examples of mimicry exist among snakes. For example, the nontoxic toad-eating snake *Xenodon rhabdocephalus* varies considerably in color pattern, but in most localities, its pattern closely resembles the local pattern of either *Bothrops asper* in Central America or *Bothrops atrox* in South America. When captured, *X. rhabdocephalus* adds to the deception by opening its mouth and erecting what appear to be large, movable fangs, similar to species of *Bothrops*. The teeth of *Xenodon* are enlarged rear fangs mounted on a movable maxillary bone and used to puncture toads that have filled with air. The snakes do not produce venom.

Mimicry of invertebrates by amphibians and reptiles may be widespread but is only beginning to be appreciated. Juveniles of the Kalahari lizard, *Heliobolus lugubris*, are black with fine white markings and, when disturbed, arch their backs and walk stiff-legged (Fig. 11.7; Huey and Pianka, 1981b). Their cryptic tails are pressed against the ground to further enhance a beetle-like appearance. Overall, their coloration and behavior closely resemble that of an oogpister carabid beetle that produces noxious chemicals for defense. The adults of *H. lugubris*, which are much larger than the beetles, do not have coloration or locomotion similar to beetles. Similarly, juveniles of the Brazilian anguid lizard *Diploglossus lessonae* are similar in size, color, and pattern to an abundant rhinocricid millipede that produces a variety of noxious and toxic substances for defense (Vitt, 1992b). The juveniles appear during the wet season when the millipedes are abundant, live in the same microhabitats as the millipedes, and, when the dry season ends and millipedes disappear, the lizards, having reached a larger body size than the millipedes, lose the banded coloration of the millipedes (Fig. 11.7). Other lizards appear to mimic scorpions and centipedes but neither comparative nor experimental studies have verified that a mimicry system is involved (e.g., Autumn and Han, 1989). Considering the high density of noxious or toxic invertebrates and the fact that they were highly diversified long before the diversification of amphibians and reptiles, invertebrate mimicry by amphibians and reptiles could be common.

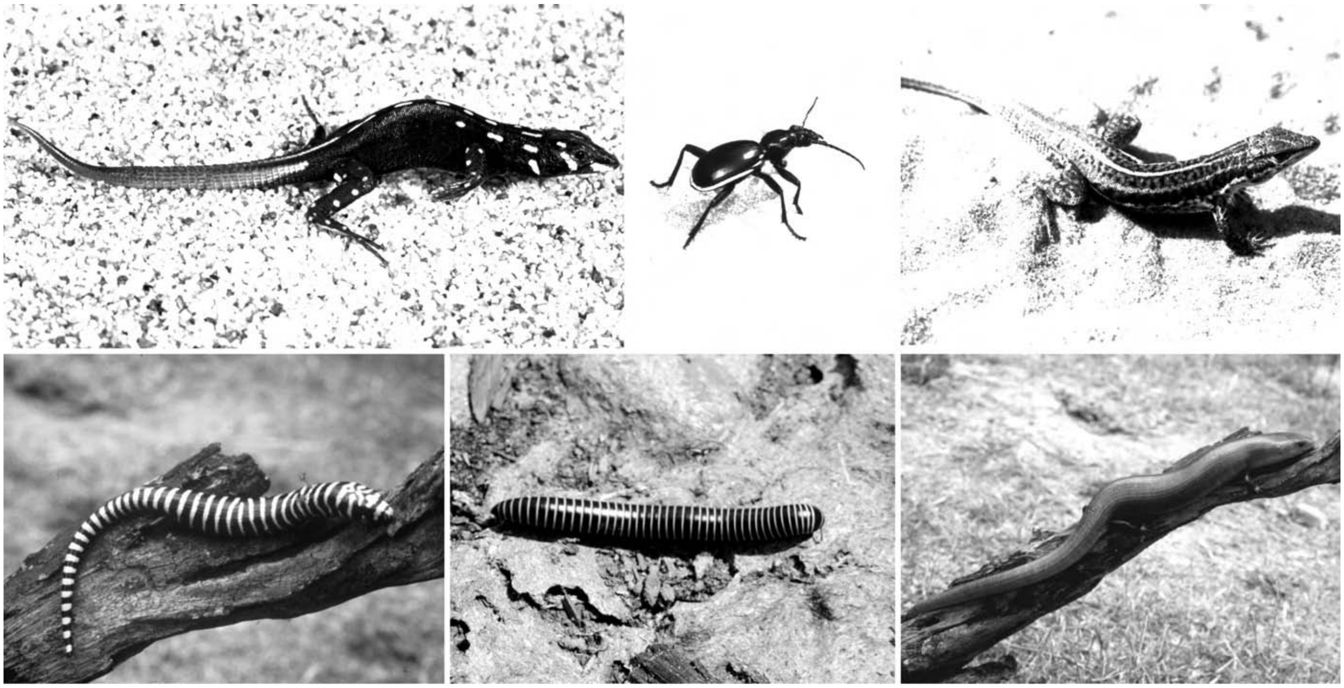


FIGURE 11.7 Some juvenile lizards mimic bad-tasting or potentially poisonous invertebrates. Top left and middle: the juvenile lizard *Heliobolus lugubris* mimics the oogpister beetle in the Namib Desert of Africa. Bottom left and middle: the juvenile lizard *Diploglossus lessonae* mimics a toxic rhinocricid millipede in northeastern Brazil. In both cases, the adults (right) do not have the color pattern of the model or mimic. Adapted from Huey and Pianka (1981b) and Vitt (1992b). Photographs by R. B. Huey and L. J. Vitt, respectively.

Among amphibians, mimicry is best known in salamanders. The red eft stage of *Notophthalmus viridescens* is terrestrial and unpalatable to birds because of its toxic skin (Brodie, 1968). A variety of other terrestrial salamanders occur in various parts of the range of red efts and appear to gain some benefit by resembling them. Birds avoid *Pseudotriton ruber* and red morphs of *Plethodon cinereus* based on their similarity to red efts (Howard and Brodie, 1973; Brodie and Brodie, 1980; Tilley et al., 1982). Likewise, *Plethodon jordani* in the southern Appalachians has brilliant red markings that warn of its distastefulness. The markings are on the cheeks or legs depending on locality. In areas where the salamander has red cheeks, the palatable look-alike salamander *Desmognathus imitator* has red cheeks, whereas in areas where *P. jordani* has red legs, *D. imitator* also has red legs (Howard and Brodie, 1973).

A complex mimicry system may exist among small leaf litter frogs that inhabit Amazonian rain forests. Many species have similar coloration and patterns, consisting primarily of bright white or yellow dorsolateral stripes on a dark background; some have bright yellow or orange flash colors in the groin and on the hidden surfaces of the thighs. Some species, including the leptodactylids *Lithodytes lineatus* and *Eleutherodactylus gaigeae*, and the dendrobatids *Epipedobates femoralis* and *Phyllobates lugubris*, have nontoxic skin. Other species, primarily dendrobatids such as *Epipedobates trivittatus* and *Epipedobates pictus*, have the same pattern but have toxic skin alkaloids produced by granular glands. Two or more of these species frequently occur together. These frogs, along with many similar species, may form a geographically widespread system of models and mimics (Fig. 11.8). Many species of frogs have large eyespots on the posterior surface of the body that they expose when disturbed. Whether the eyespots represent mimicry of large, potentially dangerous animals or simply direct the attention of a predator to areas where noxious chemicals are produced is poorly studied, and both may be occurring (see below).

Mimicry may dupe other senses of predators, although this area remains unexplored. One possibility is auditory mimicry of the saw-toothed viper *Echis carinatus* by the gecko *Teratoscincus scincus*. Both the snake and the lizard produce a rasping sound by rubbing scales together. The rasping sound would seem effective against nocturnal mammalian predators. Mimicry involving sensing systems other than sight are poorly known but could be widespread. Considering the widespread occurrence of chemical cues in prey detection by salamanders and scleroglossan lizards (including snakes), there is every reason to suspect that mimicry systems involve chemical cues.

Mimicry of inanimate objects in the environment has also been suggested as a defense mechanism. Some

FIGURE 11.8 A possible mimicry complex among Amazonian leaf litter frogs. Clockwise from upper left: *Epipedobates femoralis*, a nontoxic dendrobatid; *Epipedobates pictus*, a toxic dendrobatid; *Epipedobates trivittatus*, a toxic dendrobatid; and *Lithodytes lineatus*, a nontoxic leptodactylid. Photographs by J. P. Caldwell.

horned lizards (*Phrynosoma modestum*) assume postures and have a morphology and coloration that makes them resemble small rocks common in their microhabitats (Sherbrooke and Montanucci, 1988), and many other amphibians and reptiles have morphologies and perform behaviors that give the impression that they are "mimicking" attributes of the physical environment. Strictly speaking, these behaviors fall into the category of crypsis in that there is no animate "model." These examples show how predator-escape mechanisms sometimes cannot be easily categorized.

Escaping Approach

Species that move while foraging or have bright coloration are easily detected by predators and, as a result, rely less on crypsis and immobility. The most common response by potential prey to approaching predators, once aware that they have been detected, is locomotion away from the predator. For actively foraging lizards, this is the primary escape mechanism. The lizards often continue foraging while keeping track of approaching animals. When an animal moves within a critical distance or makes a dash at the lizard, the lizard runs to a safe distance and begins foraging again. Many aquatic snakes (e.g., *Nerodia*) and arboreal lizards (e.g., *Iguana, Uranoscodon, Crocodilurus, Physignathus*) bask on top of vegetation overhanging water and dive into the water to escape predators approaching from the land or within the vegetation. Basking crocodylians and turtles enter the water when potential predators approach. Nearly all amphibians and reptiles that use crevices or burrows rapidly enter their crevice or burrow when predators approach. Some, such as the chuckwalla (*Sauromalus obesus*), inflate their lungs with air and press their skin against the walls of the crevice to make themselves nearly impossible to extract. In the tropical arboreal lizard *Tropidurus flaviceps*, all individuals in a tree often enter the same hollow when approached from within the tree (Vitt and Zani, 1996b). Most frog species simply jump when a predator approaches, and nearly all shoreline frogs jump into water when approached. Some lizards (e.g., *Ptychozoon, Thecadactylus, Draco*), snakes (e.g., *Chrysopelea*), and frogs (e.g., *Agalychnis moreletii, Hyla miliaria*, species of *Rhacophorus*) parachute to safety by extending their limbs and spreading their toes to stretch webbing, or by using other skin extensions as airfoils. Terrestrial species, such as dendrobatids, retreat with a series of jumps that takes them well out of reach of predators. Arboreal frogs jump to other perches that protect them from predators incapable of jumping. Some, such as *Phyllomedusa hypochondrialis*, fall to the ground when disturbed and roll into a motionless (thus cryptic) ball on the forest floor.

Numerous threat displays cause predators to discontinue approach. The rattling of rattlesnakes and hissing sounds produced by many snakes and some lizards deter approach, particularly if combined with body, neck, or head expansion (Rossman and Williams, 1966; Greene, 1997). The expanded hoods of cobras, open mouth displays of cottonmouths, and brilliant colors on the inside of lizard mouths cause many predators to keep their distance (Fig. 11.9). Some frogs, including the hylid *Hemiphractus*, open their mouths and expose their bright orange tongues as threat displays similar to those of lizards when disturbed (Duellman and Trueb, 1986).

Escaping Subjugation and Capture

Skin, Armor, and Spines

Skin and other structures on the outside of the bodies of amphibians and reptiles can aid in resisting a predator attack. The softer, more permeable skin of amphibians has fewer structural modifications to increase its resistance to predator attacks (but see chemical defenses below). Aside from the assorted bony or keratinous spines that occur on the limbs and trunks of some frogs (most are associated with reproduction or digging), only the fusion of the skin to the dorsal skull roof may be defensive (Duellman and Trueb, 1986). This fusion provides strength to both skin and skull. For a few species, the top of the head may be used to block entry to retreats. The heavily keratinized skin of reptiles provides a durable body armor, and many modifications have evolved to give it even greater strength. The turtle shell composed of thick dermal plates is a most obvious defense structure. The ability to entirely close the shell as in *Terrapene* protects these turtles from most predators. Crocodylians, some lizards, and some amphibians have the epidermal scutes or scales underlain by bony osteoderms; this combined barrier makes penetration by a predator's teeth difficult, and both crocodylians and lizards use a spinning, thrashing movement to escape from the jaws of predators. Enlarged and spiny scales make a biting grip painful and difficult to hold. The horns of horned lizards (*Phrynosoma*) are longest in the areas of highest predator densities. Field observations of predators, such as the coachwhip *Masticophis flagellum*, dying from puncture wounds after swallowing horned lizards verify the effectiveness of spines. The spiny tails of *Ctenosaura, Uromastyx*, and many other lizards strike painful blows, often cutting into flesh. Jaws and claws of large-bodied lizards and turtles can inflict painful wounds when the animals are grasped, often resulting in escape. Even hatchlings of some turtles, including *Trachemys scripta* and *Chrysemys picta*, can inflict wounds to predators substantial enough to deter predation

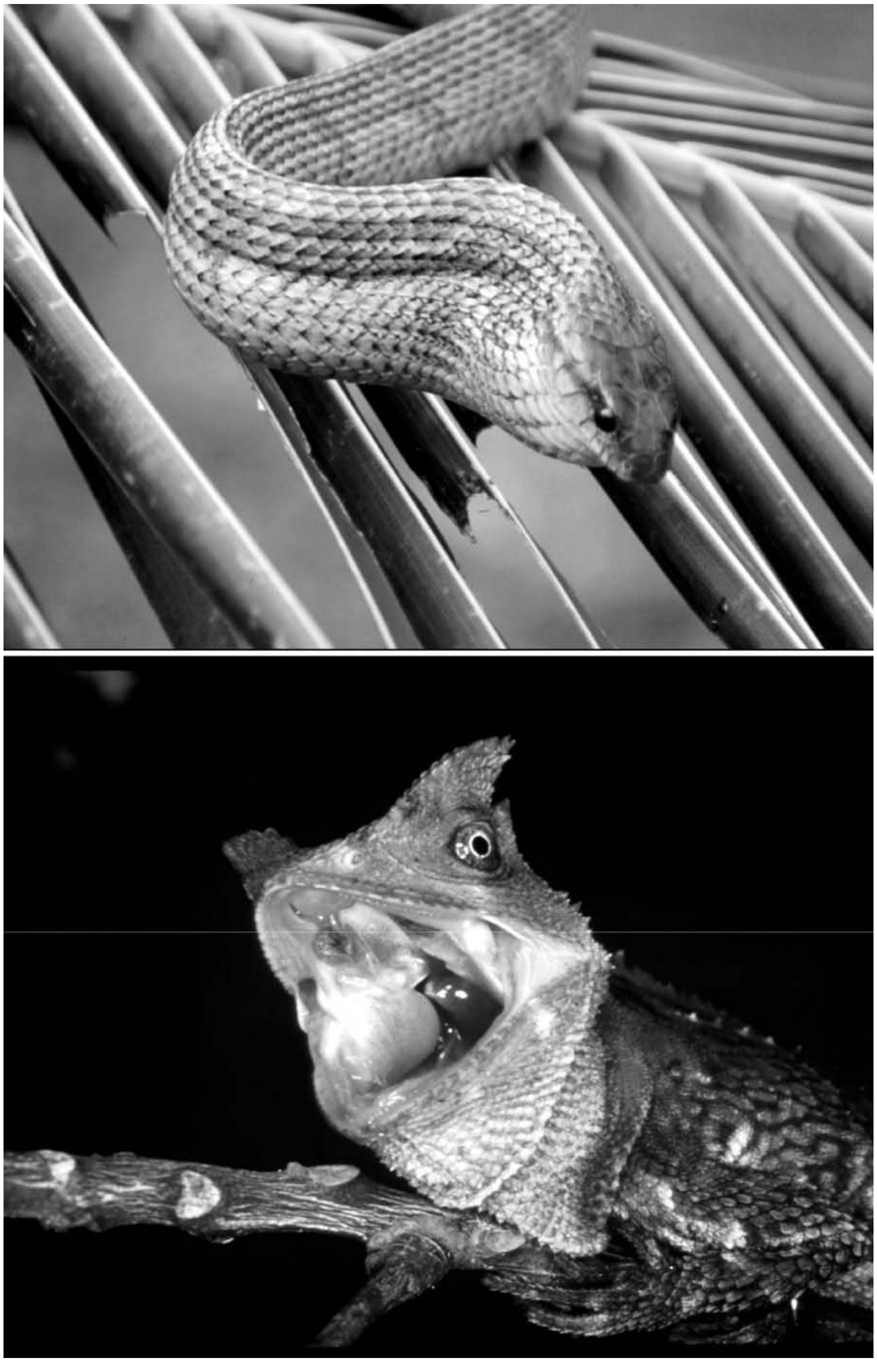


FIGURE 11.9 Threat displays by snakes and lizards. The Neotropical snake *Pseustes poeciolinotus* expands its throat and upper body, makes loud hissing sounds, and strikes, usually with the mouth closed. The Amazonian hoplocercine *Enyalioides palpebralis* faces an intruder and opens the jaws to expose bright orange mouth and throat coloration. Photographs by L. J. Vitt.

(Britson and Gutzke, 1993). Hatchlings of *T. scripta* and *C. picta* have brightly colored plastrons, and bass appear to avoid them whereas the fish do not avoid dull-colored *Chelydra serpentina*, which they only reject after attempting to eat (Britson, 1998). The bright plastral colors appear to warn the fish that the hatchlings are dangerous.

Other, more subtle structural modifications protect many smaller species. The tiny chameleons *Brookesia* have the transverse processes of the vertebrae curved

FIGURE 11.10 Some lizards, such as this Amazonian gecko (*Gonatodes hasemani*), can escape the grasp of predators by losing patches of skin. Photograph by L. J. Vitt.

dorsally over the neural arches to form a shield over the spinal cord. When touched, *Brookesia* freezes, releases its grip on the branch, and falls to the ground; during the fall, it rights itself so that it always lands with the vertebral shield upright, and birds treat it as an inedible object. Many gekkonids and some scincids, in addition to autotomizing tails when grasped by predators, can lose large patches of skin when grabbed by a potential predator (Bauer et al., 1989). As long as the body wall is not broken, the lizards heal with minimal scarring (Fig. 11.10).

Chemical Defense

Amphibians and reptiles produce a wide range of antipredator chemicals (Weldon, 1990; Daly, 1998). The amphibians, with their granular skin glands, produce chemicals ranging from irritating and mildly distasteful to emetic and lethal. The granular glands may be evenly spread across the dorsal surface as in dendrobatids or concentrated in large glandular masses as in the parotoid glands and warts of bufonids. The glandular masses are evident on many salamanders and frogs, and their locations complement their use in defense behaviors. *Bufo* and *Ambystoma* have large parotoid glands on their heads and meet their predators head-on. Salamanders that use tail lashing (e.g., *Bolitoglossa, Eurycea*) have heavy concentrations of glands that produce chemicals on the tail. The predator cannot approach and grab the prey without being exposed to gland secretions. Some species, such as *Salamandra salamandra*, can spray defensive chemicals from pressurized glands up to 200 cm (Fig. 11.11). Even in species with less striking defense behaviors and glandular concentrations (e.g., *Hyla, Rana*), the predator receives a dose of secretions from their granular glands as soon as it takes the prey into its mouth, and irritating secretions usually are sufficient to cause the prey to be released. Some frogs, such as *Phrynohyas venulosa*, produce a noxious skin secretion that is also gluelike, causing leaves and other debris to adhere to the jaws and mouth of the predator, facilitating escape. Many of the gluelike compounds have impressive adhesive properties (e.g., Evans and Brodie, 1994). When attacked by small garter snakes (*Thamnophis couchi*), the tiny salamander *Batrachoseps attenuatus* coils around the neck of the snake, making it nearly impossible for the snake to continue swallowing it (Arnold, 1982). Moreover, skin secretions from the salamander are wiped on the snake, causing nearly everything, including other parts of the snake, to adhere, allowing the salamander to escape predation. The salamanders and frogs do not stick to their own secretions.

A remarkable number of noxious and toxic components have been identified from amphibian skin, and

FIGURE 11.11 Examples of defense mechanisms involving squirting or spraying of noxious or toxic substances. Clockwise from upper left: the Australian gecko *Diplodactylus spinigerus* explosively sprays an unpalatable, sticky substance from glands in the tail; by cooling the lizards and prodding the skin with an electrode, the tail secretions of *D. ciliaris* are released as droplets on the tail; the European fire salamander, *Salamandra salamandra*, squirts chemicals from skin glands when disturbed; and the horned lizard *Phrynosoma cornutum* squirts blood from sinuses in the eyes when disturbed. The blood tastes bad, causing canids to release the lizard. Adapted from Rosenberg and Russell (1980); Rosenberg et al. (1984); Brodie and Smatresk (1990); and Middendorf and Sherbrooke (1992), respectively. Photographs provided by H. I. Rosenberg and A. P. Russell (*Diplodactylus*), E. D. Brodie, Jr. (*Salamandra*), and R. Mendez (*Phrynosoma*).

many of these are used for chemical defense (e.g., Daly et al., 1987; Daly, 1998; Erspamer, 1994). The known compounds fall into four groups: biogenic amines, peptides, bufodienolides, and alkaloids. The biogenic amines include serotonin, epinephrine, and dopamine; all affect the normal function of the vascular and nervous systems. The peptides comprise compounds such as bradykinin that modify cardiac function. The bufodienolides and alkaloids are similarly disruptive of normal cellular transport and metabolism and are often highly toxic.

The source of many chemicals that occur in amphibian skin appears to be the arthropods in their diets, particularly ants. Clades within the Bufonidae (e.g., *Bufo*), Microhylidae (e.g., Microhylinae), Ranidae (e.g., *Mantella*), and Dendrobatidae (e.g., *Dendrobates*) specialize on ants and produce some of the most toxic skin compounds. The suggestion that some frogs may optimize chemical intake for defense when selecting prey is supported by comparisons of the diets of frogs and lizards from the same microhabitats (Caldwell and Vitt, 1999). Many leaf litter frogs of Amazonian forest feed on ants even though more energetically profitable prey are available based on diets of lizards in the same microhabitat. The ant-eating frogs produce noxious chemicals in the skin. The correlation between ant-eating (myrmecophagy) and skin toxins is best supported for dendrobatid frogs (Toft, 1995; Caldwell, 1996a). All members of the genus *Dendrobates* eat ants, produce noxious or toxic chemicals in the skin, and are aposematically colored. Based on their presumed phylogenetic relationships, these traits have evolved together (see Fig. 10.23). A number of behavioral and life history traits have evolved concordant with myrmecophagy, including increased activity, reduced clutch size, and more extended parental care, including either prolonged feeding of tadpoles or long-term pair-bonds in some lineages (Caldwell, 1997). The possibility exists that release from predation by visually oriented predators has relaxed some of the constraints imposed by low levels of activity in cryptic species like *Colostethus,* resulting in the evolution of complex social behaviors involving high levels of activity in *Dendrobates. Colostethus* eats few ants, is not aposematically colored (with one possible exception), does not produce skin toxins, and relies on crypsis for escape from detection by predators. A nearly identical set of independently derived characteristics occurs among species in the ranid frog *Mantella* (Vences et al., 1997/1998). Species of *Mantella* feed on very small prey, mostly ants, produce alkaloids in the skin, are diurnal, and have aposematic coloration similar to that found in *Dendrobates.*

Larvae of many amphibians are distasteful, which provides them some protection from predation, particularly predation by fish (e.g., Kats et al., 1988). Palatability varies among species within the same general habitat as well as among closely related species (Wassersug, 1971; Blouin, 1990). Amphibian larvae use chemical cues to detect predators and spend more time in refuges when predators are present (Petranka et al., 1987).

With the exception of snake venoms, the chemical defenses of reptiles are more disagreeable than harmful. Turtles have musk (Rathke's) glands that open on the bridge of their shells; musk secretions have not been demonstrated as defensive, but to the human nose, the odor of kinosternid and chelid turtles is repugnant. Snakes have paired cloacal glands that are aimed at and emptied on predators. Some snakes, such as *Leptotyphlops dulcis*, produce chemicals that are effective in holding social insects at bay (Watkins et al., 1969). Geckos also have cloacal glands that may or may not be used in defense; however, the squirting tail glands of the Australian gecko *Diplodactylus spinigerus* produce a sticky, odiferous compound that appears defensive against vertebrates due to its odor or taste (Rosenberg and Russell, 1980). It may also be effective against some invertebrate predators such as spiders (Fig. 11.11), and it can be squirted up to one meter.

Most lizards do not have glands from which they can squirt chemicals for defense, but some horned lizards (*Phrynosoma*) involve their circulatory system in chemical defense. When captured by a potential predator, *Phrynosoma cornutum* squirts blood from the sinuses of the eyes (Fig. 11.11). At one time it was thought that blood squirted from the eyes of horned lizards gave a predator the false impression that it had been wounded by the sharp horns. However, blood of these horned lizards apparently tastes bad and causes canids to release the horned lizards (Middendorf and Sherbrooke, 1992). The source of bad-tasting chemicals remains unknown but may come from chemicals produced by the ants that they eat.

The glands of any amphibian or reptile can have multiple roles. Their secretions, even the most poisonous ones, probably also serve other functions, including individual and species recognition for reproductive and territorial behaviors, lubrication, waterproofing, or protection from bacteria, fungus, and parasites.

Death Feigning

Death feigning occurs in some frogs, salamanders, lizards, and snakes. In species that appear to feign death after falling from perches, the primary role of death feigning appears to be enhancing crypsis by ceasing movement. A Madagascar chameleon or an Amazonian *Phyllomedusa*, for example, that falls to the forest floor and ceases movement would seemingly disappear in the leaf litter. In North American *Heterodon* and Neotropical *Xenodon*, "death feigning" does not appear to enhance crypsis (Fig. 11.12). The snakes flatten their bodies, hiss, and often strike when first approached. When that threat display fails to have an effect, the snakes roll on their backs, often in a coiled or semicoiled position, open their mouths, and even drag their open mouth and tongue in the dirt. This may or may not be followed by defecation over much of the body. Exactly how this ridiculous behavior protects the snakes from

FIGURE 11.12 Defensive display of *Heterodon platirhinos.* Photographs by L. J. Vitt.

predation remains unclear, but it has been suggested that the feces contain toxins from toads eaten by the snakes and thus chemical defense may be involved. Other snakes simply roll into tight balls or flatten out in a tight coil when disturbed. The tropical leaf litter snake *Xenopholis scalaris* is bright red, which suggests aposematism or possible mimicry (Fig. 11.13).

Tail Displays and Autotomy

A large number of salamanders, lizards, and snakes display their tails when first disturbed. For salamanders and a few lizards, the display is associated with the production of noxious chemicals that discourage the predator from attacking or continuing to attack. In many snakes and lizards, no chemicals are produced and it appears that the primary function of the tail displays is to distract a potential predator away from more vulnerable parts of the body (Fig. 11.14). *Amphisbaena alba* not only raises its headlike tail off the ground when disturbed, but its head with mouth open is also raised, usually near the tail. Whether this gives a predator the impression that the animal has two aggressive heads or simply provides a 50% probability that the predator will attack the tail and allow the *Amphisbaena* to inflict a painful bite remains unknown. However, the effect is so stereotyped that nearly every rural citizen of countries where these animals live calls them "two-headed snakes." Rattlesnakes produce a loud, distinctive rattle from their specialized tail tip that not only distracts a potential predator away from the more vulnerable body as the snake crawls away to cover, but also serves to warn a potential predator that there is a high cost to any potential encounter. In this case, the cues are both visual and auditory.

FIGURE 11.13 When disturbed, many snakes, such as this red-bodied *Xenopholis scalaris*, coil tightly and flatten out while hiding the head and exposing bright coloration. Photograph by L. J. Vitt.

Larvae of many amphibians have bright or high-contrast tail tips that redirect predator attacks from the body to the tail, thus facilitating escape. In the northern cricket frog, *Acris crepitans,* larvae in temporary ponds where the primary predators are large dragonfly naiads (*Anax*) have black tail tips and suffer high rates of tail-tip damage as the result of misdirected naiad attacks, indicating the effectiveness of this defense strategy (Fig. 11.15). Larvae in lakes and streams where the primary predators are fish have translucent tails that allow the tadpoles to remain cryptic against the underwater substrate, thus reducing detection by predatory fish (Caldwell, 1982).

Among the most spectacular escape mechanisms in amphibians and reptiles is tail autotomy with subsequent regeneration. Tails of many salamanders, most lizards, and a few snakes can be released when grabbed by a predator, leaving the predator holding a thrashing and expendable body part while its owner flees to safety (Maiorana, 1977; Congdon et al., 1974; Dial and Fitzpatrick, 1983; Arnold, 1984, 1988; Wake and Dresner, 1967). Thus, tail loss not only allows immediate escape from a predator's grasp but also provides time for the salamander or lizard to escape while the predator is

FIGURE 11.14 Reptile tail displays. Clockwise from upper left: the Neotropical amphisbaenid *Amphisbaena alba* waves its headlike tail above the ground while also raising its head with mouth open; the North American gekkonid *Coleonyx variegatus* stops moving once it detects that a predator is close and then raises its tail off the ground and moves it back and forth to redirect the predator attack; the Amazonian coral snake *Micrurus surinamensis* hides its head in its coils and waves its short tail above the body; and the Neotropical rattlesnake *Crotalus durissus* produces a loud sound with its rattle that not only distracts a potential predator away from more vulnerable parts of the body, but also signals the predator that it is dangerous. Photographs by L. J. Vitt.

distracted by the tail. Because tails contain energy, the distracted predator does gain by continuing to devour the tail (Vitt et al., 1977). Regenerated tails can be smaller, similar to, or larger than original tails but contain cartilaginous support rather than the skeletal support of the original tail (Figs. 11.16 and 11.17).

In many species of lizards, coloration, size, or shape of the tail renders it conspicuous compared to the body and, although conspicuous tails can attract the attention of potential predators, the costs of attracting predators are outweighed by the benefits accrued by being able to detect the presence of a predator (Cooper and Vitt, 1991). For example, tails of juvenile *Eumeces fasciatus* are brilliant blue, tails of *Vanzosaurus rubricauda* are red or orange, and regenerated tails of *Hemidactylus agrius* are bulbous. Experiments with natural predators of *Coleonyx variegatus* and *Eumeces fasciatus* reveal that these lizards raise the tail off of the ground, distracting the attention of snakes to the tail rather than the more vulnerable body parts (Congdon et al., 1974; Cooper and Vitt, 1985). Tails are not immediately lost when grabbed by the predator. Rather, the lizards appear to allow the snake to gain a secure hold on the tail prior to releasing it. The tail is released by the lizard as the result of powerful muscle contractions. Segmented myomeres are exposed but are not torn, and little bleeding or fluid loss occurs as the tail is released. The tails immediately begin to thrash violently using anaerobic metabolism and continue to thrash for extended time periods (Dial, 1981; Dial and Fitzpatrick, 1983). Snake predators swallow the tails, increasing the rate of ingestion as the thrashing of the tail becomes less vigorous.

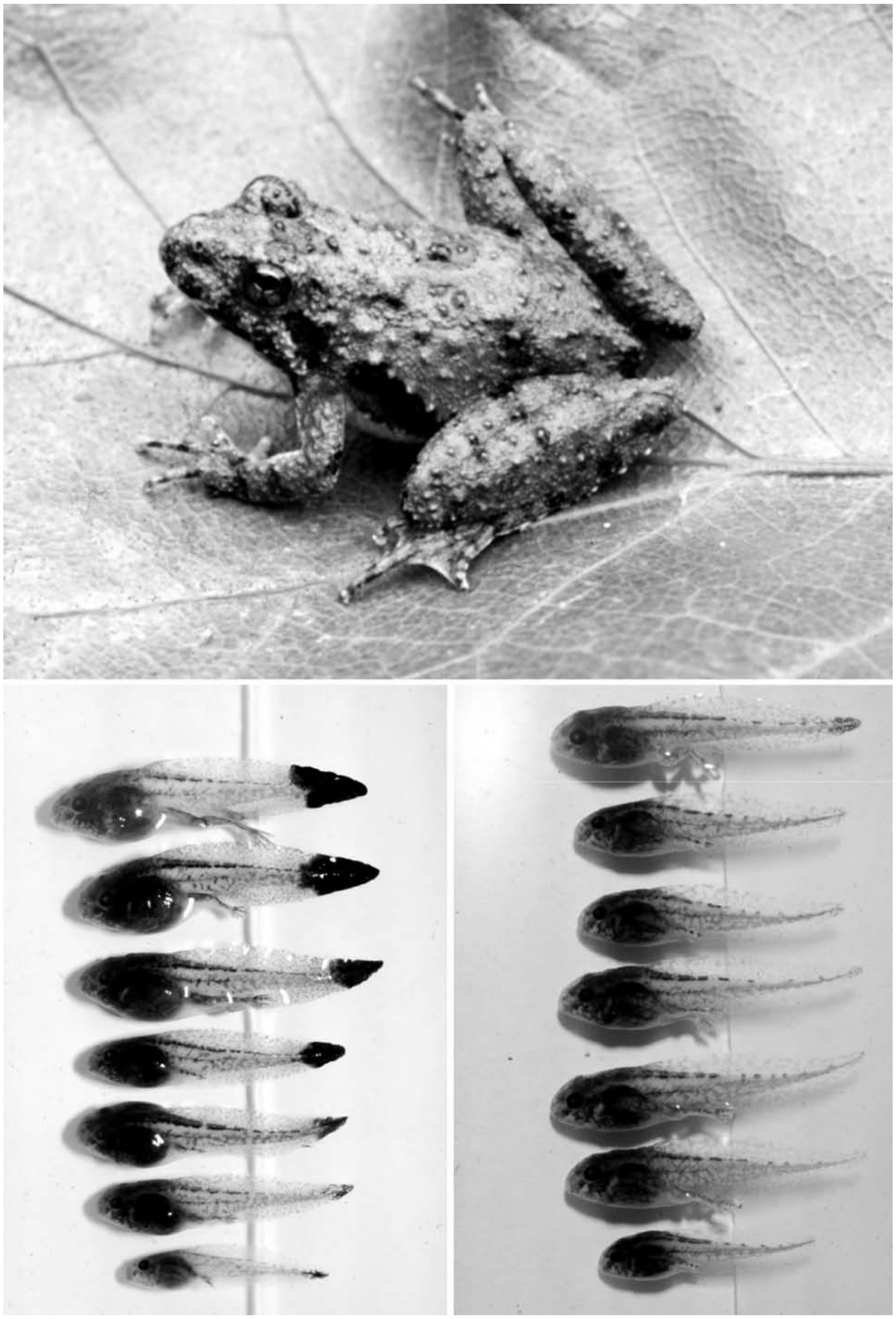


FIGURE 11.15 Tadpoles of the cricket frog *Acris crepitans* have black tails that direct attacks away from the body (lower left) when they occur in pools or small ponds with predaceous dragonfly larvae. They have clear tails (lower right) when they occur in lakes or streams where maintaining crypsis is important to avoid detection by fish predators. Photographs by J. P. Caldwell.

Loss of tails by lizards and salamanders has potential energetic, social, and survival costs. Tails of salamanders and lizards are often used as fat-storage organs (e.g., Bustard, 1967). Stored fat can be important for energetic support of reproduction and social behavior. *Coleonyx brevis* produces smaller eggs or no eggs following tail autotomy, and *Eumeces* appears to produce smaller clutches following tail autotomy (Dial and Fitzpatrick, 1981; Vitt and Cooper, 1986a,b). Some lizards, such as *Uta stansburiana,* suffer reduced social status as the

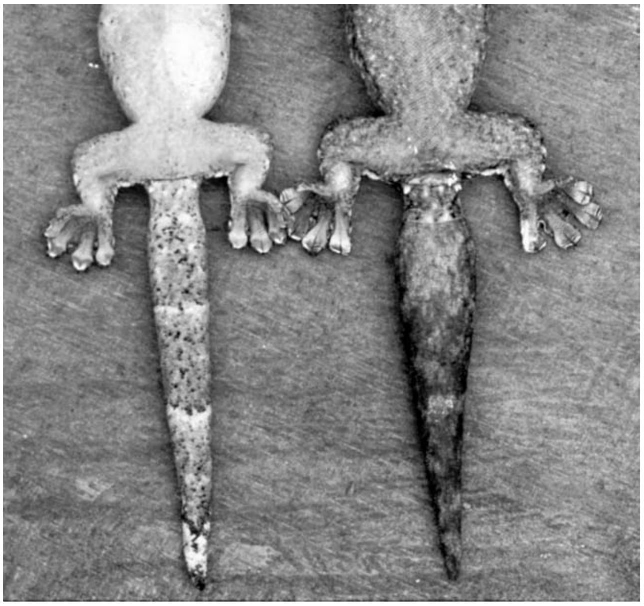


FIGURE 11.16 Although original (left) and regenerated (right) tails of lizards are superficially similar, regenerated tails can be larger than the original as in this tropical gecko, *Thecadactylus rapicauda*. Photograph by L. J. Vitt.

result of tail loss (Fox and Rostker, 1982; Fox et al., 1990). In other species such as *Lacerta monticola*, mating success is reduced (Martin and Salvador, 1993). In still others, long-term effects include reduced home range size and reduced access to females (Salvador et al., 1996). All salamanders and lizards that lose their tails are without tail autotomy as a defense mechanism during tail regeneration.

Costs of tail loss and regeneration can also vary ontogenetically. Because juveniles do not invest directly in reproduction, tail loss has a reproductive cost only if regeneration delays the attainment of sexual maturity or results in reduced size at sexual maturity. In juvenile skinks (*Eumeces*), lizards that lose tails not only regenerate the tails, but growth rates increase enough to counter the effects of the loss of a relatively large portion of their body (Fig. 11.18). In adults, tails and their energy reserves are important for reproduction and, as a result, the cost-benefit ratio for tail autotomy changes. Tails of adult *Eumeces* are cryptically colored similar to the body and other predator escape mechanisms become more important than tail autotomy.

Although an apparent cost of tail loss in salamanders and lizards might be reduced performance and hence higher risk of mortality, this is not always the case. In some lizard species, individuals without tails perform better than individuals with tails intact (Daniels, 1983). An experimental study in which tails were removed from hatchlings of *Uta stansburiana* in the field, with their subsequent growth and survival monitored, revealed reduced growth rates in lizards that lost their tails but no apparent reduction in survival when compared to hatchlings with intact tails over a 3-year period (Niewiarowski et al., 1997). In 1 year of the study, female hatchlings with broken tails survived better than those with intact tails.

The ground skink, *Scincella lateralis*, has taken the strategy of tail loss to the extreme. Not only do the lizards autotomize tails when attacked by a predator, both the skink and the autotomized tail have a high escape probability. The skinks and their tails disappear

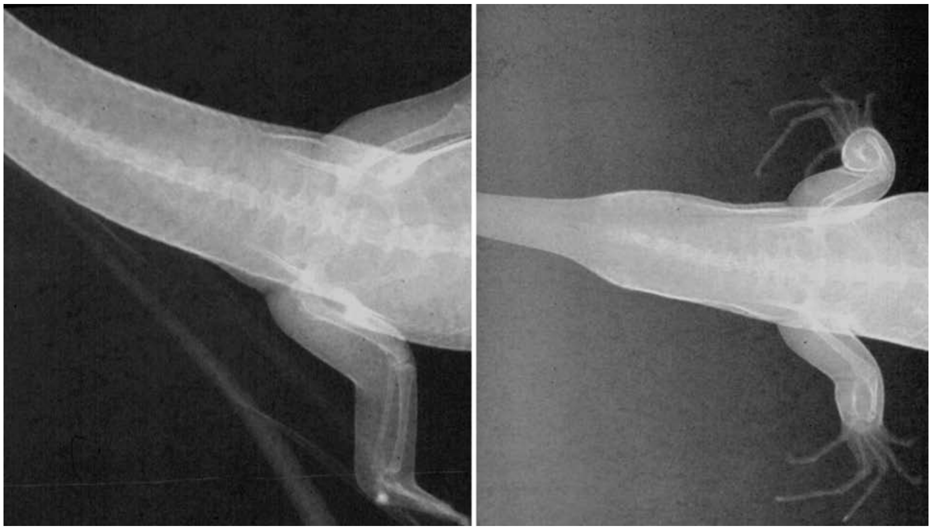


FIGURE 11.17 These x-rays of tails of *Eumeces laticeps* show that the vertebrae of an original tail (left) are replaced by a cartilaginous rod (left) in the regenerated tail. Provided by L. J. Vitt.

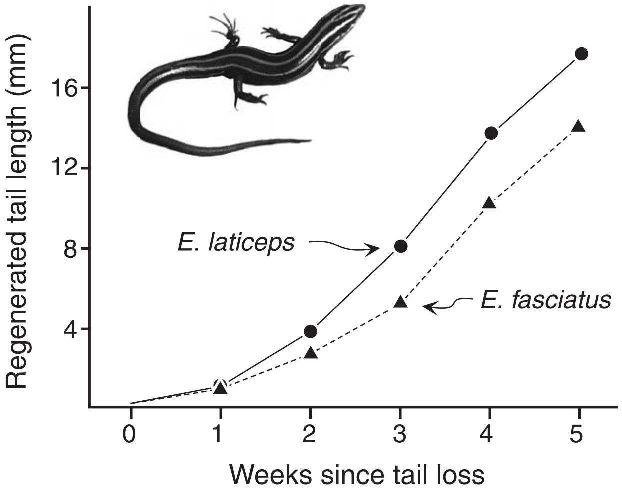


FIGURE 11.18 Tail regeneration rates in *Eumeces fasciatus* and *Eumeces laticeps*. Adapted from Vitt and Cooper (1986b).

into leaf litter, and the thrashing tail distracts the predator away from the escaping lizard. Ground skinks that have lost their tails return to the site of tail loss and if they can find their lost tails, they ingest them and regain much of the energy lost (Clark, 1971).

Although rates or frequencies of regenerated tails (indicating that the tail has been lost at least once) in natural populations have been used as relative measures of predation, tail loss rates do not necessarily estimate predation intensity because salamanders or lizards with regenerated tails are survivors of predation attempts—there is no easy method to determine mortality among animals that did not lose their tails (Schoener, 1979; Schoener and Schoener, 1982). Consequently, high frequency of tail loss could indicate the success of tail autotomy as a defense strategy rather than a high mortality due to predator attacks.

Schooling and Other Aggregations

Many amphibian larvae occur in what appear to be social groups, often referred to as schools (Wassersug et al., 1981; Branch, 1983; Caldwell, 1989). Tadpole schools are known from a variety of frog taxa, including the Bufonidae, Ranidae, Hylidae, and Leptodactylidae. Large numbers of larvae move around in ponds as a group, spreading out and reorganizing as the group moves about (Fig. 11.19). The possibility exists that a large school is perceived by some predators as something other than many individual tadpoles and is thus avoided. From the perspective of an individual tadpole, being a member of a large school reduces the probability that any specific individual will be the next one captured, sort of a low-probability Russian roulette. Tadpoles of the tropical frog *Leptodactylus macrosternum* form large schools that extend from the surface of the water where the tadpoles gulp air to the pond bottom where they fan out and graze for a brief period. The schools are continually reorganizing and individuals are always moving toward the center of the school. In northern Brazil, adults of the frog *Pseudis paradoxa* repeatedly dive into the schools from the water surface and feed on these tadpoles. Larvae of dragonflies on the pond bottom pick off tadpoles from the bottom of the school, and dytiscid beetle larvae prey on tadpoles that lag behind the school. Although the schools move around throughout the pond, it is not clear whether they do so to find richer foraging sites or to avoid intense predation. In some populations of *Leptodactylus bolivianus* and *Leptodactylus ocellatus*, females remain with the school of tadpoles and either direct the tadpole movements or aggressively defend the schools from potential predators (Vaz-Ferreira and Gehrau, 1975; Wells and Bard, 1988).

Miscellaneous Behaviors

A wide variety of other behaviors are utilized by amphibians and reptiles to escape once predators initiate attacks. Some lizards seize parts of their own body, rendering them nearly impossible to swallow. *Cordylus cataphractus*, for example, bites and holds on to its own tail, making a loop of its body and exposing its large, armored scales to a predator (Rose, 1962). The elapid snake *Vermicella annulata* elevates loops of its body to make it difficult for predators to secure a grip on the snake (Shine, 1980b). A diversity of snakes coil in a ball or hide their heads within coils (Greene, 1988).

Life History Responses to Predation

In a general way, life history responses to predation are relatively easy to visualize. For example, in species where mortality on juveniles is density dependent, production of fewer, larger, and more competitive offspring should be the evolutionary response. In species where mortality on juveniles is density independent, production of greater numbers of offspring should be the evolutionary response. Because energy for reproduction is typically limited (see Chapters 4 and 5), production of more offspring means that those offspring will be smaller. Both of these represent life history responses to predation or other mortality sources. The possible combinations of life history responses are nearly unlimited given the many variables that influence the evolution of life histories. The life histories of two species of frogs that breed in the same microhabitat exemplify the complexities of life history responses to predation. *Dendrobates castaneoticus* and *Bufo castaneoticus* breed in open, abandoned fruit

FIGURE 11.19 Individual tadpoles are afforded some protection from predation by forming large schools. Clockwise from upper left: large schools of *Hyla geographica* move around in ponds, lakes, and rivers; tadpoles of *Leptodactylus macrosternum* surface to gulp air as their large schools move about in ponds; schools of *L. macrosternum* extend from the surface to the bottom, with individual tadpoles continually cycling through the school (at the surface they are eaten by frogs [*Pseudis paradoxa*] and in the water column they are attacked by dragonfly and dytiscid larvae); and a female *Leptodactylus ocellatus* remains with its large tadpole school and actually attacks intruders. Photographs by J. P. Caldwell.

capsules of the Brazil nut tree in Amazonian Brazil (Caldwell, 1993). The capsules fall to the forest floor, agoutis gnaw the top off of the capsules and remove the Brazil nuts, and the capsules fill with water during rain storms (Fig. 11.20). Mosquitoes, giant damselflies, and both species of frogs use the capsules for breeding. A single tadpole is transported to a capsule by *D. castaneoticus*. About 250 eggs are deposited in a capsule by *B. castaneoticus*. The *Dendrobates* larva is predaceous, feeding on insect larvae and *Bufo* tadpoles if any are in the capsule. Larvae of one mosquito species and the giant damselflies are predaceous and feed on both tadpole species if the tadpoles are small enough. The tiny *Bufo* larvae develop rapidly in a race to metamorphose before all are eaten. The density of predators likely determines how many, if any, of the *Bufo* tadpoles survive to metamorphosis. The relative size of mosquito, damselfly, and *Dendrobates* larvae and the order of colonization determine which of these organisms will survive to metamorphosis. For example, if a *Dendrobates* tadpole is deposited before the insects, it feeds on all insect larvae subsequently deposited, grows, and ultimately metamorphoses. If one of the insect larvae is deposited first and grows large enough to kill a *Dendrobates* tadpole, the insect larvae will grow and metamorphose. Experiments have shown that a 7-mm damselfly larva can kill a large tadpole. Thus, both relative size and sequence of deposition determine survival in this microcosm. On the one hand, *Dendrobates* has evolved a life history in which a few large and highly competitive offspring are produced to enter a competitive system. On the other hand, *Bufo* has evolved a life history that includes a reduced clutch size compared to other species of *Bufo,* allowing it to use the small breeding site and produce enough individual offspring to ensure that at least some survive to metamorphosis.

FIGURE 11.20 Life histories of two frog species using the same breeding microhabitat illustrate the evolution of complex responses to predation. After falling to the forest floor, the indehiscent fruits of the Brazil nut tree are opened by agoutis (top left), which remove the seeds (top right) known as Brazil nuts (center) and leave the open fruit capsule on the forest floor. After the capsule fills with water, it is colonized by two frog species and a variety of insects. The frog *Dendrobates castaneoticus* (middle right) transports a single tadpole to the capsule (bottom right), whereas the toad *Bufo castaneoticus* (bottom left) deposits a small clutch of eggs (middle left). The sequence of arrival and the composition of the fauna in the capsule determine reproductive success in both frogs (see text). Adapted from Caldwell (1993). Photograph of agouti, M. A. Mares; all others, J. P. Caldwell.

OFFSETTING THE EFFECTS OF PARASITISM

The long-term effects of parasites on amphibians and reptiles are relatively poorly known. Parasites can have a nearly undetectable impact on their hosts or, in some instances, can kill their hosts. If the fitness of hosts is negatively affected by parasitism, then parasites are effectively predators because the likelihood of an infected individual's genes being represented in future generations is reduced. Potential negative effects of parasitism include anemia and reduced performance followed by reduced survival, competitiveness, social status, ability to sequester mates, and, for females, reduced fecundity (Bull and Burzacott, 1993). Ectoparasites such as ticks and mites may also introduce endoparasites such as filarial worms and *Plasmodium* (Fig. 11.21). Parasitism is so widespread and common among amphibians and reptiles that nearly every scenario is possible. Lists of parasite species exist and new species are described continually from amphibians and reptiles, but few data are available on parasite life histories; how infestation affects an individual amphibian's or reptile's health, growth, and reproductive output; or the effects on population structure and dynamics. When mass die-offs occur, such as the microsporidian epidemic of English *Bufo bufo* in the early 1960s, the decimation of *Rana pipiens* populations across northern North America in early 1970s, or the

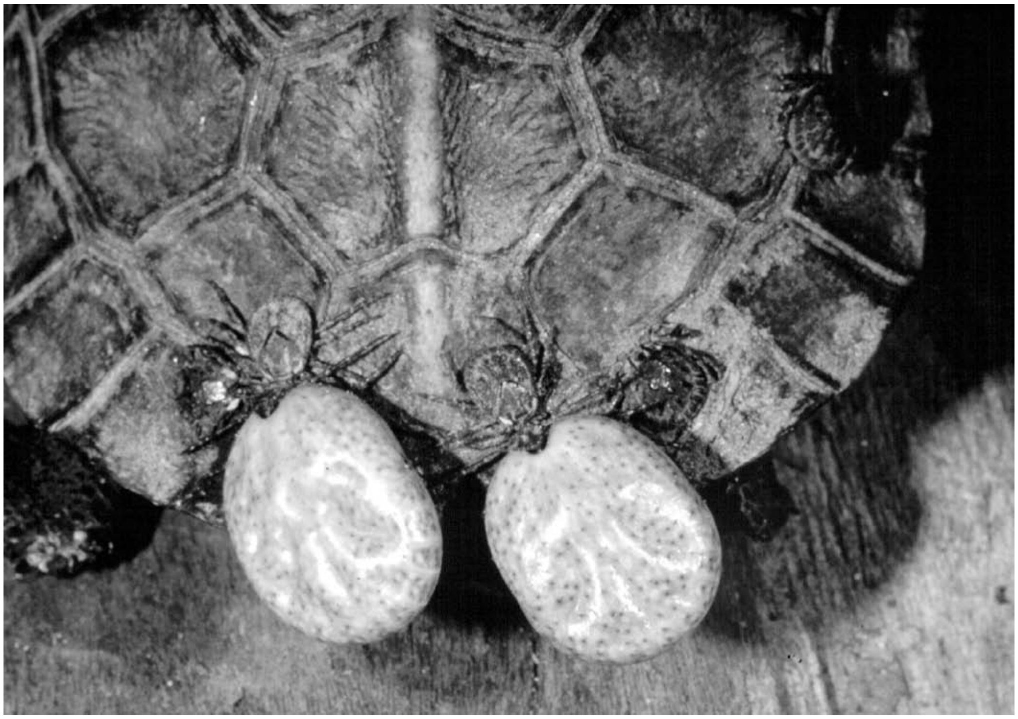


FIGURE 11.21 Ticks embedded in the shell of *Rhinoclemmys annulata*. Photograph by K. Miyata.

high incidence of viral-induced papilloma in Florida populations of *Chelonia mydas*, we are reminded of the impact parasites can have on natural populations.

Amphibians and reptiles are hosts to the usual vertebrate parasites. Internally they include bacteria, protozoans, and various groups of parasitic "worms." External parasites include helminths and arthropods, primarily mites and ticks. All individuals likely have endoparasites of one kind or another as well as one or more ectoparasites. The level of virulence is usually unknown, but in most populations, individual amphibians and reptiles generally appear healthy, so many parasites must be benign and/or the host must be resistant to some degree, at least.

Amphibians and reptiles share many of the features of the immune system of mammals and, as a consequence, similar mechanisms modulate parasite infections. One mechanism for combating bacterial infection is elevation of body temperature, because high temperature inactivates or kills bacteria. Some lizards, snakes, and turtles behaviorally select and maintain body temperatures significantly above their normal activity temperatures (Vaughn et al., 1974; Monagas and Gatten, 1983; Ortega et al., 1991; Burns et al., 1996). This behavioral fever mechanism appears to reduce the infection and improve the reptile's resistance. Amphibian granular and mucous glands may also function to offset parasite infection. The toxicity of the chemicals produced in most amphibians appears low to nonexistent for many invertebrate and vertebrate predators. These glands may have appeared early in amphibian evolution to protect against bacterial and fungal infections of the moist skin and still serve that function today. Magainins, isolated from the skin of *Xenopus*, have exceptional antibiotic and antifungal properties. They or related compounds likely exist in other amphibians. Other chemicals in the skin of some amphibians act as insect repellents and likely reduce exposure to insect-borne blood parasites.

Among the most common and geographically widespread parasites is malaria (*Plasmodium*), and a large number of species are known to infect amphibians and reptiles (Ayala, 1977). In northern California, about 40% of the populations of *Sceloporus occidentalis* have malarial parasites (Schall, 1983). Within these populations, fewer than one-third of the individuals are infected, and males are more commonly infected than females. Performance of infected lizards is adversely affected by infection (Table 11.1), although no apparent differences in structure and dynamics between infected and noninfected populations is detectable. In Panamanian populations of *Anolis limifrons*, adult males also have the highest incidence of malarial infection during all seasons; however, no evidence of differences in general health, feeding, or reproductive behavior between noninfected and infected males exists.

TABLE 11.1 The Effect of Malaria on the Performance of Western Fence Lizards *Sceloporus occidentalis*

Criterion	Performance (%)
Hemoglobin concentration	76
Metabolic rate, active	85
Burst running speed	89
Running stamina (2 min)	83
Fat stored, female	75
Clutch size	86
Growth rate	96
Mortality	114

Source: Adapted from Schall (1983).

Note: The values are the level of performance (percent) of a sample of malaria-infected lizards compared to noninfected lizards, which are assumed to perform at 100%.

Parasitism can influence the outcome of competitive interactions among species. On the island of St. Martins in the Caribbean, the lizard *Anolis gingivinus* occurs throughout the island and is a superior competitor over *Anolis wattsi*, but *A. wattsi* is restricted to the central hills. A malarial parasite *Plasmodium azurophilum* infects *A. gingivinus* but rarely infects *A. wattsi* (Schall, 1992). In areas where *A. gingivinus* is not infected, *A. wattsi* is absent, but in areas where *A. gingivinus* is infected, *A. wattsi* is present. The spatial distribution of the parasite in *A. gingivinus* is nearly identical to the spatial distribution of *A. wattsi*, which suggests that its presence renders *A. gingivinus* a poorer competitor when infected. In addition, *P. azurophilum* is known to reduce hemoglobin and negatively influence the immune system of *A. gingivinus*. Parasite-mediated competition may be common in amphibians and reptiles but is poorly documented.

Although parasitism appears to affect physiological function in some species, it does not affect others. Frillneck lizards, *Clamydosaurus kingii*, that are infected with mosquito-transmitted filarial parasites perform equally as well as uninfected lizards (Christian and Bedford, 1995). Aerobic capacity, body condition, hematocrit, and hemoglobin concentration are not related to the number of microfilariae in the blood of lizards and are not related to whether lizards are infected or not infected. Although larger lizards at the site where the parasite occurs have higher levels of infection, no effect of size (and hence parasite infection) is detectable on any of the performance parameters measured.

A variety of mites and ticks infest reptiles and amphibians. Many lizard species have mite pockets—folds of skin that often are completely packed with mites. In some lizards, folds of skin form mite pockets on the lateral surfaces of the neck anterior to the insertion of the front legs. These are often so packed with mites that large red patches are visible on the lizards from considerable distances. Exactly why lizards have mite pockets is controversial. One hypothesis is that mite pockets concentrate mites and restrict their damage to a few small areas (Arnold, 1986). Another is that mite pockets reflect phylogenetic or structural constraints; the folds are present and mites use them (Bauer et al., 1990, 1993). Implicit in the first hypothesis is the idea that overall mite loads would be reduced and thus overall damage would be less. Whether lizards actually gain anything by having mite pockets remains to be demonstrated; no apparent reason exists for mites to restrict themselves just to mite pockets. Moreover, the overall impact of tick and mite infestations remains poorly documented for amphibians and reptiles. Infestation of the mite *Hannemani dunni* is found in 100% of the salamanders *Plethodon ouachitae*. Each individual has an average of 20 mites on its body, and many individuals have clusters of mites on their appendages, causing deformities of the toes (Winter et al., 1986). The sympatric *Plethodon serratus*, which occurs in the same microhabitat as *P. ouachitae*, is not infected with mites. The reason why *P. serratus* is not attacked by mites is unknown, as is whether the mite infestation has any detrimental effects on reproduction or population structure in *P. ouachitae*. In sleepy lizards, *Tiliqua rugosa*, two species of ticks infect lizards at different localities (Bull and Burzacott, 1993). Long-term studies on the lizards reveal that longevity is not reduced in lizards infected with ticks. Individual lizards appear to maintain their tick loads from year to year. Lizards with the largest numbers of ticks reach the largest body size and are more likely to be in mating pairs than lizards with low tick loads. Thus there is no evidence in these lizards that parasite infection reduces fitness.

Elimination of a parasitic infection is possible, although the mechanism is unknown. Nearly all male spadefoots, *Scaphiopus couchii*, leave their breeding aggregations with a monogenean trematode infection, yet 50% have lost the parasites prior to hibernating (Tinsley, 1990).

ADDITIONAL READING

Arnold, E. N. (1988). Caudal autotomy as a defense. *In* "Biology of the Reptilia, Vol. 16, Ecology B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 235–273. Alan R. Liss, Inc., New York.

Daly, J. W. (1998). Thirty years of discovering arthropod alkaloids in amphibian skin. *J. Nat. Prod.* **61**: 162–172.

Duellman, W. E., and Trueb, L. (1986). “Biology of Amphibians.” McGraw-Hill, New York.

Endler, J. A. (1978). A predator’s view of animal color patterns. *In* “Evolutionary Biology, Vol. 11” (M. K. Hecht, W. C. Steere, and B. Wallace, Eds.), pp. 319–364. Plenum, New York.

Erspamer, V. (1994). Bioactive secretions of the amphibian integument. *In* “Amphibian Biology, Vol. 1, The Integument” (H. Heatwole and G. T. Barthalmus, Eds.), pp. 178–350. Surrey Beatty & Sons, Chipping Norton, NSW.

Greene, H. W. (1988). Antipredator mechanisms in reptiles. *In* “Biology of the Reptilia, Vol. 16, Ecology B. Defense and Life History” (C. Gans and R. B. Huey, Eds.), pp. 1–152. Alan R. Liss, Inc., New York.

Pough, F. H. (1988). Mimicry and related phenomenona. *In* “Biology of the Reptilia, Vol. 16, Ecology B. Defense and Life History” (C. Gans and R. B. Huey, Eds.), pp. 153–234. Alan R. Liss, Inc., New York.

REFERENCES

General: Schall and Pianka, 1980; Stebbins and Cohen, 1995.

Predator Avoidance: Escaping Detection: Brodie et al., 1974; Endler, 1978; Greene, 1988; Morey, 1990.

Escaping or Misdirecting Identification: Autumn and Han, 1989; Brodie, 1968, 1993; Brodie and Brodie, 1980; Brodie and Janzen, 1995; Greene, 1988; Greene and McDiarmid, 1981; Howard and Brodie, 1973; Huey and Pianka, 1981b; Pough, 1988; Sazima and Abe, 1991; Sherbrooke and Montanucci, 1988; Smith, 1975, 1977; Tilley et al., 1982; Vitt, 1992b.

Escaping Approach: Duellman and Trueb, 1986; Greene, 1997; Rossman and Williams, 1966; Vitt and Zani, 1996b.

Escaping Subjugation and Capture: Arnold, 1982; Arnold, 1984, 1988; Bauer et al., 1989; Blouin, 1990; Branch, 1983; Britson, 1998; Britson and Gutzke, 1993; Bustard, 1967; Caldwell, 1982, 1989, 1996a, 1997; Caldwell and Vitt, 1999; Clark, 1971; Congdon et al., 1974; Cooper and Vitt, 1985, 1991; Daly, 1998; Daly et al., 1987; Daniels, 1983; Dial, 1981; Dial and Fitzpatrick, 1981, 1983; Duellman and Trueb, 1986; Erspamer, 1994; Evans and Brodie, 1994; Fox and Rostker, 1982; Fox et al., 1990; Greene, 1988; Kats et al., 1988; Maiorana, 1977; Martin and Salvador, 1993; Middendorf and Sherbrooke, 1992; Niewiarowski et al., 1997; Petranka et al., 1987; Rose, 1962; Rosenberg and Russell, 1980; Salvador et al., 1996; Schoener, 1979; Schoener and Schoener, 1982; Shine, 1980b; Toft, 1995; Vaz-Ferreira and Gehrau, 1975; Vences et al., 1997/1998; Vitt and Cooper, 1986a,b; Vitt et al., 1977; Wake and Dresner, 1967; Wassersug, 1971; Wassersug et al., 1981; Watkins et al., 1969; Weldon, 1990; Wells and Bard, 1988.

Life History Responses to Predation: Caldwell, 1993.

Offsetting the Effects of Parasitism: Arnold, 1986; Ayala, 1977; Bauer et al., 1990, 1993. Bull and Burzacott, 1993; Burns et al., 1996; Christian and Bedford, 1995; Monagas and Gatten, 1983; Ortega et al., 1991; Schall, 1983, 1992; Tinsley, 1990; Vaughn et al., 1974; Winter et al., 1986.

Part V

POPULATION AND COMMUNITY ECOLOGY

But you should not be deceived into believing that
ecology is founded on exact quantitative laws that
serve to predict events with the same authority as the
equations of, say, physics or physical chemistry. An
ecosystem is vastly more complex than a gas-filled
balloon or a flask of reagents. Proceed cautiously. . . .
E. O. Wilson and W. H. Bossert, 1971

In natural environments, interbreeding individuals compose populations, and interacting populations of many species compose communities. Both populations and communities have characteristics unique to them. Populations have age structure, age-specific survivorships, and replacement rates. Communities contain interacting populations of many species that compete for limited resources and prey on, or are preyed upon by, other members of the community. Competition and predation are generally thought of as community processes (although intraspecific competition and predation also occur). Unlike most physical phenomena, population- and community-level phenomena are extremely complex, so much so that only portions of population or community phenomena are studied by most ecologists. For example, ecologists interested in competition might design experiments to determine the effects of density on competition between several species of amphibian larvae or conduct transplant experiments with *Anolis* lizards to determine the effects of island size and species composition on colonization ability. One reason that populations and communities are so complex is that they are affected by every biotic and abiotic variable in their environment. Moreover, communities comprise animal and plant species that have evolutionary histories that are independent to varying and often unknown degrees.

Recent advances in ecological theory have provided models designed to explain some of the population- and community-level events observed in natural systems. Reptiles and amphibians have played critical roles in the development and testing of ecological models. Populations of lizards and larval frogs and salamanders, in particular, are extremely amenable to experimental manipulations. Complex, and sometimes surprising, population- and community-level responses to species interactions have been identified in studies with amphibians and reptiles. Nevertheless, these areas remain relatively unexplored.

Chapter

12

Population Structure and Dynamics

A population is typically defined as a group of interbreeding individuals of the same species living in the same area. Each individual is potentially able to mate with any other individual of the opposite sex. Consequently, each population represents a single gene pool, and all individuals share a recent common ancestry. Although the potential for interbreeding is seldom, if ever, realized within a single generation, complete mixing of genes (panmixis) may occur over generations in small, localized populations. Asexually reproducing organisms (e.g., parthenogenetic *Cnemidophorus*) do not fit this definition because each individual is reproductively isolated from all others. Nevertheless, they experience many of the same population phenomena as sexually reproducing species.

Populations can be variously delimited. All box turtles (*Terrapene carolina*) in eastern North America, hellbenders (*Cryptobranchus alleganiensis*) in the Ozark River drainage, or black toads (*Bufo exsul*) in Deep Springs Valley represent populations. Although each is a biological population, the local population (= deme) is usually the unit of interest to biologists. The local population responds to local conditions: growing, shrinking, evolving, or even disappearing (extinction). Each local population is semi-isolated from other similar populations by minor or major habitat discontinuities, but few are totally isolated (closed) and most receive occasional immigrants from nearby or distant populations and lose members via emigration.

CHARACTERISTICS OF POPULATIONS

Even though each population can be viewed as a single entity that experiences birth, juvenile and mature phases, and eventually death, such a view oversimplifies the complexities of a population's history and persistence. The characteristics and stability of a population derive from the lives and deaths of its members. Each population has a size, an age distribution, a sex ratio, birth and death rates, and a gene frequency. These population traits and others vary temporally within a population as well as among populations of the same species in response to local environmental (abiotic and biotic) conditions. The variability of responses arises from fluctuations in environmental conditions, the initial state of a population when experiencing the changing conditions, and the life history characteristics of the species.

A snapshot of the structure of a population is provided by a life table (an actuary table or survivorship/mortality schedule). A life table gives an age-specific summary of the fate of a cohort, which is a group of organisms all hatched or born during the same time interval. The life table is based on data on births and deaths of members of the cohort from the time of deposition of eggs or birth until death of all cohort members (Table 12.1A). Life table data are presented as the actual number (n_x) of individuals observed or transformed to a standard cohort size of 100 or 1000 individuals or to decimal proportions (l_x). Often the life table is expanded to include the population's fecundity schedule to provide an age-specific summary of reproductive productivity ($l_x m_x$; Table 12.1B,C,D).

Life tables provide a summary of a population's current state and may suggest whether the population is likely to persist. Life tables also permit intra- and interspecific comparisons of populations. Primary components of life tables are the average age of sexual maturity (i.e., age at which individuals first begin to reproduce) and age-specific mortality and fecundity. A number of other measures of a population's state can

TABLE 12.1 Life Tables and Fecundity Schedules[a]

A. Life table for a French population of wall lizards, *Podarcis muralis*.

Age,	Survivors		Mortality		Life expectancy
x	n_x	l_x	d_x	q_x	e_x
0–1	570	1.000	376	0.66	1.01
1–2	194	0.340	146	0.75	0.99
2–3	48	0.084	23	0.48	1.48
3–4	25	0.044	13	0.52	1.36
4–5	12	0.021	*6*	*0.50*	*1.31*
5–6	*6*	*0.011*	*3*	*0.50*	*1.05*
6–7	*3*	*0.005*	*2*	*0.50*	*0.70*
7–8	*1*	*0.002*	*1*	*1.00*	

Source: Data from Barbault and Mou (1988).

Note: Italicized values are hypothetical, assuming constant q_x for adults.

B. Survivorship and fecundity schedule for a South Carolina population of female slider turtles, *Trachemys scripta*.

x	l_x	m_x	$l_x m_x$	q_x	
0	1.000	0.00	0.000	0.89	
1	0.105	0.00	0.000	0.46	
2	0.057	0.00	0.000	0.17	
.					
6	0.026	0.00	0.000	0.186	
7	0.021	1.28	0.027	0.186	
.					
10	0.011	1.28	0.014	0.186	
.					
15	0.044	1.28	0.005	0.186	
.					
20	0.001	1.28	0.002	0.186	
.					
22	<0.001	—	—	—	$R_o = 0.137$

Source: Data from Frazer et al. (1990).

C. Survivorship and fecundity schedule for a North Carolina population of Appalachian dusky salamanders, *Desmognathus ocoee* (formerly *ochrophaeus*).

x	l_x	m_x	$l_x m_x$	
0	1.000	0.0	0.000	
.				
4	0.087	4.5	0.392	
5	0.055	4.5	0.248	
6	0.034	4.5	0.153	
.				
8	0.013	4.5	0.058	
.				
10	0.005	4.5	0.022	
.				
12	0.002	4.5	0.009	$R_0 = 1.026$

Source: Data from Tilley (1980).

D. Survivorship and fecundity schedule for a Utah population of female western yellow-bellied racers, *Coluber constrictor*.

x	l_x	m_x	$l_x m_x$	
0	1.000	0.0	0.000	
1	0.170	0.0	0.000	
2	0.125	0.2	0.023	
3	0.102	1.8	0.188	
4	0.078	1.8	0.178	
5	0.068	2.4	0.160	
.				
10	0.010	2.7	0.055	
.				
15	0.006	2.9	0.017	$R_0 = 1.187$

Source: Data from Brown and Parker (1984).

[a] Abbreviations and explanations for tables A–D are x, age interval (years); n_x, actual number of members alive at beginning of age interval; l_x, proportion of cohort alive at beginning of interval; d_x, number of cohort members dying during age interval; q_x, age-specific death rate (proportion of individuals dying during interval that were alive at beginning of interval); e_x, average life (years) expectancy for members alive at beginning of interval; m_x, age-specific fecundity rate (average number of offspring produced by surviving cohort during each interval); $l_x m_x$, total fecundity of surviving cohort members in each interval; and R_o, net reproductive rate (average lifetime fecundity for each cohort member).

be derived from these data, including mean generation time (T), net reproductive rate (R_0, also called the replacement rate), reproductive value (v_x), intrinsic rate of natural increase (r), and others. R_0 is especially informative; it ranges between 0 and ≈ 10 for vertebrates. A value of 1.0 indicates that the population is stable (births = deaths). Declining populations have $R_0 < 1.0$ and increasing populations have $R_0 > 1.0$.

Survivorship (l_x) and mortality (d_x and q_x) are different aspects of the same population phenomenon, the rate of mortality of a cohort. Survivorship (l_x) maps the cohort's decline from its first appearance to the death of its last member. Age-specific mortality (q_x) records the probability of death for the surviving cohort members during each time interval. The pattern of a cohort decline is often shown by plotting survivorship against time. Four hypothetical survivorship curves represent the extremes and medians of possible survivorship patterns (Fig. 12.1). In Type I (rectangular convex curve), survivorship is high (i.e., early mortality low, $q_x < 0.01$) through juvenile and adult life, and then all cohort members die nearly simultaneously ($q_x = 1.0$). Type III is the opposite pattern (rectangular concave curve) where mortality is extremely high ($q_x > 0.9$) in the early life stages and then abruptly reverses to almost no mortality ($q_x < 0.01$) for the remainder of the cohort existence. The Type II patterns occupy the middle ground, either with a constant number of deaths (d_x) or a constant death rate (q_x). In Type II patterns with a constant death rate (q_x), survivorship declines more rapidly because the actual number of deaths at any time is based on a percentage of the remaining population. Although these idealized patterns are never matched precisely by natural populations, the patterns offer a convenient descriptive shorthand for comparing population data.

Most amphibians with indirect development, crocodylians, and turtles have Type III survivorship. Amphibian eggs and larvae commonly experience high predation. Increased size resulting from growth may temporarily render older larvae less subject to predation by aquatic predators, but predation is again high during metamorphosis and early terrestrial life. For those species that breed in temporary ponds, death of entire cohorts is a regular threat because ponds may dry prior to metamorphosis. Many turtle populations suffer high nest predation; freshwater species and seaturtles often have 80–90% of their nests destroyed within a day or two of egg deposition. The majority of the remaining amphibians and reptiles have Type II-like patterns with moderate and fluctuating mortality during early life and then a moderate to low and constant death rate during late juvenile and adult life stages (Fig. 12.2). Weather (e.g., too wet or too dry) appears to be the major cause of juvenile mortality in many Type II species. No amphibian or reptile attains a close match to a Type I survivorship. Among reptiles, *Xantusia vigilis* approaches this pattern (Fig. 12.2). Species with parental care may have an initial low mortality, but even crocodylians cease parental care well before their offspring are fully predator- and weatherproof.

Populations do not have fixed survivorship patterns. Annual patterns are most similar in populations with a nearly constant age structure, but even these populations can shift from one pattern to another due to a catastrophic event or an exceptional year of light or heavy mortality. Males and females in the same cohort may have different survivorship curves, and if the difference is great, the resulting population will have an unequal sex ratio.

Natality and fecundity are used interchangeably and denote the number of eggs or neonates produced per individual (female and male) in the population; however,

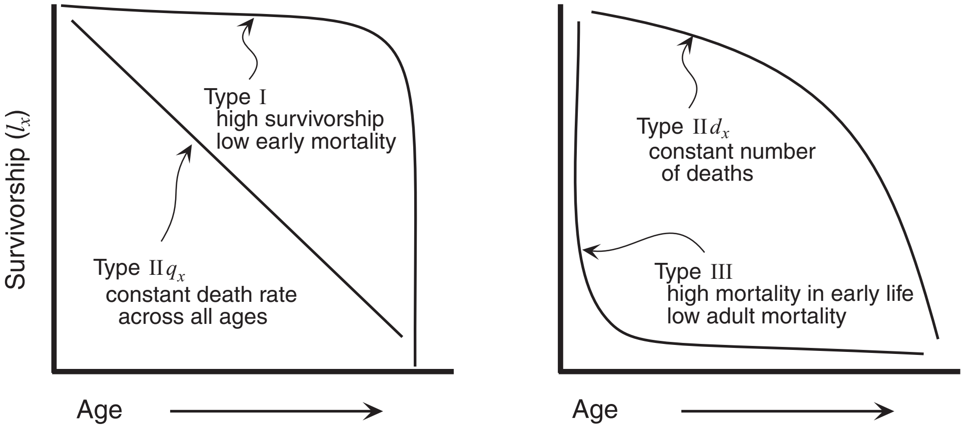


FIGURE 12.1 Hypothetical survivorship curves for animal populations (see text).

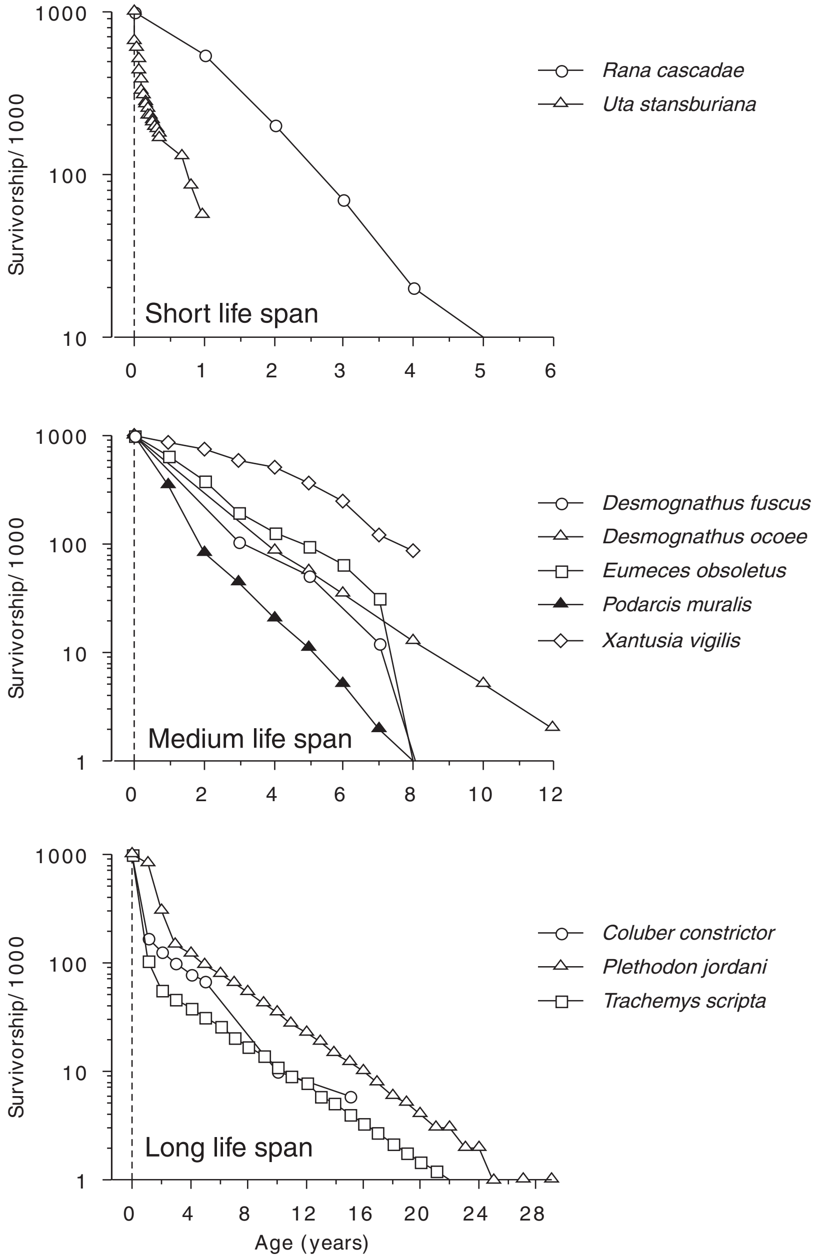


FIGURE 12.2 Representative survivorship curves for amphibians and reptiles. Data for amphibians are *Df*, Danstedt (1975); *Do*, Tilley (1980); *Pj*, Hairston (1983); and *Rc*, Briggs and Storm (1970). Data for reptiles are *Cc*, Brown and Parker (1984); *Eo*, Hall and Fitch (1972); *Ts*, Frazer et al. (1990); *Us*, Tinkle (1967); and *Xv*, Zwiefel and Lowe (1966).

most fecundity schedules are for females only and the cohort's average output is halved. Average clutch and litter sizes range from 1 to 50,000+ in amphibians and reptiles, but these values are not an accurate measure of a cohort's realized fecundity. First, these reproductive outputs are without reference to time. Fecundity addresses output in a specific time domain: average offspring production per cohort member per unit time (typically years, but weeks or months may be the appropriate interval for short-lived species). The reproductive output of a cohort must be adjusted to account for clutch size, the frequency of clutch production, and the number of members reproducing in each age interval. For example, many lizard populations produce multiple clutches each year, although the number of clutches differs among different age classes. Second, clutch size is often a function of body size. Among species and within species with variable clutch size, the number of eggs increases with female size (= age). Third, clutch size can differ seasonally owing to differential availability of energy resources in the production of their first, second, and subsequent clutches. The resulting fecundity value must account for these variables and estimate offspring production for each time interval. Such data are not easily or quickly gathered, and, even in the best field studies, fecundity values may rest on untested assumptions. The difference between a species' average clutch size and its fecundity is typically great, for example, 6.25 versus 1.28 eggs, respectively, in *Trachemys scripta* (Table 12.1; Frazer et al., 1990). Also, since fecundity may increase or decrease with time (Table 12.1, *Coluber constrictor*; Brown and Parker, 1984), a population's age-specific realized fecundity ($l_x m_x$) potentially can increase, although it seldom does because survivorship (l_x) usually declines at a faster rate than fecundity (m_x) increases.

The estimates of age-specific realized fecundity are useful demographic parameters that permit ecologists to predict a population's future (R_o) and assess its mean generation time (T). As noted earlier, R_o, or net reproductive rate, shows whether population size is increasing or decreasing; R_o is the sum of age-specific realized fecundities ($l_x m_x$). Mean generation time is also calculated from the $l_x m_x$ values and denotes the average age of parenthood for the population. T is never less than the age of sexual maturity, but it nearly equals maturity in short-lived species and shifts upward in long-lived species, especially those species with high adult survivorship and increasing fecundity (m_x).

Age of sexual maturity marks the point in the life history at which individuals begin to reproduce. Depending upon the shape of the survivorship curve, many or few of the initial cohort remain to reproduce. Only in Type I populations is a major portion of the original cohort available for reproduction. In the other patterns, less than 1/10 of the original cohort typically survives to reproduce in amphibians and reptiles (Table 12.1 and Fig. 12.2). Rapid attainment of sexual maturity usually results in small body size at sexual maturity. Because smaller females produce smaller clutches, rapid maturity has an associated fecundity cost. Rapid attainment of sexual maturity may allow escape from high mortality of certain life history stages (e.g., amphibian larvae).

POPULATION STRUCTURE AND GROWTH

Demography is the study of age structures and growth rates among populations. Age of maturity (and its corollary, longevity), survivorship, and fecundity are the principal determinants of population size, structure, and growth.

Size, Abundance, and Density

Of all population parameters, population size is the simplest to measure, although counting all individuals in a population is not an easy task. The abundance or number of individuals in a population imparts little information without reference to the delineation of a population. A nesting population of 500 Kemp's ridley seaturtles compared to 250 green seaturtles indicates that the ridley population is larger than the green population, until the reader realizes that the 500 turtles represent the total adult female ridley population whereas the 250 green seaturtles represent the number of females present one night on one of a thousand nesting beaches. In addition to defining the population censused, most comparisons convert abundance to density, the number of individuals per square *unit of space*. Density values need not be restricted to areal units and may be more meaningful if given as number of *Rana* per linear meter of shoreline or *Anolis* per tree. The goal is to have a density value that provides an immediate impression of the rarity or commonness of animals and is biologically meaningful in comparison with other populations. The simplicity and convenience of areal values promote the regular use of these density values. Comparisons cannot be easily made between one-dimensional (shoreline), two-dimensional (forest floor), and three-dimensional (canopy) estimates of population density.

Contrasts in density of populations are often striking (Table 12.2). Explanations and determinants of density variation are not always apparent or rigorously tested. Densities typically reflect the relative availability of resources but are also influenced by climatic events or levels of predation. The presence of abundant food and shelter and low predation permit high densities in many populations. That 27,200 red-backed salamanders (*Plethodon cinereus*) per hectare occur in a New England forest is particularly impressive, even more so considering that the combined biomass of this and three other salamander species exceeds the combined total biomass for birds and mammals in this forest (Burton and Likens, 1975). High densities of resident populations are not uncommon for small amphibians and reptiles (Table 12.2), and where comparative data are available, reduced predation often appears to be a major factor. For example, anole populations are commonly two to four times larger on islands of the West Indies than on the Central American mainland. Competition for food, especially with insect-eating birds, may be less intense on islands; however, the number of anole species increases

TABLE 12.2 Population Densities of Some Amphibians and Reptiles

Taxon	Density	Body size	Habit/habitat
Bolitoglossa subpalmata	4,790	42	Terrestrial/trop. forest
Plethodon glutinosus	8,135	63	Terrestrial/tem. forest
Arthroleptis poecilonotus	325	20	Semiaquatic/trop. savanna
Bufo marinus	160	90	Terrestrial/trop. scrub
Eleutherodactylus coqui	100	36	Terrestrial/trop. forest
Eleutherodactylus coqui	23,000	36	Terrestrial/trop. forest
Geochelone gigantea	27	400	Terrestrial/trop. scrub
Sternotherus odoratus	194	66	Aquatic/tem. lake & river
Apalone muticus	1,267	210	Aquatic/tem. lake & river
Alligator mississippiensis	0.2	1830[a]	Semiaquatic/tem. marsh
Lacerta vivipara	784	56	Terrestrial/tem. forest
Mabuya buettneri	17	78	Arboreal/trop. savanna
Uromastyx acanthinurus	0.15	110	Terrestrial/subtrop. desert
Varanus komodoensis	0.09	1470	Terrestrial/trop. scrub
Xantusia riversiana	3,200	70	Terrestrial/tem. scrub
Agkistrodon contortrix	9	540	Terrestrial/tem. savanna
Coluber constrictor	0.3	630	Terrestrial/tem. scrub
Enhydrina schistosa	0.9	730	Aquatic/trop. tidal river
Opheodrys aestivus	429	360	Arboreal/tem. forest
Regina alleni	1,289	400	Aquatic/subtrop. marsh

Sources: For salamanders, Bs (Vial, 1968) and Pg (Semlitsch, 1980). For frogs, Ap (Barbault and Rodrigues, 1979); Bm (Zug and Zug, 1979); and Ec (Stewart and Pough, 1983). For turtles, Gg (Bourn and Coe, 1978); So (Mitchell, 1988); and Tm (Plummer, 1977a). For crocodylians, Aa (Turner, 1977). For lizards, Lv (Pilorge, 1987); Vk (Auffenberg, 1978); and Xr (Fellers and Drost, 1991). For snakes, Ac (Fitch, 1960); Cc (Brown and Parker, 1984); Es (Voris, 1985); Oa (Plummer, 1985); and Ra (Godley, 1980).

[a] Total length.

Note: Density is the mean number of individuals per hectare; body size is length (SVL—CL for turtles—in millimeters) of adult females. Trop., tropical; tem., temperate.

with the size of islands, contributing to overall high densities of anoles. High densities of anoles on islands (> 1000 individuals ha^{-1}) are possible because, like other ectotherms, they have relatively low energy demands. High densities (large populations) reduce the likelihood of population extinction by environmental stochasticity (Schoener and Schoener, 1980). High densities may also be a response to the patchy distribution of resources. Limited breeding areas may be a common concentrating factor as well. Densities of breeding anurans commonly exceed 500 frogs per hectare in temperate and tropical areas (Table 12.2). Such high densities and competition for reproductive space are not limited to small-bodied species. Before heavy human predation, many seaturtle and *Podocnemis* populations experienced high levels of nest destruction by nesting females digging up the eggs of earlier-nesting females. High densities also arise from environmental fluctuations, such as the seasonal concentration of caimans and sideneck turtles in the drying pools of the Venezuelan llanos or single- and mixed-species aggregations of snakes in hibernacula.

Crocodylian and giant tortoise populations may also be dense (Table 12.2). In these taxa, which are physiologically long-lived and free of predators once they reach adult size, the relatively low energy needs combined with longevity over several decades produce large populations of adults. Not all crocodylian populations are dense, and the density of other large reptilian predators may be one to two individuals per hectare or less, depending upon the availability of resources—both food and space. Adult *Alligator mississippiensis* or *Crocodylus porosus* do not tolerate other adults or large juveniles within their territories and prey upon the smaller individuals. Density regulation due to territoriality limiting availability of space occurs in a variety of amphibians (*Atelopus varius, Rana virgatipes*) and reptiles (*Sceloporus undulatus*) of various sizes (Crump, 1986; Given, 1988; Ferguson et al., 1983).

Because densities reflect the availability of resources and the intensity of predation, population densities can show considerable fluctuation from year to year and site to site. The density of a Puerto Rican frog, *Eleutherodactylus coqui*, was nearly doubled by experimentally adding nest boxes. Populations of newts, *Notophthalmus viridescens*, differed nearly 100-fold in adjacent forest pools, apparently as a result of lower food availability and higher parasite densities in some pools. Density of an Australian gecko, *Oedura monilis*, varied ninefold in the same forest; local density was dependent upon the availability of loose bark for shelter. Densities of *Anolis limifrons* in Panama varied from 0 to more than 150 in 890 m^2 plots during a 22-year period (Fig. 12.3). The length of the dry season and the relative amount of rain during the wet season appear to determine anole population

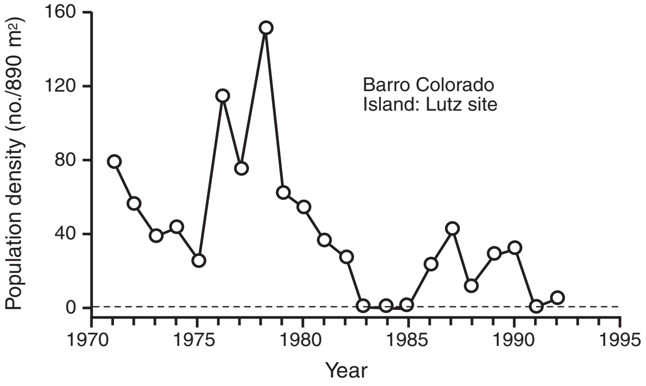


FIGURE 12.3 Annual variation in population density of *Anolis limifrons* on Barro Colorado Island. Adapted from Andrews and Wright (1994).

density. Short dry seasons (during which little breeding takes place) increases the time available for breeding (wet season) and results in more clutches produced by anoles. If the wet season is too wet, egg mortality is higher, negatively influencing population density (Andrews and Wright, 1994).

Similar variation in population size can occur in long-lived reptiles. During a 7-year period, the population size of the Australian skink *Tiliqua rugosa* increased by more than 50% (Fig. 12.4). Adult survival fluctuated considerably during the same time period but was nearly identical at the end of the 7-year period as at the beginning (Fig. 12.4). In a tropical savanna of Africa, frog abundance increased just after the end of the wet season, as did one lizard species (Fig. 12.5). Abundance of another lizard species decreased following the rainy season. Interpreting changes in relative and absolute abundances of amphibians and reptiles is complicated by the interactions between climatic factors, resource availabilities, and species interactions.

Age Distribution

Life tables chart the size of each age class of a cohort through the life of the cohort. Age distribution analysis examines the size of each age class within a population at a single moment in time (Fig. 12.6). Age-class size can be either the actual number of individuals in the class or the proportion of the total population. The age distribution pattern for a population may be stable through time if its survivorship (l_x) and fecundity (m_x) schedules remain constant. In a stable age distribution, the proportion of individuals in each class remains constant. Some salamander populations, such as plethodontids in a climax Appalachian forest, appear to have nearly stable age distributions. Annual population loss through mortality, emigration, and aging in each age class is matched by recruitment through aging and immigration. Equilibrium population size in these salamanders derives from a longevity greater than 10 years, a stable environment, low predation, and occupation of all suitable habitat by adults.

A stable or predictable environment, adequate resources, and low predation are requirements for the appearance of stable age distributions in all amphibian and reptilian populations. For most populations, climate, resource availability, and predation differ widely each year, causing survivorship and fecundity to vary from season to season and from year to year. Changing age structures are most visible in annual populations, in which a new generation is present each year. Small species of lizards and frogs in seasonally cyclic climates typically have annual populations. Juveniles hatch and

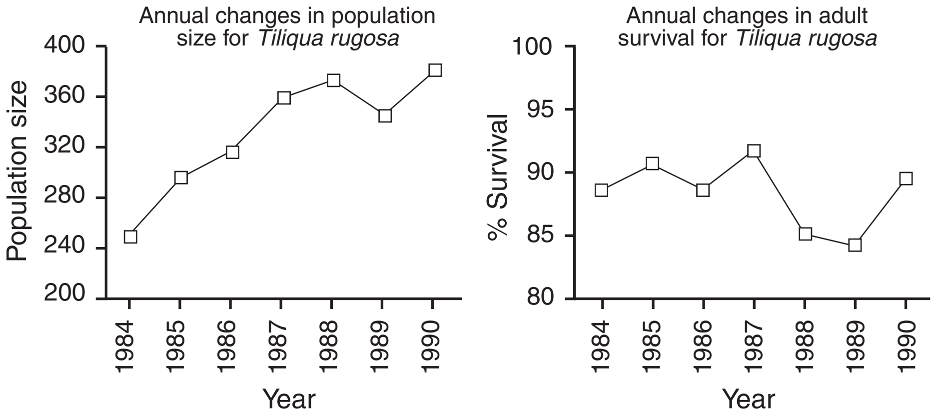


FIGURE 12.4 Yearly variation in population density and adult survivorship of *Tiliqua rugosa*. Adapted from Bull (1994).

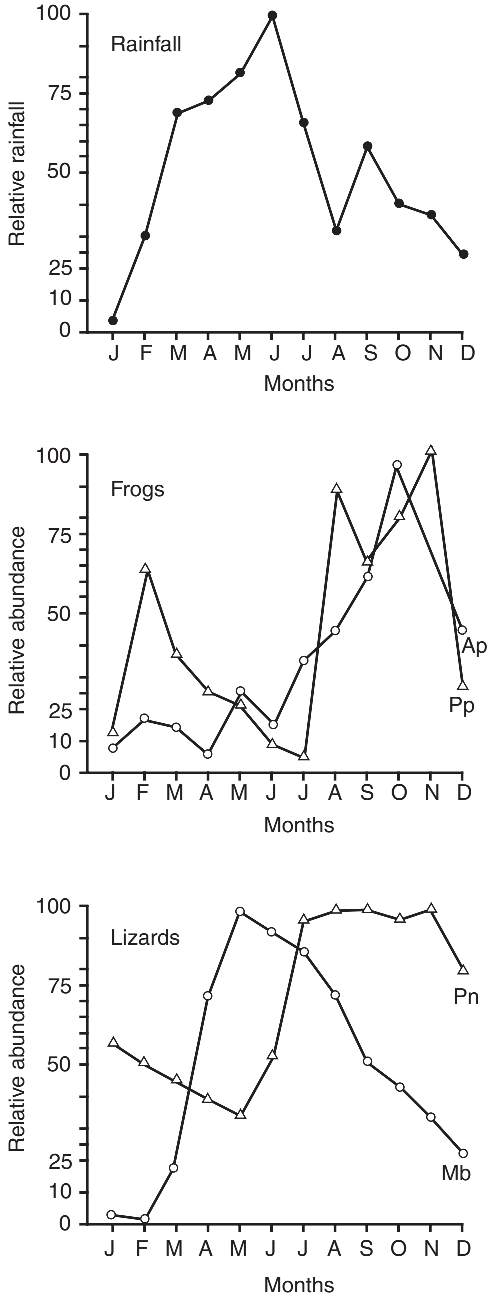


FIGURE 12.5 Seasonal fluctuations in abundance of frogs (*Arthroleptis poecilonotus, Phrynobatrachus plicatus*) and lizards (*Mabuya buettneri, Panaspis nimbaensis*) living in a highly seasonal tropical environment (savanna in Lamto, Ivory Coast). Relative rainfall and abundances are scaled to the highest monthly average rainfall and densities. Data from Barbault (1972, 1975, 1976a) and Barbault and Rodrigues (1978, 1979).

grow during an equable season, have slow or no growth during a harsh season (dry or cold), and reach sexual maturity at the beginning of the next equable season. Adults mate and lay eggs during what is likely to be their only reproductive season. These adults usually deposit several clutches and invest the maximum possible amount of energy in reproduction. Although a few individuals may survive until the next breeding period, most do not. Thus, at any instant, the age structure of an annual population is uniform, that is, all members have identical ages (usually within 4–8 weeks of one another), and the age of the population matches the age of the cohort (Fig. 12.6; Tinkle, 1967).

Another aspect of age distribution is the sex ratio, which is the proportion of males to females in the population. An equal sex ratio is 1:1 or 0.5. The sex ratio is a critical demographic feature, because it directly affects the growth potential of a population ($\geq l_x m_x / R_o$): more females in the population result in production of more offspring. For bisexual diploid species, the primary sex ratio (number of males:females at fertilization) is 1:1, because the heterogametic parents produce equal numbers of male and female gametes. Sex ratios for species with other reproductive modes (e.g., unisexual, polyploidy) deviate from 1:1 because of altered gametogenic and fertilization mechanisms that produce unequal numbers of female and male gametes. Differential gamete mortality or fertilization may produce a skewed sex ratio in bisexual species.

Determination of primary sex ratios requires karyotypic examination of early zygotes, a technique that has not been established directly in amphibians and reptiles. Estimates are derived from secondary sex ratios at birth or hatching, and even these data are difficult to obtain because of the absence of external secondary sex characteristics in most species. In the majority of bisexual species, with the exception of reptiles with temperature-dependent sex determination, the secondary sex ratios approximate 1:1.

Although many populations have 1:1 sex ratios, unequal sex ratios are regularly reported for adult populations of amphibians and reptiles. Assuming equality for primary and secondary sex ratios, unequal adult sex ratios require differential mortality during the juvenile stage or differential survivorship of adult males and females. The inequality variously favors males or females. Only in lizards (based on a small sample) is a trend evident, and it shows a higher mortality among males. For other reptiles and amphibians, roughly equal numbers of species or populations have female-dominated ratios and male-dominated ratios. In some populations, the inequality has shifted from one sex to the other in successive years. The apparent lack of trends and annual shifts in sex ratios suggests that many of the reported inequalities are more apparent than real, reflecting the difficulties of accurately censusing amphibian and reptilian populations and not the actual numbers of females and males in these populations.

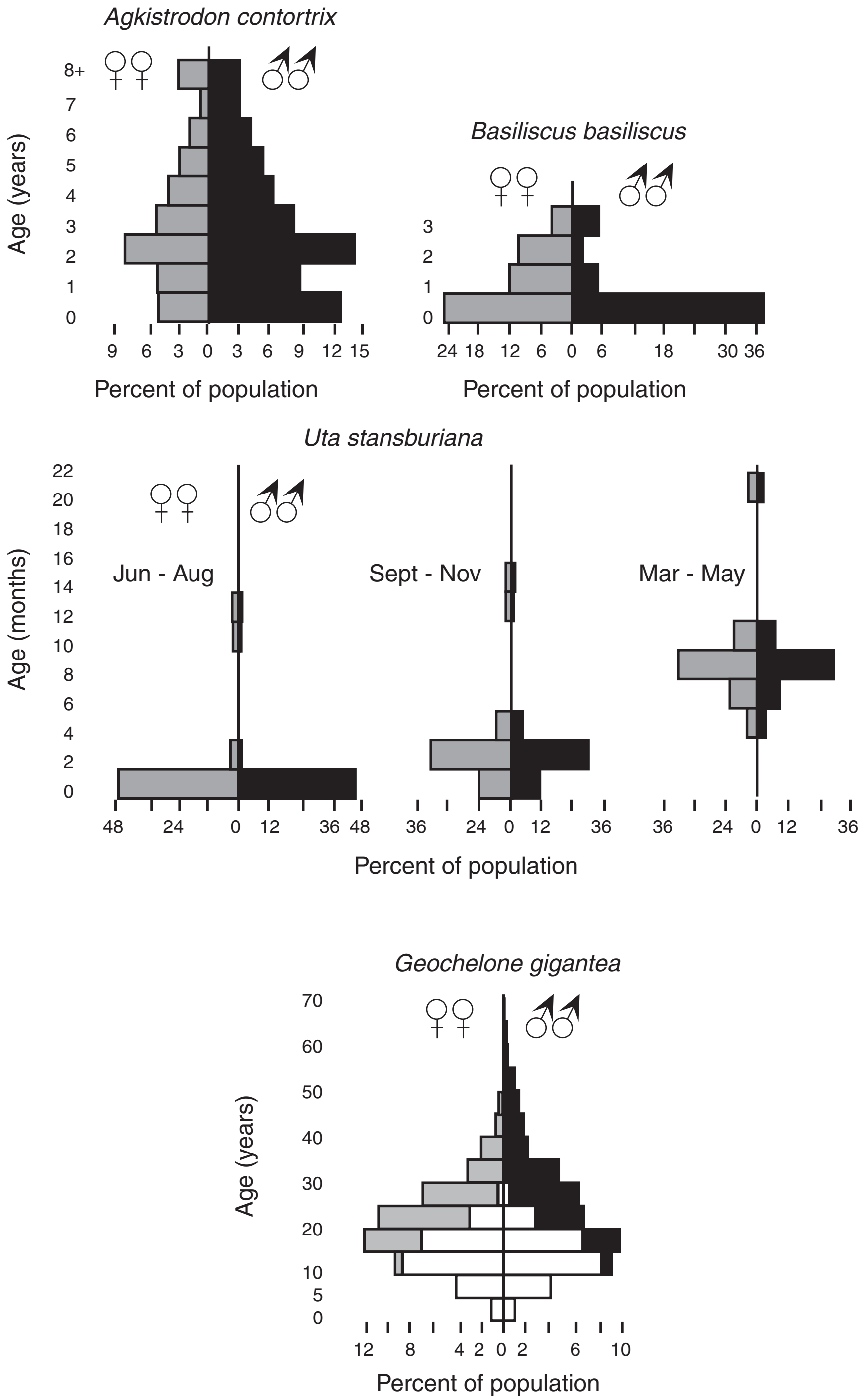


FIGURE 12.6 Age distribution patterns of some amphibian and reptile populations: seasonal patterns for an annual lizard, *Uta stansburiana* (Tinkle, 1967), and point-in-time patterns for a moderate-lived snake, *Agkistrodon contortrix* (Vial et al., 1977), a short-lived lizard, *Basiliscus basiliscus* (Van Devender, 1982), and a long-lived tortoise, *Geochelone gigantea* (Bourn and Coe, 1978). The bars denote the percentage (of total population) of males or females present in each age class: open bars, unsexed individuals; stippled bars, females; and solid bars, males.

Population Growth

Population growth may be positive or negative, resulting in increasing or decreasing population sizes, respectively. Few, if any, amphibian and reptilian populations are stable (at equilibrium), with size remaining constant from year to year. Short-lived species, such as many small-bodied anuran and lizard species, have mean generation times (T) of 1 year or less, and their population sizes change monthly (Fig. 12.5). Population size in these semiannual and annual species is highest at the end of the reproductive season when eggs hatch and juveniles enter the population; the number of individuals slowly declines until the next reproductive season. As average longevity or generation time increases, stability of population size increases, particularly in the adult segment of populations that have reached the carrying capacity of their habitat. This is possible because amphibians and reptiles commonly have Type III survivorship curves. In long-lived species, annual survivorship of adults is high and recruitment of new individuals into the population is low, but balances adult mortality (but see Fig. 12.4).

Population growth is the change in number (N) of individuals per unit time (dN/dt) and is the balance between the population's recruitment and loss of members. Recruitment occurs through hatching or birth and immigration, and loss occurs because of death and emigration. Two models or equations are relevant to the examination of population growth: the exponential equation, $dN/dt = rN$, and the logistic equation, $dN/dt = rN(K - N/K)$. Both are oversimplifications of the factors affecting population growth, but both contain parameters (r and K) that offer insights into, and permit comparison of, the dynamics of different populations (Pianka, 1970). The intrinsic rate of increase (r) measures the balance between recruitment and loss and is approximated by the relationship of net reproductive rate to mean generation time ($\ln R_0/T$). When $r > 0$, the population is increasing, and when $r < 0$, the population is decreasing. Since a population can increase or decrease exponentially for only a brief period of time without becoming unrealistically large or going extinct, the logistic equation better matches the growth of most biological populations. In these population growth models, K represents the carrying capacity, or resource limits, of the environment. When population size (N) exceeds the carrying capacity (K), the population will decrease, and when $N < K$, the population increases; thus, K represents an equilibrium population size (Fig. 12.7).

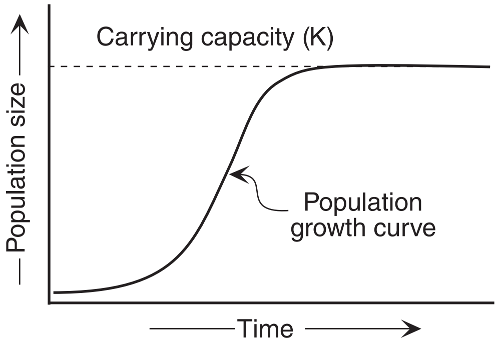


FIGURE 12.7 Diagrammatic representation of population growth as it approaches the carrying capacity of the environment (K) and after it has reached K. The shape of the population growth curve depends on the intrinsic rate of increase (r).

K and r do not remain constant for a population of organisms. They are simply estimates of resource availability of the environment and the population's growth rate during the period of study. K and r vary seasonally or yearly as abiotic and biotic factors impinge on individuals and population sizes change. The relative values of r and K and their ranges of variation reflect a species' reproductive potential, adult body size, longevity, type and pattern of resource use, and other life history aspects. Although K is easy to understand conceptually, it can be difficult to measure. Carrying capacity for a population depends not only on the absolute amount of the critical resource, but also on the degree to which other species (competitors) use the resource and the risk (e.g., predation) to acquire it. Species are often categorized as either r- or K-selected "strategists" (Table 12.3) because two contrasting sets of life history traits appear to be at least superficially associated with a species' position relative to K. No "strategy" (in a planning sense) by individuals, populations, or species is involved. Small-bodied, short-lived species generally have high population turnover and high r. Large-bodied, long-lived species generally have large adult populations and low r. The underlying logic is that in environments where resources are unlimited (i.e., the population density is low with respect to K), the production of many small offspring will maximize r, and thus females producing many, small young will be at a selective advantage. In resource-limited environments (i.e., the population is at K), larger offspring will be better able to compete for the limited resources. Thus, females that produce fewer, larger offspring will be at a selective advantage. Viewing species as r- or K-selected entities oversimplifies the evolution of life history characteristics, partially because alternative strategies such as "bet hedging" produce the same sets of life history traits predicted by r- and K-selection when adult mortality is variable but opposite predictions when juvenile mortality is variable (Stearns, 1976, 1977). When juvenile mortality is variable and the environment is stable (i.e., predictable), early maturity, greater

TABLE 12.3 Demographic and Life History Traits Associated with r-and K-Type Populations of Amphibians and Reptiles

Attributes	r-type	K-type
Population size (density)	Seasonally variable; highest after breeding season, lowest at beginning of breeding season	High to low, but relatively stable from year to year
Age structure	Seasonally and annually variable; most numerous in younger classes, least in adults; usually ≤ 3 year classes	Adult age classes relatively stable; most numerous in adult classes; multiple year classes
Sex ratio	Variable, often balanced	Variable, often balanced
Survivorship	Almost always Type III	Types II and III
Mean generation time	Equivalent to age of sexual maturity	Often exceeds age of sexual maturity
Population turnover	Usually annual, rarely beyond 2 years	Variable, often >1.5 times age of sexual maturity to decades
Age of sexual maturity	Usually ≤ 2 years	Usually ≥ 4 years
Longevity	Rarely ≥ 4 years	Commonly >8 years
Body size	Small, relative to taxonomic group	Small to large
Clutch size	Moderate to large	Small to large
Clutch frequency	Usually single breeding season, often multiple times within season	Multiple breeding seasons, usually once each year
Annual reproductive effort	High	Low to moderate

Source: In part from Pianka (1970).

number of offspring, and fewer reproductive events will be at a selective advantage. However, when the environment is fluctuating, late maturity with fewer offspring spread over a longer time interval provides a selective advantage. Females hedge their bets by producing offspring a number of times over a long time interval, gambling that some will survive to reproduce. Females that invest all of their reproductive efforts into a single episode are much more likely to lose their entire investment. Much of the confusion over r- and K-selection resides with its application rather than the underlying theory. Species with so-called "r-traits" or "K-traits" (Table 12.3) are frequently called r-selected or K-selected with no knowledge of the underlying evolutionary mechanism that produced those sets of traits. To determine whether the life history traits of an organism fit into one of these categories requires evidence that natural selection operated in a density-independent (r-selection) or density-dependent (K-selection) manner, and this critical information is often lacking.

The direction and rate of population growth reflect the interaction between recruitment and loss. Recruitment into a population may be viewed in two ways: all individuals, irrespective of age, enter the absolute population or juveniles enter the reproductive population as they become sexually mature. The manner and timing of recruitment depend on the reproductive pattern of a population. In populations with a single, brief reproductive period each year, all members of the new generation hatch or are born simultaneously. In contrast, as the length of the breeding period increases, recruitment occurs over an increasingly longer interval.

These generalizations apply to both amphibians and reptiles, although different reproductive patterns and life history characteristics affect how and when recruitment occurs. In amphibians with complex life cycles, recruitment occurs during a brief period in explosive breeders, but it occurs over a longer period or may be continuous in prolonged breeders. Recruitment begins when eggs are laid or young are born. The fate of offspring is independent of the parents in species with no parental care. For the explosive-breeding spadefoot toads (*Pelobates, Scaphiopus*, and *Spea*), a population will surge from a few dozen adult toads to several hundreds or thousands of individuals after a single night of breeding. The population immediately begins to decline through deaths by predation and developmental failures. If the pond dries prior to metamorphosis, the population returns to a level near its prebreeding size and structure; if metamorphosis occurs, the new cohort adds a juvenile component to the age structure and the potential of recruitment into the breeding population in a year or two. For annual species with extended breeding seasons (whether for a frog, *Acris crepitans*, or a lizard, *Uta stansburiana*), recruitment occurs over a 1–3 month breeding season and is maximal near the end of the season, just prior to a surge of adult deaths; thereafter, population size declines until the following year's breeding season. Few if any adults survive a second year; hence, annual recruitment into the adult population is essential for survival of the population. Taxa with longevity greater than 10 years (e.g., salamanders, turtles) have relatively stable adult populations but variable-sized and -aged cohorts of maturing individuals; the breeding season may be brief (1–2 nights for some mole salamanders, *Ambystoma*) or extended (2–3 months for seaturtles). Survival of each new cohort to the following year is variable, typically between 0 and 20%. Because of the extended and variable period of maturity in long-lived taxa, members of a single cohort enter the adult population over several years (e.g., 2–8 years for the red-spotted newt, *Notophthalmus viridescens*, and 6–20 years in Blanding's turtle, *Emydoidea* *blandingii*). Stability of adult population size is maintained by high survivorship of adults and continual, although low, annual recruitment.

Dispersal also affects population growth: emigration is the loss of individuals and immigration is the gain of individuals. Emigration is difficult to distinguish from mortality, because disappearance by emigration can be confirmed only if individuals reappear or are found elsewhere. Immigration is easier to recognize but only if the entire population is marked. Because of these logistic difficulties, emigration and immigration are assumed to balance one another and are subsumed in the mortality and natality estimates in survivorship and fecundity schedules. Dispersal is important in two other aspects: colonization or origin of new populations, and gene flow by the potential introduction of new alleles into other populations and/or changing gene frequency of parental or new populations (see Chapter 10).

Factors affecting recruitment and loss segregate into density-dependent and density-independent effects. In the former, a direct correlation exists between a population's density and its rate of recruitment or loss. Viewed from the perspective of loss, density-dependent factors increase loss (mortality and/or emigration) as density increases. Predation and competition are the most apparent density-dependent factors; as density increases, individuals are more often encountered and captured by predators, thus increasing mortality in absolute as well as proportionate numbers. Increasing density eventually reaches a level where one or more resources are in short supply and competition among individuals for resources intensifies. Inadequate food leads to malnutrition or starvation for some or all members of the population, and lack of shelter exposes more individuals to predators or displaces some individuals into suboptimal habitats. Field experiments on frog and salamander populations (single- and multiple-species protocols) regularly demonstrate that growth rates of individuals are reduced by crowding. Crowding leads to increased predation because larvae require longer to grow to sizes that reduce vulnerability to predators. A longer time to metamorphosis increases the likelihood that the pond will dry prior to the cohort's metamorphosis; thus, a density-independent effect on mortality may result from a density-dependent effect.

Floods, fires, volcanic eruptions, and other catastrophic events are usually considered to be density-independent, affecting all species and members of a population equally. Pond drying annually threatens temporary-pond breeding amphibians, and if ponds dry before any larvae metamorphose, mortality is density-independent. Likewise, drowning of seaturtle nests by storm-driven high tides on nesting beaches is density-independent. Some evidence suggests that mortality resulting from large-scale catastrophic events may not always be entirely density-independent and may differentially affect species. For example, Hurricane Hugo, a storm of moderate intensity that passed over eastern Puerto Rico in 1989, provided an opportunity to study the effects of a catastrophic weather event on populations of amphibians and reptiles. Adult survivorship of the frog *Eleutherodactylus coqui* was unchanged immediately after the storm, but 1 year later, adult density was four times higher than prestorm levels (Woolbright, 1991). An increase in quality retreat sites because of forest debris and a reduction in invertebrate predators contributed to the increase. Juvenile recruitment of *E. coqui* remained low after the hurricane, possibly because the adults attained a smaller size in disturbed areas caused by the storm—clutch size is correlated with female body size. A study of four species of *Anolis* lizards before and after the hurricane revealed that absolute abundance did not change, but anole distribution and habitat use were different (Reagan, 1991). Activity of all species, including high-canopy species, was confined to within 3 m above ground because of the extensive destruction of the canopy. Response of one species was keyed to change in habitat structure, whereas that of another species was keyed to change in microclimate. Thus, even when catastrophic events occur, some species of amphibians and reptiles may respond to the event in different ways.

Population size and growth are regulated by complex interactions among density-independent and density-dependent factors. For example, a small isolated population of fence lizards, *Sceloporus undulatus*, studied in eastern Kansas seldom reached a density where resource availability was exceeded. Population size appeared to be regulated by summer and fall predation on egg-laying females that was proportionately greater at higher densities. Stability did not occur because irregular flooding drowned nests and adults, and low spring temperatures periodically increased individuals' susceptibility to predation. Each year, density-independent mortality appeared to have the greatest effect on annual survivorship (Ferguson et al., 1980).

Metapopulations

A metapopulation is the "set of local populations within some larger area, where migration from one local population to at least some other patches is possible" (Hanski and Simberloff, 1997). This view of populations adds spatial scale in dealing with population phenomena and has particularly powerful applications to conservation biology. Populations of organisms are not often distributed evenly in the environment; rather, subpopulations exist in environmental patches that provide appropriate microhabitats for the species. For example, chuckwallas, *Sauromalus obesus*, have a large distribution in the southwestern United States and northern Mexico. Most subpopulations are restricted to ''islands'' of rocky habitats in otherwise open desert habitats. The subpopulations on each rock habitat island have their own independent dynamics (Case, 1976a; Tracy, 1999), and the rate of exchange of individuals among rock habitats is low enough that immigration has no apparent effect on the dynamics of each population. Amphibians that breed in temporary ponds could experience local extinctions due to early pond drying or extended drought, only to be reestablished by colonists from other patches when conditions are more favorable. Understanding metapopulation dynamics is potentially critical to determining the potential persistence of species in natural environments (Hecnar and M'Closkey, 1996). Metapopulation biology is a relatively new area in herpetology; nevertheless, some interesting research suggests that understanding the spatial distribution and dynamics of amphibian and reptile populations can provide new insights into persistence of populations on a landscape scale. For many species of amphibians and reptiles, simply determining whether the ''population'' is a metapopulation (e.g., comprising subpopulations with some level of interchange) can be an onerous task (Burke et al., 1995).

A long-term study of the red-spotted newt, *Notophthalmus viridescens*, revealed that the population was divided into numerous subpopulations centered around a pattern of breeding ponds in Virginia (Gill, 1978). Adults are philopatric (they almost always return to their home pond), and when removed they return to their home pond. As a result, little exchange of genes takes place between subpopulations. Moreover, because breeding success is zero in some ponds, immigrants from other ponds appear responsible for the founding of subsequent populations. Even when large numbers of newts are translocated to other ponds, a majority return to their pond of origin (Gill, 1979).

Water pythons, *Liasis fuscus*, in the Northern Territory of Australia, comprise three distinct subpopulations based to a large extent on the availability of nest sites (Madsen and Shine, 1998). The three subpopulations differ in body size, seasonality, and reproductive status, and individuals within each subpopulation appear to be philopatric during the dry season when breeding occurs. During the wet season, the snakes occur side by side as they all move to the floodplain of the Adelaide River. Nevertheless, characteristics of each subpopulation are maintained due to philopatry to home breeding sites. Metapopulation dynamics are revisited in Chapter 14.

ADDITIONAL READING

Gill, D. E. (1978). The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens*. *Ecol. Monog*. **48**: 145–166.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Q. Rev. Biol.* **51**: 3–47.

Stearns, S. C. (1977). The evolution of life history traits: A critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst*. **8**: 145–171.

Tinkle, D. W. (1967). The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publ. Mus. Zool., Univ. Michigan* **132**: 1–182.

Wilson, E. O., and Bossert, W. H. (1971). ''A Primer of Population Biology.'' Sinauer Assoc., Inc., Stamford, CT.

REFERENCES

Population Structure and Dynamics: General: Wilson and Bossert, 1971.

Characteristics of Populations: Brown and Parker, 1984; Frazer et al., 1990.

Population Structure and Growth: Size, Abundance, and Density: Andrews and Wright, 1994; Crump, 1986; Burton and Likens, 1975; Ferguson et al., 1983; Given, 1988; Schoener and Schoener, 1980.

Age Distribution: Tinkle, 1967.

Population Growth: Ferguson et al., 1980; Pianka, 1970; Stearns, 1976, 1977; Reagan, 1991; Woolbright, 1991.

Metapopulations: Burke et al., 1995; Case, 1976a; Gill, 1978, 1979; Hanski and Simberloff, 1997; Hecnar and M'Closkey, 1996; Madsen and Shine, 1998; Tracy 1999.

Chapter

13

Community and Geographical Ecology

Most ecosystems contain many species of plants and animals, some of which interact with and influence the ecology of amphibians and reptiles. The biotic component of ecosystems (i.e., the plants and animals) is the community, which is the entire complex (trophic network) of interacting organisms in one location, including all organisms from the energy-capturing plants to the tertiary predators and decomposers. Community is used rarely in this all-encompassing sense. For both logistic and philosophical reasons, studies of communities are most often restricted to tractable sets of interacting species. Logistically, it would be nearly impossible to quantify interactions of all organisms in one community, even if it were a simple community (i.e., one with low species diversity). Philosophically, it is much more useful to examine interactions among similar taxa (e.g., all frogs) or taxa using a particular microhabitat (e.g., leaf litter vertebrates) because the more significant interactions can be identified and traced. Interactions among species most closely related phylogenetically should be more intense than interactions between distantly related species. Similar evolutionary histories lead to relatively similar morphologies and behaviors and a greater likelihood that species will compete for similar resources. In restricted microhabitats (e.g., small temporary ponds), however, interactions with and among more distantly related taxa (e.g., *Acris* larvae and aquatic insects) might be more intense than interactions between more closely related taxa (e.g., *Acris* and *Rana* larvae that breed in large permanent ponds). Community ecologists often refer to these subsets of organisms as assemblages (e.g., *Anolis* lizard assemblages or temporary pond assemblages) to distinguish them from the entire community.

COMMUNITIES

Communities have characteristics that populations and species do not have, including species richness (the number of species), species diversity (the number of species combined with their relative densities), and interspecific competition and predation. Communities typically also have structure that persists even though species composition and abundances change. They are composed of sets of species that are producers (plants), primary consumers (herbivores), secondary consumers (carnivores), and decomposers (bacteria, etc.). Parasites on animals are secondary consumers. Guilds are sets of species that use particular resources in the same manner; for example, there might be an ant-eating guild, and these specialized resource groups are often identifiable in communities. Intraguild predation and competition may occur among different stages or size classes within a guild. Because communities are components of ecosystems, they play a role in nutrient and energy cycling. Amphibians and reptiles have been used to develop and test much theory in community ecology, partially because their abundance and high species richness make them model organisms among vertebrates for both comparative and experimental community studies.

Natural environments, even within areas as small as a hectare or 0.1 ha, offer each organism a mosaic of choices for shelter, feeding, and reproduction. Because environments vary considerably in physical characteristics such as temperature, season length, and structural diversity of the habitat, different environments contain different combinations of amphibian and reptile species. The geographical location of habitats also influences the potential interacting species that might be found at any given place simply because colonization usually involves species from taxa that are already in the area. For example, we would not expect to find teiid lizards in an Australian desert even though the habitat might appear ideal for teiid lizards. Teiid lizards do not occur in Australia or on any Old World continents. Consequently, no mechanism exists, other than introduction by man, for teiid lizards to colonize and diversify in Australia.

Defining local amphibian and reptile communities requires macrodescriptors, names that delimit the area or kind of environment of interest. Some examples are the herpetofaunal community of a lowland tropical forest, a desert flatland habitat, or a temporary pond in South Carolina. Each description provides limits within which patterns of species richness, diversity, and species interactions can be understood. The questions asked in community ecology often determine the macrodescriptors. ‘‘Interactions among tadpoles in leaf axils of tropical plants’’ is a macrodescriptor indicating that interactions among tadpoles (a taxonomic restriction) in leaf axils of tropical plants (a habitat restriction) are being studied, even though the findings might have much broader application. A more general macrodescriptor, such as ‘‘the ecology of a tropical forest community,’’ even though correct, lacks specificity and provides little relevant information.

Characteristics of Communities

No matter how broadly or narrowly defined, a community’s structure is its species composition, the abundance of each species, and the interactions among species. Even though the patterns of co-occurrence are evident and relatively easy to quantify, the causes for these associations are not. Factors governing the presence or absence of a species and the abundance of its members are numerous and sort into abiotic and biotic ones. Abiotic (a = ‘‘without,’’ bio = ‘‘life’’) factors are a function of the physical environment and each species’ physiological tolerances with respect to environmental variables (Chapters 6 and 7). Biotic factors are resource related and concern interactions with other species. These interactions may be direct (catching prey or being captured as prey) or indirect (shade from a tree or high humidity of a forest); they have positive, negative, or neutral effects on an individual’s survival and reproduction, hence influencing persistence or extinction of a population. Direct interactions include predation, mutualism, and competition, major factors that shape community structure. Historical factors include colonization and extinction events, which also determine species composition. Interactions that led to the present-day structure of many communities are often subtle because a long history of interactions leads to equilibrium; the species interactions that produce present-day structure may have occurred long ago. Moreover, existing differences among species at first contact might be sufficient to allow coexistence with little or no interaction. The available species pool can also have considerable impact on the structure of communities.

At one level, the basic organization of all communities follows energy flow through the various life-forms from plants to consumers and decomposers. Life’s energy derives entirely from the sun. Plants capture this radiant energy and convert it into plant tissue; herbivores eat the plants and convert the energy to animal tissue. Predators eat herbivores, and some high-order predators feed on other predators as well as on herbivores. At each step (trophic level; see the inset of Fig. 13.1) in the food or energy chain, energy is lost as a by-product of metabolic activities (i.e., respiration) and because individuals are unable to assimilate all food obtained. Assimilation efficiency is typically lowest in herbivores and highest in top-order predators. Trophic pyramids reflect the sequential energy loss through trophic levels. It should be obvious, given differences in assimilation efficiencies among trophic levels, that biomass of primary producers is greatest, and biomass of each successive trophic level is lower. Amphibians and reptiles are mainly primary and secondary predators, eating other consumers and in turn being eaten. Consequently, herpetological communities occupy the middle region of the trophic chain or food web (Fig. 13.1).

Local Species Assemblages

Amphibian and reptile communities (i.e., limited-membership communities) are diverse (Table 13.1), reflecting the availability of energy and shelter, species

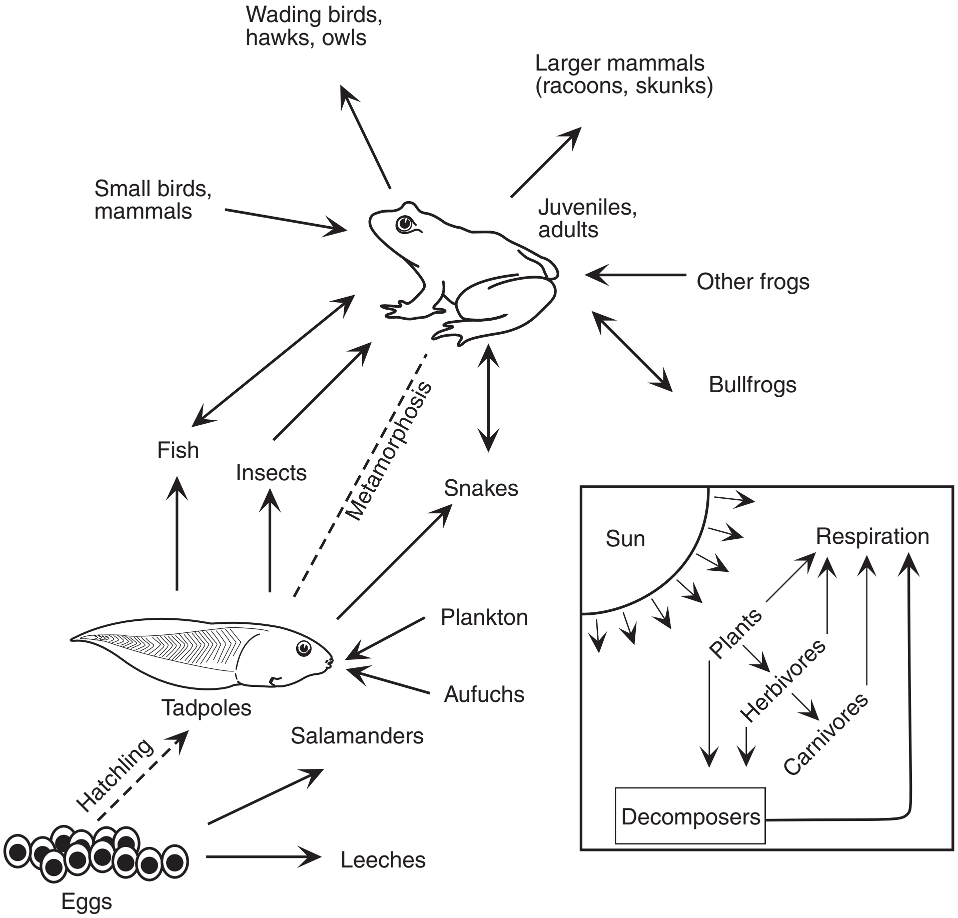


FIGURE 13.1 A generalized food web for an eastern North American pond showing the bullfrog (*Rana catesbeiana*) as the focal point. Arrows denote direction of energy flow, i.e., consumption. The inset (lower right) shows the general pattern of energy flow through communities. Adapted from Bury and Whelan (1984).

source pools from which to draw colonists, and rigors of the abiotic–biotic environment. The trend is for the number of species (species density) to increase from cold-temperate to tropical areas (possibly total biomass as well, although comparable data are unavailable); however, countertrends occur in some groups. For example, turtle communities are more diverse in midlatitudes in the northern hemisphere than in the tropics; plethodontid salamander communities share similar species numbers when forest microclimates are matched, regardless of whether they are tropical (cloud forests) or temperate (deciduous forests). Lizard communities at the same latitude (within a single continent) commonly are more diverse in more arid regions; the reverse trend occurs in amphibians and turtles. Such generalities have many exceptions and often the differences reflect sampling success and protocol (e.g., duration, completeness, and area of sampling). The Savannah River Site in South Carolina (Table 13.1) has an extremely rich herpetofauna in comparison to some tropical sites. The Savannah River Site has numerous aquatic and terrestrial habitats, is within an area of high species diversity, is not isolated by natural and man-made barriers from other natural areas, and has been exceptionally well sampled (continuous sampling for 30+ years). No tropical sites have had comparable sampling (although sites in Thailand and Borneo have been sampled thoroughly for 1–2 years). The fauna of Barro Colorado Island (within the Panama Canal) lacks free interchange of fauna with the adjacent mainland forest. A striking feature of all subtropical and tropical assemblages is the high diversity of frogs and snakes; frogs partition space and time, whereas snakes partition food.

The nature of the physical environment, the composition of the species source pool, and the interactions of community members are major factors contributing to community structure. Whether the climate is tropical or arctic, or the soil rocky or sandy, a myriad of other

TABLE 13.1 Composition of Continental Herpetological Assemblages[a] from Different Climates

Site	Caecilians	Frogs	Salamanders	Turtles	Lizards	Snakes	Crocodylians	Totals	Latitude
Andrew Exp. Forest (forest)	0	3	7	0	3	3	0	16	44°N
U. of Kansas Natural Reserve (grassland and forest)	0	9	1	4	7	16	0	37	39°N
Prince William (forest)	0	10	10	4	4	13	0	41	38°N
Savannah R. Site (swamp and forest)	0	23	16	12	9	35	1	95	33°N
Barro Colorado (forest)	1	29	0	5	22	39	2	98	9°N
Santa Cecilia (forest)	3	81	2	6	28	51	2	173	0°N
Tucumán (forest)	0	16	0	1	26	24	0	67	28°S
Vienna (fields and forest)	0	12	5	1	5	5	0	28	48°N
Rota (grassland and forest)	0	6	2	1	10	5	0	24	37°N
Lamto (savanna)	0	17	0	0	10	12	0	39	8°N
Kivu (forest)	0	29	0	2	10	38	1	80	2°S
Vernon Crookes Reserve (grassland and forest)	0	17	0	0	8	14	0	39	30°S
Lazo Nature Reserve (forest)	0	6	0	0	1	6	0	13	43°N
Chitwan (grassland and forest)	0	11	0	7	10	24	2	54	28°N
Sakaerat (fields and forests)	1	24	0	2	30	47	0	104	14°N
Ponmudi (forest)	2	24	0	0	16	14	0	56	9°N
Nanga Tekalit (forest)	1	47	0	0	40	47	0	135	3°N
Big Desert (scrub)	0	4	0	0	18	2	0	24	35°S

Sources: Andrew Experimental Forest, Oregon, USA (Bury and Corn, 1988); University of Kansas Natural History Reserve, Kansas, USA (Fitch, 1965); Prince William National Forest, Virginia, USA (Pague and Mitchell, unpubl.); Savannah River Plant, Georgia, USA (Gibbons and Semlitsch, 1991); Barro Colorado Biological Station, Canal Zone, PANAMA (Myers and Rand, 1969); Santa Cecilia, ECUADOR (Duellman, 1978); Tucumán (bosques chaqueros), ARGENTINA (Laurent and Teran, 1981); Vienna, AUSTRIA (Tiedemann, 1990); Rota, SPAIN (Busack, 1977); Lamto, IVORY COAST (Barbault, 1976b); Kivu, ZAIRE (Laurent, 1954); Vernon Crookes Nature Reserve, NATAL (Bourquin and Sowler, 1980); Lazo State Nature Reserve, Maritime Terr., RUSSIA (Shaldybin, 1981); Royal Chitwan National Park, NEPAL (Zug and Mitchell, 1995); Sakaerat Experiment Station, THAILAND (Inger and Colwell, 1977); Ponmudi, INDIA (Inger et al., 1984); Nanga Tekalit, SARAWAK (island; no continent at this latitude in Asia) (Lloyd et al., 1968); and Big Desert, Victoria, AUSTRALIA (Woinarski, 1989).

[a] Each assemblage represents the taxa likely to be present in a 25 km^2 area and represents multiple habitats in most cases. The data are the number of species, excluding introduced or exotic species.

physical features sets the conditions for a species' survival and reproduction. Community membership also depends strongly on what species are available to colonize an area. Numerous amphibian and reptile species are adapted for survival in arid lands, but dispersal limitations prevent most from invading new arid lands. For example, Australian *Moloch* or even shovel-nosed snakes (*Chionactis*) from the nearby Sonoran Desert are unlikely to colonize a rocky outcrop in the Chihuahuan Desert. Once a species tolerant of the physical environment reaches a site, its persistence depends upon its interactions with the current community members and future colonists.

Community organization and species membership therein have become increasingly recognized as multifaceted (Table 13.2). Interactions are not singled out here because they are more important than other factors but because recent research on herpetological communities has emphasized interactions. The major interactions are predation, symbiosis, and competition, and, of these, competition has occupied center stage for the past 50 years. Competition has been generally championed as the major biotic factor establishing community structure and driving the morphological and behavioral divergence between similar or closely related species living in the same habitat. Ongoing competition has lost its universal acceptance as "the explanation" for community organization. In part, this change results from an increasing recognition that community structure is greatly and regularly influenced by stochastic events (e.g., arrival order of colonists, adverse weather such as hurricanes), historical factors (e.g., colonization history), and a myriad of other factors. Additionally, predation has a prominent influence on community structure, particularly population densities. Perhaps more influential for the declining explanatory power of competition was the

TABLE 13.2 Properties Determining a Species' or Population's[a] Membership, Position, and Persistence in a Community

Organismic	Environmental
Body size	Severity of physical environment
Diet (trophic position)	Spatial fragmentation
Mobility	Long-term climatic variation
Homeostatic ability	Resource availability
Generation time	Resource partitioning
Number of life stages	
Recruitment	

Source: After Schoener (1986).

[a] Schoener proposes these properties to examine the structure and dynamics of assemblages (e.g., intertidal algae, island anoles). These properties also highlight factors that affect an organism's survival and reproductive success, and hence a population's or species' niche and community affiliations.

tendency of competition theory (e.g., niche compression hypothesis, species packing, resource partitioning) to accept most cases of overlapping resource use as evidence of competition. Clearly demonstrating resource competition among vertebrates is difficult and often requires long-term ecological studies in which the effect of one species on another can be directly demonstrated.

No single factor is responsible for community structure. The factors mentioned above and others operate (often intermittently) singly, in combination, in opposition, or synergistically, depending upon the circumstances, to produce the observed structure. This structure is only a temporary aspect of the population dynamics of the component species.

Factors Influencing Community Structure

Interspecific interactions are usually complex in natural communities and as the number of species increases, so does the potential number of interactions. Interactions typically involve competition and predation, but abiotic factors and phylogenetic history play important roles in structuring communities and consequently determining the distribution and abundance of species.

A basic tenet of most studies of species interactions is that resources are limited. When two species vie for limited resources at a particular locality, selection over time should lead to one of the following outcomes: (1) one species will exclude or outcompete the other for the limited resource, or (2) the two species will diverge in their use of one or more resources so that coexistence is possible. The consequences of resource competition are easy to visualize in a single-resource system in which a number of consumers use the same resource (Fig. 13.2). In this case, the available resource has been divided up among consumers, and resource partitioning is evident (Schoener, 1974a; Toft, 1985). An example might be a frog community in which frog species vary in body size, and prey size is associated with frog body size. Small species would feed on small prey, and larger species would feed on larger prey. All frog species might eat insects, but each species would eat different insects. Real communities are much more complex than this example. At least three prominent resources, food, space, and time, are partitioned (Pianka, 1973, 1986). When only two resources are involved, each species can use one resource differently but have identical use patterns of another resource. For example, two frog species might eat insects of similar size but capture those prey at different times of day. Added resources make it possible for species that occur together to have similar resource utilization patterns with respect to one of the resources. In Figure 13.3, Guild A comprises three species that overlap in use of resource 1 but separate in their use of resource 2. This is a more realistic representation of a natural community, albeit a very simplified one. This simplified community contains a specific number of species and their identities, the relative abundances of each species, the patterns of resource use by each species, and the guild structure. If all resident species used all resources in a random manner, the "community" would have no structure. Indeed, if that were the case, it would be necessary to reexamine the underlying assumption that resources are limited! Ultimately, the nonrandom use of resources determines whether a community is structured or organized.

Microhabitats are important resources partitioned for all amphibians and reptiles (Table 13.3). In amphibian larval communities in temperate and tropical regions, species often segregate more by seasons than by microhabitats, but microhabitat differences usually occur among amphibian larvae that occur at the same place during the same time of year. In snake communities prey types are partitioned. Snakes tend to be food

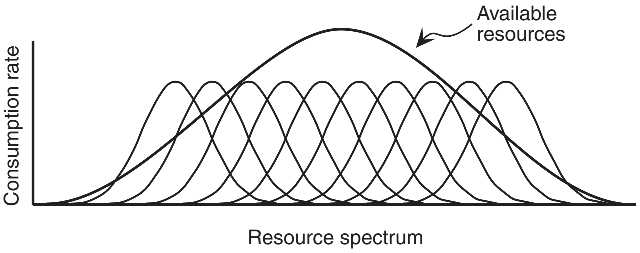


FIGURE 13.2 Graphic representation of a single-resource system in which a number of consumers partition the resource. Adapted from Pianka (1988).

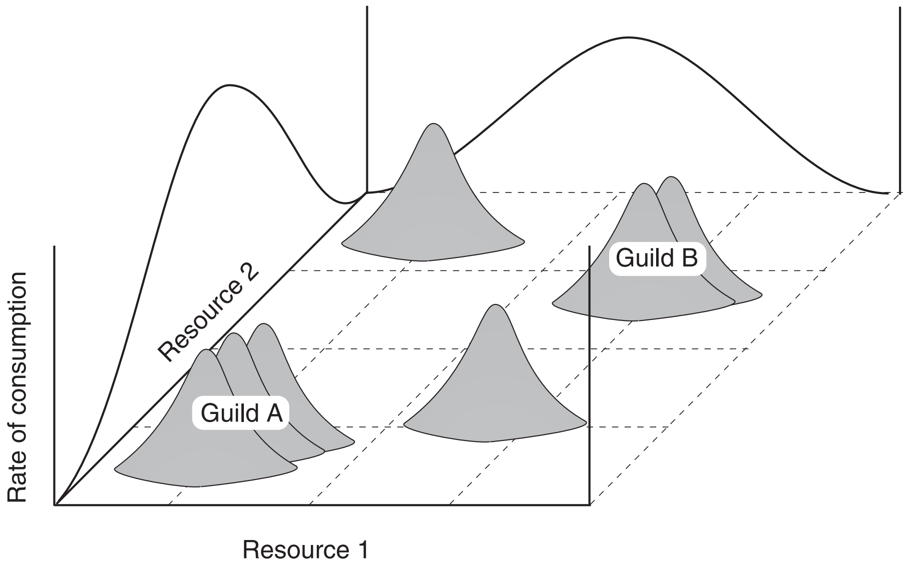


FIGURE 13.3 Graphic representation of a two-resource system showing the increase in complexity as the numbers of resources increase. Clusters of resource utilization curves represent "guilds," sets of species using one of the resources in a similar way. Adapted from Pianka (1988).

specialists, and many capture and consume large prey. In contrast, frogs, salamanders, and lizards typically partition prey resources by size or type—an expected resource axis for insectivores feeding on relatively small prey. In all communities studied (Table 13.3), partitioning occurs along two or more axes, and habitat and food partitioning exist in most. Time is a less important resource, although approximately 50% of the lizard and snake communities show some diel segregation of species, and snakes show an even higher seasonal partitioning.

TABLE 13.3 Niche Axis (Food, Space, and Time) Contributing Most to Resource Partitioning in Amphibian and Reptilian Communities

	Primary niche axis			Partitioned			
Taxa	Food	Time	Habitat	Food	Time (diel)	Time (season)	Habitat
Salamanders	25	0	75	100	15	8	87
Frogs	0	0	100	94	23	23	88
Amphibian larvae	6	88	6	75	0	88	83
Turtles	100	0	0	100	100	50	0
Lizards	53	36	11	94	45	24	91
Snakes	44	56	0	93	100	50	71

Source: After Toft (1985).

Note: The values are the percentage of studies in which one resource was the most strongly partitioned and in which a resource was partitioned.

Community studies can easily be divided into short-term and long-term studies, each of which provides different and often complementary information. Short-term studies are "snapshots" of what occurs at a given place and time. "Snapshots" taken at a variety of localities can be used to make comparisons among communities, providing insight into convergent and parallel evolution among other things. Acquiring repeated samples on a large spatial scale has been called the "far-flung approach" (Fig. 13.4; Cody, 1996). Long time periods may be necessary to gather these samples, but each sample is short term, and comparisons among samples rest on the assumption that variation within a sample (the unmeasured temporal variation) is less than variation between samples (the spatial samples). Long-term community studies at single localities allow repeated samples (the temporal samples) that provide observations on changes in community composition or structure. These studies can be interpreted within the context of abiotic or biotic changes within that particular community. Both "far-flung" and "long-term" studies can be descriptive, comparative, or experimental, and each provides unique insights into how communities function. A third type of community study involves intensive sampling at a single locality over a relatively short time period with the intent of describing in detail the structure of a particular community at one time. Individual data sets obtained using the far-flung approach are examples which, with the combination and comparison of additional data sets, provide spatial scale. When combined with innovative analyses, particularly phylogenetic

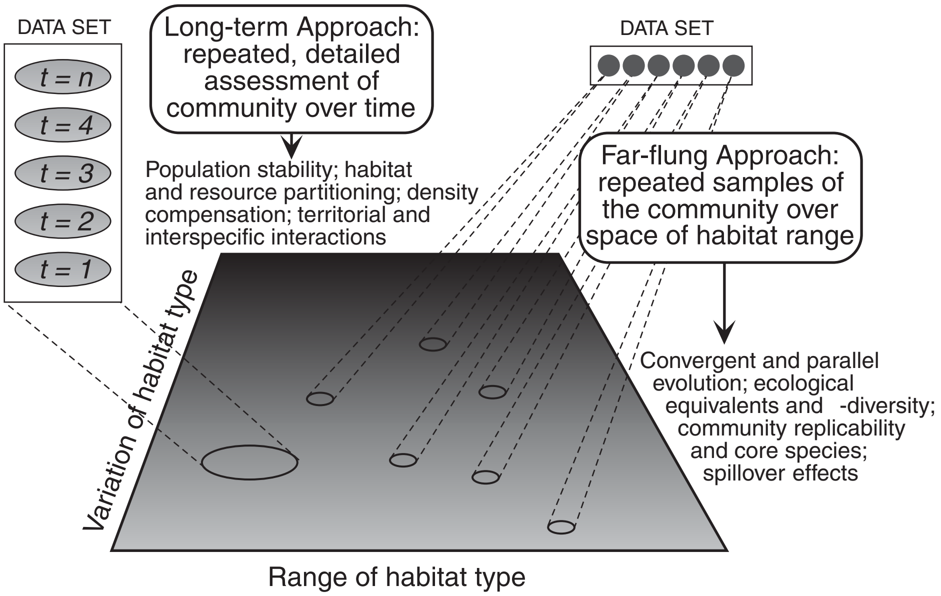


FIGURE 13.4 Graphic representation of the differences between long-term and far-flung studies in animal ecology. *t,* time. Adapted from Cody (1996).

analyses, these single snapshots can often be illuminating in themselves.

Short-Term Studies (Single Sample and Far-Flung Approaches)

Descriptive Studies These studies document similarities and differences in resource use among species within a particular community and serve to generate hypotheses that address the causes of observed structure. For example, streams in Borneo contain at least 29 species of frog larvae associated with distinct microhabitats. Among these, 5 species use leaf drifts; 3 use riffles, shingle areas, and open pools; 3 use potholes; and 2 use side-pools and potholes (Inger et al., 1986). Larvae inhabiting each of the four microhabitats consist of heterogeneous taxonomic groups, and morphology of some species appears to dictate where they feed. Feeding behavior also differs among species but is influenced to some degree by morphology. On a community level, food is the resource partitioned, but food partitioning is somewhat dependent on the distribution of tadpoles within the stream. In this particular larval community, present-day species interactions appear relatively unimportant. Reproductive behavior of adults and existing morphological and behavioral characteristics of the larvae (which are not independent of phylogeny) appear to be the primary causes of structure.

In a transition Amazon rain forest habitat in northern Brazil, 9 species of frogs and 7 species of lizards occur together in the leaf litter (Caldwell and Vitt, 1999). Many of the frogs and lizards are juveniles, but some are adults of tiny species (e.g., the frog *Pseudopaludicola boliviana* and the lizard *Coleodactylus amazonicus*). Even though the 16 species live in leaf litter, their diets vary considerably. An ant–termite guild of 2 species is evident, and leaf litter frogs and lizards (a microhabitat guild) separate on the basis of prey types and sizes. Prey size is associated with predator body size within most species and across nearly all species (Fig. 13.5). Frogs in the assemblage consume many more ants than do lizards in the same microhabitat. These observations suggest the hypothesis that frogs might be feeding on ants to optimize intake of chemicals to be used for defense (see Chapter 11), whereas lizards might be selecting prey to optimize energy intake.

Comparative Studies Comparisons of one or more communities represent repeated and independent samples on a spatial scale. The scale can vary considerably; studies within or across habitat gradients provide information on species turnover and ecological equivalents (species replacement), whereas studies between continents or even islands can provide information on convergence of communities with relatively independent evolutionary histories. For example, such studies led Williams (1972) to propose the ecomorph model for Caribbean *Anolis* assemblages and Pianka (1975) to search for convergence in structure of desert lizard communities.

Comparisons of contiguous communities along habitat gradients (see Fig. 13.4) often provide insight into

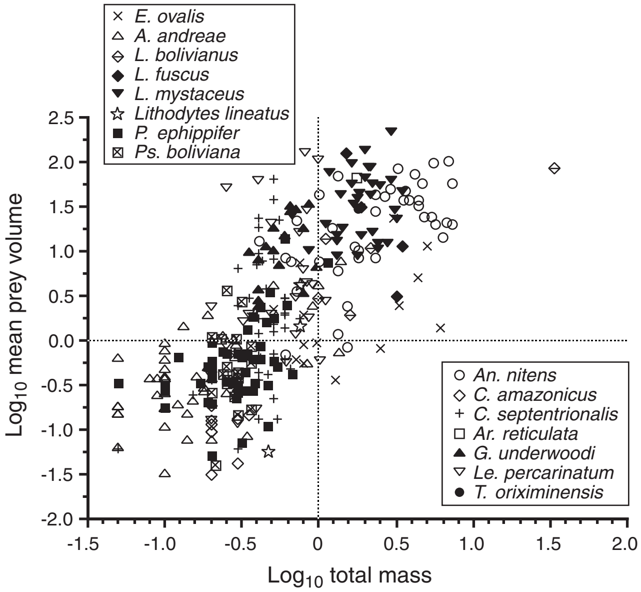


FIGURE 13.5 Relationship between body size (mass) and mean prey size (both log transformed) for frogs and lizards from Roraima, Brazil. Sixty percent of the variation in prey size is attributable to variation in consumer size. Genera are, from top to bottom, *E* = *Elachistocleis, A* = *Adenomera, L* = *Leptodactylus, P* = *Physalaemus, Ps* = *Pseudopaludicola, An* = *Anolis, C* = *Coleodactylus, Ar* = *Arthrosaura, G* = *Gymnophthalmus, Le* = *Leposoma,* and *T* = *Tretioscincus.* Adapted from Caldwell and Vitt (1999).

factors that maintain structure in undisturbed communities. For example, 105 species of reptiles and amphibians that differ in species composition, relative abundance, and microhabitat use occur across three distinct habitats in Borneo (Lloyd et al., 1968). The three environments taken together comprise a gradient from undisturbed broadleaf evergreen forest to deciduous dipterocarp forest and into agricultural land. The evergreen forest contains the highest diversity of reptiles and amphibians (77 species) and the agricultural area contains the lowest diversity (55 species); the dipterocarp forest is intermediate (67 species). A similar trend occurs in the number of resource states (microhabitats) used by the resident species. Niche breadths are lower in evergreen forest, and the average niche overlaps, or similarities in use of resources, are higher. Niche breadths reflect the relative frequency of use of different microhabitats. Species with low niche breadths use one or a few microhabitats, whereas species with high niche breadths might use a large number of microhabitats equally. Overlaps indicate similarity between species in the use of a particular set of resources (microhabitats in this case). Low niche breadths and higher average niche overlaps indicate that species in the evergreen forest are more similar to each other with respect to resource use than those in the other two habitats. When species are very similar in resource use, they are referred to as tightly packed. Species in the evergreen forest have high overlaps, that is, they are similar to each other in microhabitat use, thus forming microhabitat guilds (see Fig. 13.3). The guilds are distinctly different from each other (low overlap). For example, one very tight terrestrial guild (low overlaps among members) contains 4 species of lizards, 1 frog, and 1 snake. A riparian guild contains 2 frogs and a turtle. The conclusions from this study, based on spatial comparisons along a habitat gradient, are that more predictable environments (evergreen forest) promote the formation of guilds that allow greater species richness. Additional information on other niche axes might make the pattern even more clear.

Community comparisons at a continental level have been made with desert lizards (Pianka, 1973, 1975, 1985, 1986). Although an expectation might be that desert lizard communities on three continents converge in structure, Pianka's studies show that climatological, historical, and resource-based differences between continents have shaped desert lizard assemblages in different ways. Nevertheless, average diet and microhabitat niche breadths of lizards are similar among the deserts, and, even though the communities cannot be considered convergent, taxonomically unrelated species pairs have converged in morphology and ecology (Fig. 13.6). Differences are apparent in numbers of species, taxonomic composition of communities, and other ecological characteristics (Table 13.4). Even when species compositions of identifiably similar microhabitats are compared, striking differences exist. Saltbush (Chenopodiaceae) shrub sites occur in the Kalahari Desert and North American and Australian deserts. Six lizard species live in these sites in North American deserts, 13 in the Kalahari, and 18 in Australian deserts.

Continental comparisons of the number of species and individuals in tropical forests reveal that Costa Rican forests harbor many more individuals and species of amphibians and reptiles when compared with Bornean forests (Scott, 1976). In Costa Rica, terrestrially breeding *Eleutherodactylus* form a major component of the leaf litter fauna, whereas in Borneo, viviparous skinks appear to have similar ecological roles. Subsequent work in Borneo, Thailand, and Indo-Malayan rain forests also reveals much lower amphibian and reptile densities compared with Costa Rica (Inger, 1980). Although the differences were initially attributed to differences in "routes and rates of energy flow" associated with differences in leaf litter, additional data suggest alternative explanations (Scott, 1976). Scott observed reduced leaf litter in the Bornean forest site. Later studies in Borneo, Thailand, and the Indo-Malayan rain forest were conducted in areas with high leaf litter, yet amphibian and reptile density remained low. The impact of insect production

FIGURE 13.6 The agamid lizard *Moloch horridus* (left) of Australia is an ecological equivalent of the iguanid lizard *Phrynosoma platyrhinos* (right) of North America. Both species are ant specialists in arid habitats. Photographs by E. R. Pianka (left) and L. J. Vitt (right).

related to fruiting of dipterocarp trees likely accounts for lower densities in Borneo. Climatic change that has resulted in the habitat becoming drier appears to account for reduced frog density in Thailand. The shorter hydroperiod of temporary breeding pools increases larval mortality. Data were not sufficient to suggest hypotheses to account for low densities in Indo-Malayan forest. This example shows that on a global level, differences and similarities in community structure may have independent explanations.

Experimental Studies The use of cattle tanks and other temporary artificial ponds for replicated experiments with anuran and salamander larvae spawned an entire generation of ecologists focused on unraveling the intricacies of complex species interactions (e.g., Brockelman, 1969; Wilbur, 1972, 1987). The advantages of artificial enclosures center around control of exogenous variables. In natural ponds, an unknown number of variables influence larval survival, and, because natural ponds are not uniform in structure, habitat gradients exist that also introduce undocumented variation. Artificial ponds can be designed to minimize or eliminate effects of unmeasured variables, inoculated with predetermined densities of potential competitors and predators, and set up in appropriate

TABLE 13.4 Variation among Continental Deserts in the Structure of Lizard Communities[a]

	North America			Africa			Australia		
Mode of life	**Mean**	**Range**	**%**	**Mean**	**Range**	**%**	**Mean**	**Range**	**%**
Diurnal	6.3	4–9	86	8.2	7–10	56	18.1	9–25	60
Terrestrial	5.4	4–7	74	6.3	5.5–7.5	43	15.4	9–23.5	54
Sit-and-wait	4.4	3–6	60	2.4	1.5–2.5	16	5.3	2–7	18
Widely foraging	1.0	1	14	4.0	3–6	27	10.1	4–12	36
Arboreal	0.9	0–3	12	1.9	1.5–2.5	13	2.7	0–5.5	9
Nocturnal	1.0	0–2	14	5.1	4–6	35	10.2	8–13	36
Terrestrial	1.0	0–2	14	3.5	3–5	24	7.6	6–9	27
Arboreal	0.0	—	0	1.6	0.5–2.5	11	2.7	1–4	9
Subterranean	0.0	—	0	1.4	1–2	10	1.2	1–2	4
All terrestrial	6.4	4–8	88	9.8	9–11	67	23	15–34.5	78
All arboreal	0.9	0–3	12	3.5	2–5	24	5.4	1–9	18
Total	7.3	4–11	100	14.7	11–18	101	29.6	18–42	100

Source: After Pianka (1985).

[a] The numbers of species and their modes of life are indicated for each category and are based on multiple sites in each desert. Semi-arboreal species are assigned half to terrestrial and half to arboreal categories.

statistical designs. They are particularly relevant to studies of amphibian larval communities, because amphibian mortality mainly occurs in the larval stage, and mortality can be density dependent, density independent, or a combination of both. Drying of ponds prior to metamorphosis, for example, is density independent, whereas the effect of competition and/or predation in ponds with long hydroperiods is usually density dependent. Moreover, size and time to metamorphosis affect fitness of amphibians (Semlitsch et al., 1988; see Chapter 5).

Early experiments examined the effects of competition and predation on survivorship, length of the larval period, and size at metamorphosis in six amphibian species (Wilbur, 1972). Competition among larvae of three species of *Ambystoma* was evident; each species survived better, metamorphosed more rapidly, and reached a larger size at metamorphosis in the absence of the other two salamander species. Additional experiments revealed more complex interactions when a predator (*Ambystoma tigrinum*) was added and when an alternative prey (*Rana sylvatica* tadpoles) for that predator was also added. In the absence of the alternative prey, the predator was a competitor with the other *Ambystoma*. However, in the presence of *R. sylvatica* tadpoles, *A. tigrinum* fed on the frog larvae, grew rapidly, and became a predator on the other species of *Ambystoma*. In another study, increased predator (*Notophthalmus viridescens*) density in artificial ponds reduced survivorship of *Hyla versicolor*, but the surviving frog larvae were larger at metamorphosis because predation reduced larval density, and more resources were available for each individual (Morin, 1987). In the presence of a competitor, *Pseudacris crucifer*, size at metamorphosis was reduced in *H. versicolor*. These studies, and many others, demonstrate that competition and predation can have a major impact on fitness of amphibian larvae (e.g., Wilbur and Fauth, 1990). Competition can negatively influence body size at metamorphosis. Females that metamorphose at a small size will have a reduced clutch size. Competition can also increase time to metamorphosis, which increases the possibility that the pond will dry prior to metamorphosis (density-independent selection). Predation can reduce density, resulting in lower density-dependent mortality. The relatively fewer surviving metamorphs benefit because they have more food and metamorphose at a larger size.

Experimental studies that involve manipulation of natural communities are, by design, much more complex. Nevertheless, several large-scale experiments using enclosures in a natural habitat produced results similar to artificial pond experiments (Scott, 1990, 1994). Larval *Ambystoma opacum* at high density grew more slowly, metamorphosed at smaller body size, and had lower survival than those that were enclosed at a lower density. Slower growth in the high-density enclosures also increased the probability that all larvae would die due to pond drying. Intraspecific competition in this case was dependent on hydroperiod through its effect on larval density. The intensity of competition also increased risk of predation because larvae take greater risks to acquire resources when competition is greater. The effects of density on size at metamorphosis translated into measurable effects on adults. Females resulting from larvae that experienced low density were larger when they returned to breed than those raised at high density and, for one cohort, had larger clutch sizes (Scott, 1994).

Long-Term Studies

Descriptive Studies Even though long-term ecological studies are critical for understanding population interactions (Likens, 1989; Cody, 1996), few exist for amphibians and reptiles. Turtles at the E. S. George Reserve in Michigan have been continually monitored since 1964—a unique investigation in which the turtle populations have experienced turnover in investigators rather than the opposite. Beginning in 1953 (Sexton, 1959), turtles were marked and monitored. As each successive researcher moved on, others took over. The turtles continue to be monitored today (Congdon and Gibbons, 1996). Populations of three species, *Chrysemys picta*, *Emydoidea blandingii*, and *Chelydra serpentina*, compose more than 98% of the turtle community, and these three species have remained more or less stable over 20 years of intensive monitoring (1974–1994). The size of the *C. serpentina* population increased slowly during the 20 years, and *C. picta* underwent a major population decrease only to recover several years later (Fig. 13.7). A fourth species, *Sternotherus odoratus*, composed less than 2% of the turtle community. The population of *S. odoratus* disappeared repeatedly as a result of changes in the physical condition of marshes. No evidence suggests that species interactions are important in structuring this turtle community. Rather, environmental factors and intraspecific interactions appear to best explain patterns of population size in these and other turtles studied (e.g., Ernst, 1971; Mitchell, 1988; Zweifel, 1989).

Amphibian populations have been monitored continuously from 1979 to the present on the Savannah River Plant (SRP) in South Carolina. Sixteen years of data on all species that use ponds as breeding sites indicate that the length of time ponds contain water (hydroperiod) is the primary cause of variation in population levels of the amphibian community, either through its direct effect on larval mortality or its effect on competition and predation (Semlitsch et al., 1996). In the driest

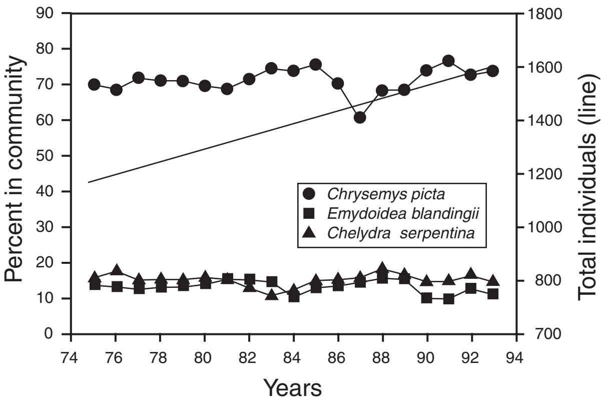


FIGURE 13.7 Annual variation in proportional representation of three turtle species in Michigan, based on capture–recapture studies. Adapted from Congdon and Gibbons (1996).

years, recruitment of juveniles into the population is controlled by the resulting short hydroperiod ($\leq$ 100 days). Larvae do not survive to reach metamorphosis; reproductive failure is complete or nearly complete for all species. In wetter years with longer hydroperiods ($\geq$ 200 days), both the diversity and the numbers of metamorphosing juveniles increase. Not all species responded similarly to variation in the length of the hydroperiod. One frog species, *Pseudacris ornata*, actually experienced lower recruitment in years with longer hydroperiods because they were able to use temporary ponds as alternate breeding sites. Longer hydroperiods increase the number and kinds of species interactions of developing larvae. If ponds persist long enough, larval densities increase, as do densities of predators, and competition and predation become major factors influencing recruitment. In this complex system, community structure appears regulated by a predictable interaction between rainfall, hydroperiod, competition, and predation.

Nutrient-poor lakes containing caimans, turtles, and fish illustrate the possible benefits of predation and its stabilizing effect on nutrient cycling (Fig. 13.8). In tropical forests, nutrients are held largely in vegetation and are rapidly recycled into plants following decomposition; streams and lakes are often nutrient poor. Annual floods inundate low-lying forests and enlarge forest lakes, and fish that normally live in the main channel migrate into forest lakes to spawn. Unexpectedly, fish diversity and population size have declined with the increased harvest of caimans. When caimans are present, they feed on the adult fish, and their feeding and defecation nearly doubles the amounts of calcium, magnesium, phosphorus, potassium, and sodium in the water, making the system much more productive for hatchling fish and other aquatic organisms. Consequently, removing

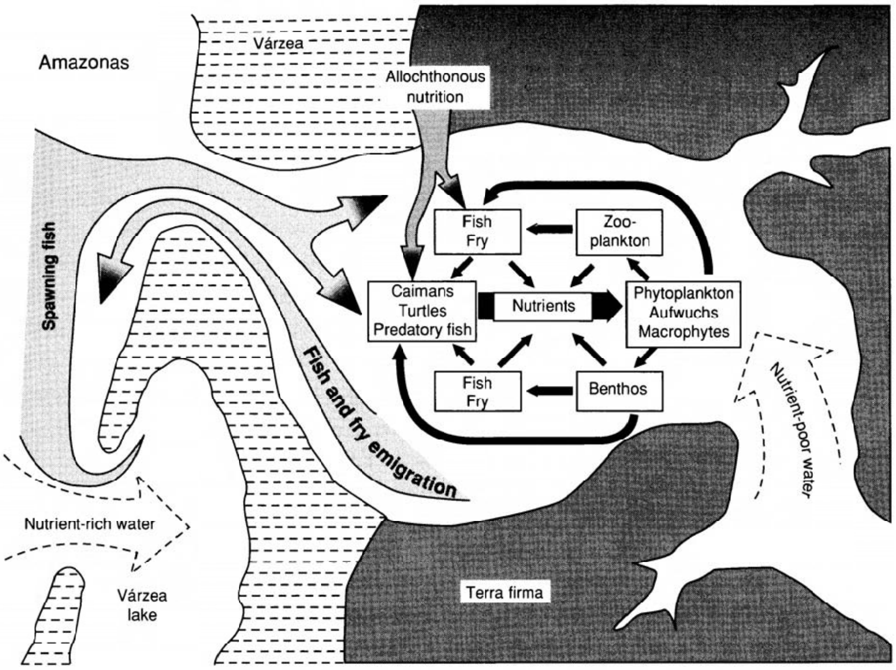


FIGURE 13.8 Caiman predation and the enhancement of the nutrient cycle in lakes at the mouth of small Amazon tributaries. Adapted from Fittkau (1970).

the caimans interferes with normal nutrient cycling and can negatively effect the entire system.

Comparative Studies The composition of lizard assemblages in a Australian desert is influenced by natural wildfires that produce a mosaic of habitat patches, each in a different state of recovery (Pianka, 1992). Dominated by porcupine grass or spinifex (*Triodea basedowi*), a highly flammable plant that regenerates rapidly following fires, the Great Victorian Desert harbors the greatest lizard diversity yet recorded—53 species at one site (Pianka, 1996). By using LandSat false-color satellite images, fire succession can be traced. Twenty-five years of lizard censusing at one site on a sandplain near Laverton and nearly 20 years of censusing at another site, Red Sands, both in Western Australia, show diverse responses to wildfires among lizard species inhabiting the sites. Species that prefer open areas increase in abundance following fires, but more specialized species, particularly those that depend on large (hence, not recently burned) spinifex tussocks, become locally extinct. Because the fires typically move in a fingerlike fashion rather than as a continuous front, populations of lizards depending on spinifex persist in isolated patches. Lizards living in sand ridges and mulga habitat patches form metapopulations, and local extinctions and periodic reinvasions maintain lizard diversity in the area. As a consequence, the lizard community is in a continual state of flux in which densities and species composition change in response to the fire mosaic. High lizard diversity results, at least in part, from the temporal and spatial diversity of habitats that result from the fire mosaic.

Experimental Studies Much of the geographic distribution of *Plethodon jordani* and *Plethodon teyahalee* in the Great Smoky Mountains is non-overlapping: *P. jordani* occurs at higher elevations and *P. teyahalee* occurs at lower elevations (Hairston, 1996). Narrow bands of coexistence vary in elevation depending upon slope orientation (e.g., E, W, N, SW) and are not associated with detectable changes in vegetation, suggesting that competition between the two species accounts for different elevational distributions. In the Balsam Mountains, the same two species overlap broadly in elevational distribution. The salamanders are terrestrial. A species removal experiment was designed to determine if interspecific competition accounted for the differences in distribution. Because the longest-lived species, *P. teyahalee,* requires 5 years to reach sexual maturity, a 5-year experiment was chosen to ensure that one full generation of species interactions would be included. In the Smoky Mountains, removal of one species resulted in an increase in abundance of the other, indicating that competition occurs and accounts for the nearly non-overlapping distributions. In the Balsams, the response was much lower. *P. teyahalee* increased in the *P. jordani* removal areas and juveniles of *P. jordani* increased in the *P. teyahalee* removal area, but only after the 4th year. This result indicates that interspecific competition is less intense in this area. Eight-year experiments in which salamanders were transferred between mountain ranges revealed that selection for increased competitive ability, especially in *P. jordani*, accounts for the restricted altitudinal distribution of *P. teyahalee* in the Great Smoky Mountains.

A 3-year experimental study on species interactions between two similar-sized lizards, *Urosaurus ornatus* and *Sceloporus merriami*, revealed that competition is intermittent and one-sided (Dunham, 1980). Lizards of each species were removed from reciprocal plots to determine if populations would respond to the absence of potential competitors. During years of high prey abundance, no population increases occurred. When prey availability was low (resources limited), *Urosaurus* density and individual growth rates increased in plots lacking *S. merriami,* but the opposite did not occur. *S. merriami* is a superior competitor, and as a result exploitative competition was asymmetrical. Neither population density nor individual growth rates of *S. merriami* increased in the absence of *U. ornatus,* indicating that *U. ornatus* had no effect on *S. merriami*.

Phylogenetic Approaches to Community Ecology

Species that compose natural communities have unique evolutionary histories that determine their ability to colonize new areas and how they will interact with other species. At higher taxonomic levels, species may be so different that little or no interaction occurs when they come into contact. For example, a turtle and lizard species would be unlikely to influence each other's abundance unless the lizards fed on the turtle eggs. Historical species sorting as opposed to recent species interactions may determine at least part of the makeup of a particular present-day community. For example, an assemblage of desert lizards might have a horned lizard species that interacts little with other lizards because of its specialized diet of ants. The particular species of horned lizard in the assemblage may result from interactions that occurred among species of horned lizards long ago and determined which species would do better in a particular habitat. The sorting among horned lizards in this example might be independent of interactions with present-day community members. Finally, as indicated earlier in this chapter, the clades available for diversification in a particular region may also impact patterns of community structure.

Historical Ecology of Tropical Snakes

New World snakes reach their highest species diversity in tropical forests, and ecological diversity among tropical snakes is also high. Snake species feed on a wide variety of other organisms and live in nearly every imaginable microhabitat. Most tropical New World snakes are colubrids that are represented by three evolutionary clades, the colubrines, the South American xenodontines, and the Central American xenodontines (Cadle and Greene, 1993). Central American xenodontines overall are smaller in body size than South American xenodontines, which are smaller than colubrines. The three clades differ in their relative use of microhabitats and prey types as well. Consequently, at least some of the ecological differences among species across the three clades can be attributed to historical factors. This hypothesis is strengthened by the observation that the three clades evolved in separate biogeographic centers (i.e., their evolutionary histories are different). A comparison of the structure of snake communities (colubrids only) from northern Central America to southern South America reveals that the proportion of the community represented by each of these three clades changes dramatically from north to south (Fig. 13.9). In northern localities, South American xenodontines are poorly represented, whereas Central American xenodontines are poorly represented in southern localities. Because the lineages differ considerably in ecological characteristics, Neotropical snake communities at various localities differ because of the nonequal representation of the three lineages. For example, most South American xenodontines are terrestrial, fossorial, or aquatic, whereas most Central American xenodontines are fossorial, cryptozoic, or arboreal, in that order. None of the colubrines is arboreal or aquatic and only one is fossorial. Likewise, most of the South American xenodontines eat snakes, all of the Central American xenodontines eat earthworms or mollusks, and none of the colubrines eats either of these prey categories—but all of them eat arthropods. There are some similarities in

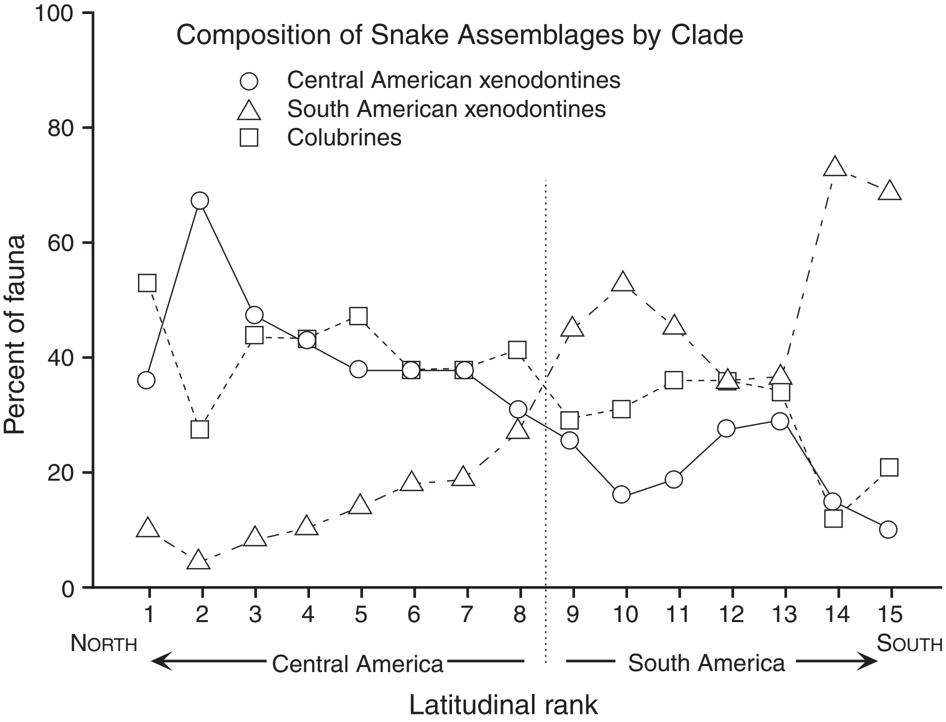


FIGURE 13.9 Changes in the proportional representation of three clades of colubrid snake species in communities across a latitudinal gradient from northern Central America to southern South America. The points at each north–south location represent specific snake communities. For example, the first set of points represents the snake fauna at Los Tuxtlas, Mexico, where 36% are Central American xenodontines (circle), 11% are South American xenodontines (triangle), and 53% are colubrines (square). Numbers along the *x* axis represent rank order of localities along the north–south gradient. Values on the *x* axis do not correspond to the original categories used by Cadle and Greene (1993). Ranking by latitude changed the positions of the five sets of points at the southern latitude end of the graph. The dashed line separates Central American from South American localities. Adapted from Cadle and Greene (1993).

diets that cut across clades. For example, species from all three clades feed on lizards, amphibians, and fish. Consequently, conclusions about a specific Neotropical snake community must include a consideration of the composition of the snake community and the history of each clade. Ecological factors may play a role in determining patterns of resource use within the specific community, but only within constraints imposed by the history of the clade represented.

Historical Ecology of Lizard Community Structure

In the central Amazon of Brazil, the 19 most common lizard species segregate on the basis of microhabitat, prey types, and prey size (Vitt et al., 1999). Overlaps among species in diets and microhabitats are relatively low but some guild structure is evident. Further analyses demonstrate that resource use (diets and microhabitats) is not random; rather, the lizard community is structured with respect to resources. An analysis in which the relative evolutionary similarities among lizard species were compared with dietary and microhabitat similarities (overlaps) shows that a historic component of patterns of prey use exists; more closely related species eat more similar prey (Fig. 13.10). The same relationship does not hold for patterns of microhabitat use. Although one explanation for the observed structure in this lizard community is that present-day species interactions led to ecological segregation, the phylogenetic analysis suggests that at least some of the differences among species have their origins deeply embedded in the evolutionary history of the various lizard clades and cannot be attributed exclusively to ongoing species interactions. Historically, species sorting may have been based on similarity of

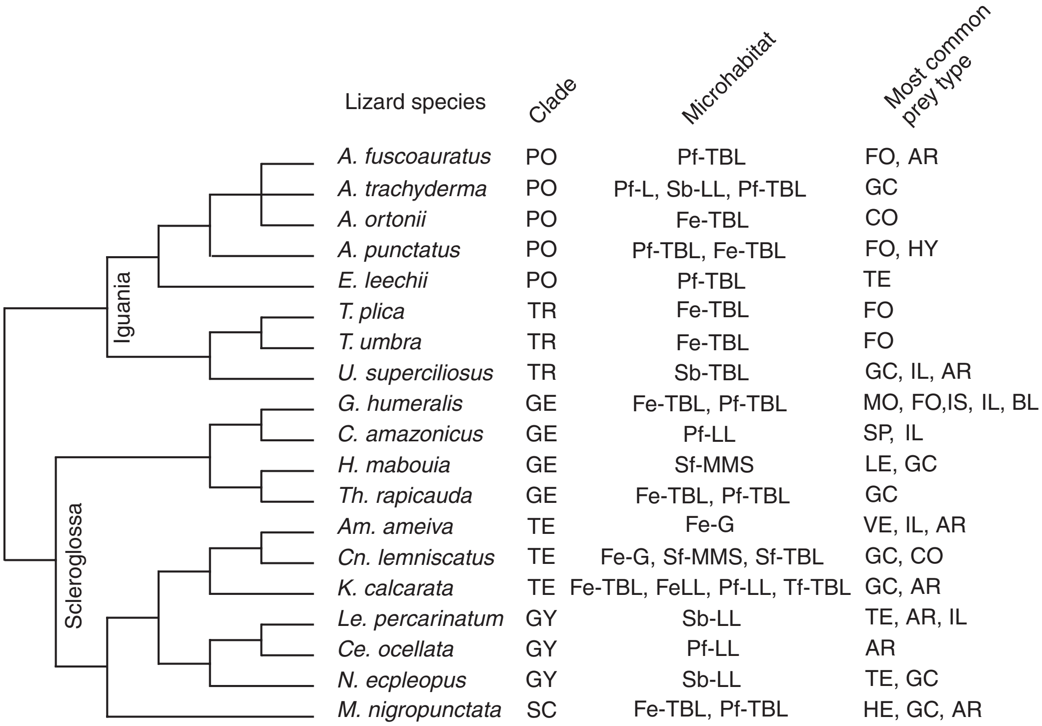


FIGURE 13.10 Phylogenetic reconstruction for lizards from the central Amazon rain forest showing the topology of ecological characters. Lizard genera, from top to bottom, are *A* = *Anolis, E* = *Enyalius, T* = *Tropidurus, U* = *Uranoscodon, G* = *Gonatodes, C* = *Coleodactylus, H* = *Hemidactylus, Th* = *Thecadactylus, Am* = *Ameiva, Cn* = *Cnemidophorus, K* = *Kentropyx, Le* = *Leposoma, Ce* = *Cercosaura, N* = *Neusticurus*, and *M* = *Mabuya*. Lizard clades are PO = Polychrotinae; TR = Tropidurinae; GE = Gekkonidae; TE = Teiidae; GY = Gymnophthalmidae; and SC = Scincidae. Microhabitat categories are Fe-G = forest edge, ground; Fe- LL = forest edge, leaf litter; Fe-TBL = forest edge, trunk, branch, limb; Pf-L = primary forest, leaf; Pf-LL = primary forest, leaf litter; Pf-TBL = primary forest, trunk, branch, limb; Sf-MMS = litter secondary forest, man-made structure; Sf-TBL = secondary forest, trunk, branch, limb; Sb-TBL = streambed, trunk, branch, limb; Sb-LL = streambed, leaf litter; and Tf-TBL = treefall, trunk, branch, limb. Prey categories are OD = odonates; GC = grasshoppers and crickets; BL = roaches; TE = termites; CO = beetles; HE = hemipterans; LE = butterflies and moths; SP = springtails; HY = hymenopterans (nonant); FO = ants; IL = insect larvae; AR = spiders; IS = isopods; MO = mollusks; and VE = vertebrates. Adapted from Vitt et al. (1999).

species and competitive interactions, but ecological differences between major clades were sufficient to allow coexistence. This result suggests the hypothesis that deep-rooted assemblages may behave differently in an ecological sense than shallow-rooted assemblages (see the next section on ecomorphs) because much of the important divergence took place long ago.

Ecomorphology

The recognition of distinct "ecomorphs" of *Anolis* lizards in the Caribbean resulted in a long-term evaluation of patterns of morphological and ecological evolution in island lizards that continues today (Williams, 1972). Williams observed that morphologically similar but unrelated anole species occupied similar microhabitats on different islands within the Lesser Antilles. The lizards had nearly the same body size, coloration, morphology, and behavior. The combined "morphotypes" and "ecotypes" composed what has become known as ecomorphs, which are morphologically similar animals of different species living in similar microhabitats (Fig. 13.11). For example, a species that lives in the crown of vegetation and has a specific associated morphology is called the crown ecomorph. Most striking was the observation that similar ecomorphs on different islands were not necessarily each other's closest relative. This observation suggests that the evolution of ecomorphs on different islands was independent (Williams, 1983).

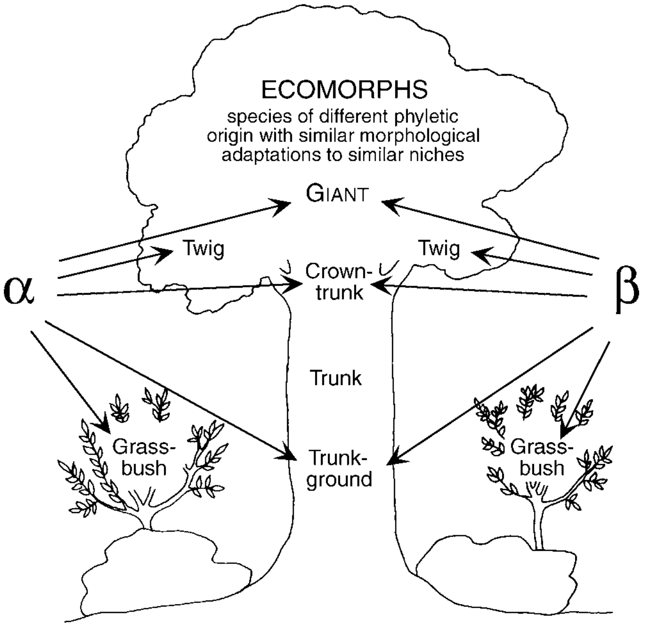


FIGURE 13.11 Ecomorphs of *Anolis* lizards in the Caribbean. α and β indicate different (independent) clades of anoles. Adapted from Williams (1983).

In both Jamaica and Puerto Rico, evolutionary patterns of community structure can be determined by examining the topology of morphological and ecological traits on independently derived cladograms (Losos, 1992). As the number of anole species increased in Jamaica (Fig. 13.12), generalist species split into two specialized species, one using the trunk–ground habitat and one using crowns of vegetation. The crown lineage then split to form one large-bodied species (crown-giant) and a smaller species that utilizes the trunk–crown interface. In Puerto Rican *Anolis*, community evolution occurred as well but the pattern of evolution was not identical to that in Jamaica (Fig. 13.12). Similar to Jamaica, the generalist species split into two new species, but one is a crown-giant and the other is a trunk–ground species. The trunk–ground lineage then produced a trunk–crown species. Finally, the trunk–ground lineage produced yet another species, this time a grass–bush species. In both instances, morphology of the lizards is closely related to habitat use. Species that are more arboreal have longer hindlimbs and more streamlined morphology. Most striking is that similar ecomorphs were produced from two initial species (twig and generalist) that are different in Jamaica and Puerto Rico. In the four species assemblages, for example, each island has the same set of ecomorphs but no species are shared. The same ecomorphs evolved independently on each island, showing that the evolution of community structure of *Anolis* in these two islands is convergent.

Symbiotic Relationships among Species

Symbiosis is an intimate association in which one species occurs on or in the body or habitation of a host species. The association may be detrimental (disease, parasitic) to the host or beneficial (mutualistic, commensal) to one or both species. Disease and parasites variously affect the performance and survival of individual amphibians and reptiles (see Chapter 11), but whether a disease or parasite species can or does exclude an amphibian or reptile species from a community is not well known. Loss of amphibian species due to disease and/or parasites is suspected to be occurring at a global scale (see Chapters 11 and 14).

In beneficial symbiosis, two species are dependent upon each other; in one case, both species benefit from the association (mutualism), and in the other, both are capable of living independently although the association benefits one species (commensalism). Mutualistic interactions between reptilian and/or amphibian species have not been identified. Several examples in which algae and other plants grow on the surface of reptile skin suggest that mutualistic interactions between reptiles and other

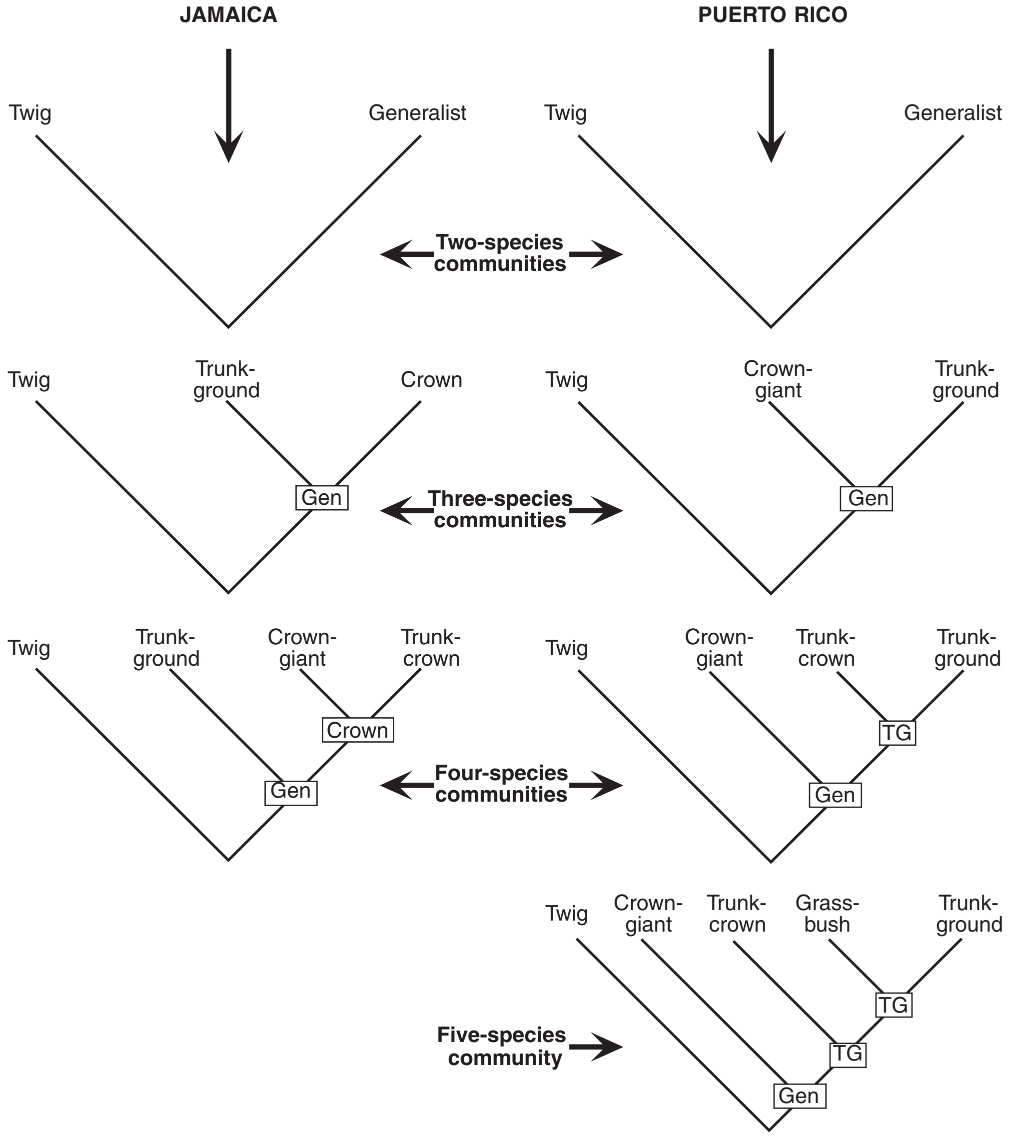


FIGURE 13.12 Patterns of community evolution in Jamaican (left) and Puerto Rican (right) *Anolis* lizards. Progression downward through communities within islands shows the evolution of anole ecomorphs. Comparison across islands (e.g., compare four-species communities) shows that evolution of ecomorphs in *Anolis* living on different islands is convergent. Adapted from Losos (1992).

organisms might be more widespread than previously thought. Algae is common on the carapace of turtles (e.g., Gibbons, 1968; Hulse, 1976), and both a bryophyte and an alga have been observed on the lizards *Corytophanes cristatus* and *Uranoscodon superciliosus* (Gradstein and Equihua, 1995; Howland et al., 1990). In *U. superciliosus*, lizards covered with algae appear more cryptic than lizards without algae because all individuals live on algae-covered trees. The algae may benefit by using the lizards as dispersers. At the community level, one member escapes predation and another is dispersed.

The herbivorous iguanine lizards and green seaturtles require the presence of a microbial gut fauna to break down cellulose and hemicellulose (Bjorndal, 1996; Troyer, 1991). Plant fiber is broken down by microbes in the colon, which is aided to some extent by mechanical action of nematodes (Nagy, 1977; Iverson, 1982). Once broken down by symbionts, the end products of fermentation are taken up by the wall of the colon. In these examples, the linkage between the herbivores and their symbionts is a critical component of community structure.

GEOGRAPHY OF POPULATIONS

Determinants of Species Distributions

Each organism has specific physiological tolerances and requirements. Populations represent a distribution of the requirements of their individual members. If an individual's tolerances are not exceeded and if its requirements are fulfilled, it survives. Survival of the individual does not ensure survival of the population; the individual must reproduce and so must its offspring for the population to persist. It is this latter aspect that makes age-specific mortality and age-specific fecundity the key life history traits (see Chapter 5) and, ultimately, the key determinants of a population's occurrence and persistent in any geographic area.

Because a species consists of multiple local populations, the species' distribution represents the total occurrences of its populations, and the borders of each species' distribution mark the areas where populations waver between extinction and self-perpetuation. In a season or year where conditions allow reproduction and survival of the young, the population grows; in the next, reproduction could be unsuccessful and the population could drift toward extinction. The factors affecting these population cycles are climate (micro and macro) relative to physiological tolerances, availability and access to resources, and interspecific interactions. A fourth factor, historical accident and dispersal ability, determines what species are likely to occur in an area and the probability of their reaching an area.

Among the thousands of amphibian and reptilian species, many can live in locations outside of their natural distribution. The success of numerous exotic lizards in Miami, Florida, of the marine toad (*Bufo marinus*) in the West Indies and the Southwest Pacific, and of the brown tree snake (*Boiga irregularis*) in Guam shows this ability. Normally, the species occupying an area derive from nearby areas, and a vacant habitat is ''filled'' by a few migrants that cross barriers (geographic or unsuitable habitats) or by the slow expansion of a population into less hospitable areas. Dispersal abilities and opportunities are variable. Small, fossorial amphibians and reptiles have poor dispersal abilities, whereas large, aquatic species tend to be good dispersers. Coastal and riverside species are more likely than inland species to be transported elsewhere. Amphibians rarely cross saltwater barriers; reptiles commonly do. These generalities have numerous exceptions and only indicate a few of the factors associated with a species' dispersal and its tolerances and preferred habitats. Dispersal ability and the nature of barriers are also critical in determining the level of gene flow among populations and local population differentiation.

It is hardly surprising that climate affects a species' occurrence. An animal will not survive in an area where one or more of its physiological tolerances are regularly or constantly exceeded. Temperature, rainfall, and their periodicity establish the climatic regimes under which individuals and populations must operate. Tolerance limits (Chapter 7) are species specific, although variation among populations exist, particularly in widespread species. Because the edges of species' ranges often closely match the isograms of rainfall and temperature, tolerance limits may define the limits of species' distributions (Fig. 13.13). Frequently, the effects of temperature and/or rainfall are greater on one life stage than on another, but the survival of each stage is critical for the survival of the population. Spring droughts may prevent temporary-pond amphibians from breeding or, if breeding does occur, larvae recruitment may fail due to ponds drying early. Adults may survive (tolerate) the drought to breed again when conditions improve. Droughts extending over several years can cause populations to go extinct locally, particularly in short-lived species. In turtles with temperature-dependent sex determination (Chapter 5), cooler summers may produce all-male cohorts, and, if this hatchling sex ratio continues, the sex ratio may be biased toward males and result in eventual population declines.

Climate, resources, and interspecific interactions vary from area to area, and each population adjusts (adapts) to its local conditions. Because the conditions are nowhere the same, each population adapts differently and is diverging genetically (evolving) from other populations. If this divergence continued, speciation would occur; however, speciation is a rare outcome because adjacent populations exchange individuals. Migrants bring new genes that are incorporated into the gene pools of adjacent populations. The rate of gene flow is a function of the closeness of the populations and the dispersal tendency of the species. The rate can be quite slow, yet still maintain the genetic continuity of distant populations. While maintaining the continuity, local populations can adapt to local conditions. Often, the adaptations most easily detected are traits associated with reproduction (Fig. 13.14; also see Chapter 5).

Biogeography—Patterns of Distribution

Throughout the world, geographic areas contain different species of plants and animals. The flora and fauna of a given area are relatively uniform in species number and composition compared to adjacent areas. The flora and fauna can persist over large or small areas and then gradually or abruptly change to a new flora and fauna. Biogeography is the study of these patterns and the factors that cause them. Biogeography has two general

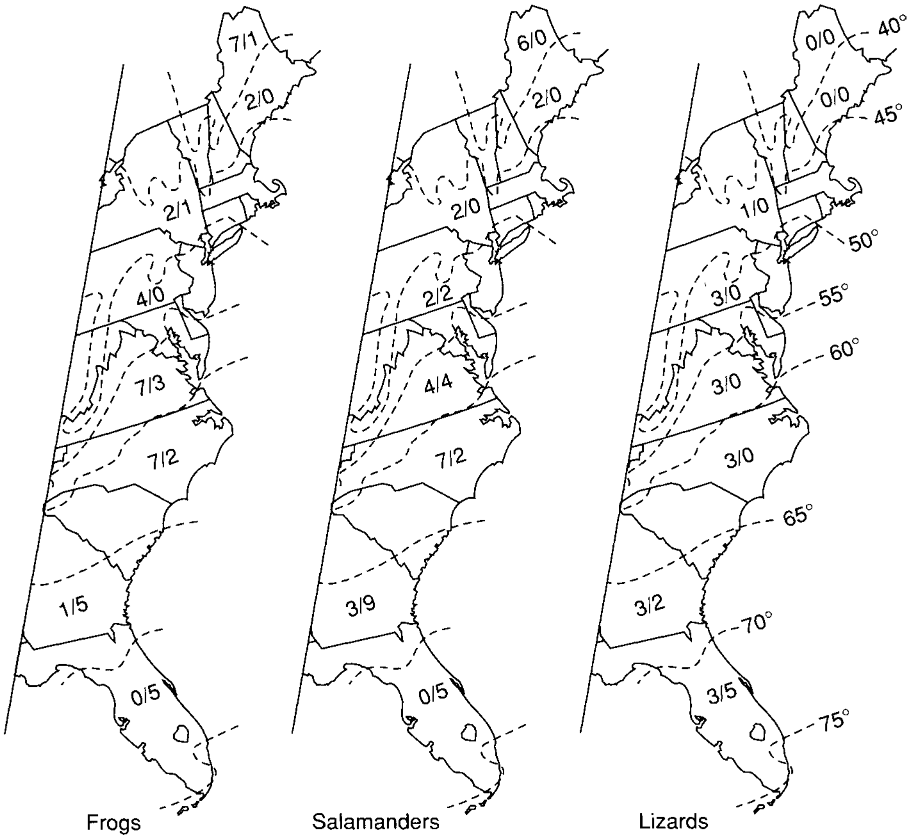


FIGURE 13.13 Temperature isotherms and the northern and southern termini of frog ($n = 30$ species), salamander (26), and lizard (16) distributions in eastern North America (piedmont and coastal plains). The isotherms are mean annual temperature (°F); the integers in each zone are number of species with ranges terminating in the interval (northern/southern termini). Isotherms from USDA (1941); distributional data from Conant and Collins (1991).

approaches. Geographical ecology (ecological biogeography) examines the structure of different communities from a perspective of resource utilization. Biogeography often examines the number of species in an area and their origins but can also examine how different species partition the available resources. Historical biogeography examines the structure of communities based on the relationship and origins of the taxa, emphasizing the phylogenetic affinities of the species and their evolutionary histories.

Biomes and Biogeographic Realms

Current worldwide distributions of communities form two patterns: biomes and biogeographic realms. Biomes are based on the similarity of the overall structure of the plant community relative to climate. Biogeographic realms are based on the phylogenetic relatedness of the component taxa. The biome concept ignores animals and recognizes communities based on plant structure (e.g., height and shape of plants, leaf structure, deciduous or evergreen vegetation) because climate is the primary determinant of vegetation. The major terrestrial biomes are tundra; boreal coniferous forest (taiga); temperate deciduous and rain forest; temperate grassland; chaparral; desert; tropical grassland and savannas; tropical scrub forest; tropical deciduous forest; and tropical rain forest. These biomes can be further subdivided in multiple ways. In all cases, biomes reflect the annual cycle of temperature and rainfall; animal distributions match the biomes in general but deviate considerably when examined in detail for amphibians and reptiles. Few amphibians or reptiles occur in tundra, and those that do, only do so marginally. Assemblages with low numbers of species are widespread in the boreal forest biome, and are dominated by amphibians. Northern temperate latitudes have salamanders; southern ones have none. The number of species and the diversity of the herpetofauna increase within the temperate biomes and into the tropics, but, unlike plants in which overall community structure matches climate, animal community composition is more influenced by taxonomic affinity.

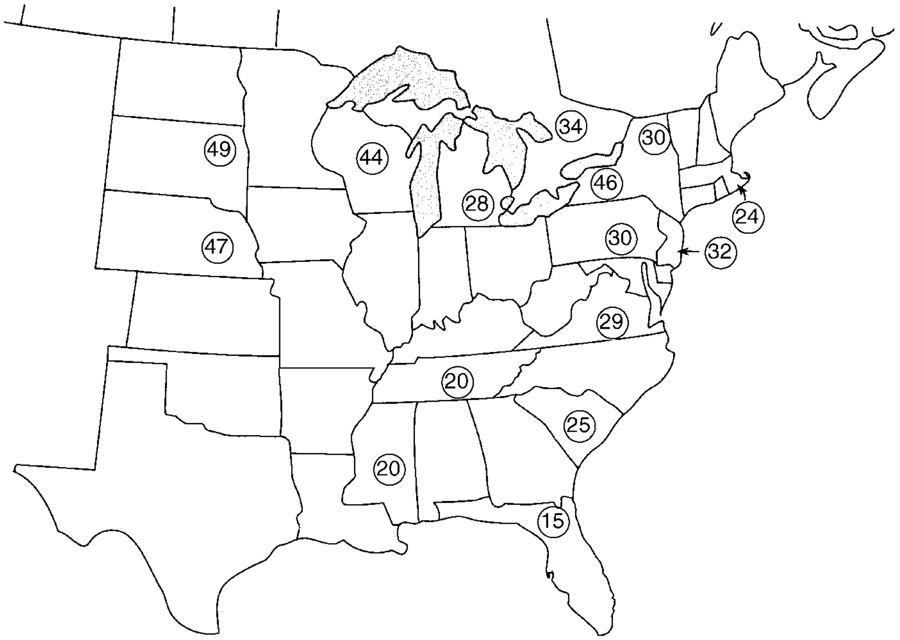


FIGURE 13.14 Geographic variation in clutch size for populations of the snapping turtle (*Chelydra serpentina*) in North America. The integers represent mean clutch sizes for their areas of placement. Data from Fitch (1985) and Iverson et al. (1997).

Biogeographic realms (Fig. 13.15) are defined in terms of animal and plant distributions based on phylogenetic affinities. The realms derive from higher-order relationships, typically relatively large clades, and reflect past geological events (continental drift, barriers and connections for species dispersal). Indeed, the present distribution of many higher taxonomic groups of amphibians and reptiles matches the past continental connections and fragmentations proposed by the plate-tectonic (drifting continents) theory (Fig. 13.16). (Compare Fig. 13.15 with the distribution maps in Chapters 15–21.) For example, salamanders occur mainly in the Holarctic (Nearctic + Palearctic) region, and frog diversity is highest in the Southern Hemisphere. These distributions match the Mesozoic split of the supercontinent of Pangaea into northern Laurasia and southern Gondwana. Ancient groups still retain a Laurasian or Gondwanan distribution. Pipid frogs occur in both Africa and South America. The distribution of pleurodiran turtles reflects the historical geologic links between Australia, southern Africa, and South America, a Gondwanan distribution. Cryptobranchid, plethodontid, and salamandrid salamanders occur both in North America and in Eurasia, suggesting an ancient distribution throughout Laurasia. Just as these interclade relationships match ancient topographies, intergenetic and interspecific distributions reflect more recent (but still ancient) geological events and climates. Each continent has been divided into biogeographic provinces that are delimited by abrupt terminations in species distributions as one community shifts to another. These discontinuities in community structure likely reveal a prior isolation of communities and speciation that occurred within each one.

Geographical Ecology

The striking differences in number of species at different localities and latitudes have long intrigued biologists (Table 13.1). Comparisons of species richness (diversity or density) provide geographic comparisons of community structure. Most attention has been directed at explaining the tendency for species diversity to increase from high-latitude habitats to tropical ones and, as for most other studies of communities, at examining the changing diversity within specific taxonomic groups such as frogs or lizards. The emphasis in most instances centers just on the number of species rather than a combination of the number of species and their relative densities. Accurate and comparable data on species abundance are largely unavailable (see below), making the most interesting comparisons difficult.

Numerous explanations have been proposed to account for the differences in richness. The primary explanations are evolutionary time, ecological time, climatic stability, climatic predictability, spatial heterogeneity, productivity, and species interactions. These explanations are not mutually exclusive, and likely

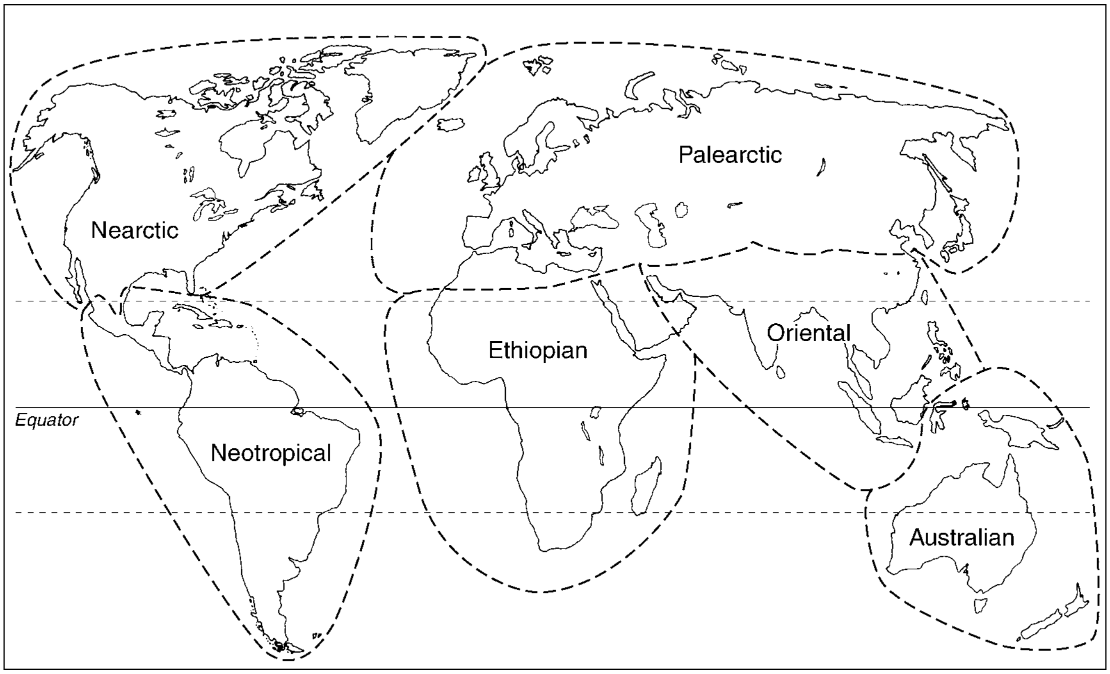


FIGURE 13.15 Biogeographic realms of the world.

multiple causes operate in different combinations at different locations and at different times.

Evolutionary and Ecological Time Two distinct timescales are typically considered in biogeographic studies. Evolutionary time refers to time periods long enough for adaptation to occur. Ecological time refers to time periods short enough that adaptation has not occurred. Older communities presumably have had more time for species to adapt to the local environment. As a result, they should contain species that exhibit adaptations to various aspects of the particular environment or community, thus reflecting the influence of evolutionary time periods. Species can colonize new or modified habitats with no apparent evolutionary change (adaptation); thus these events are considered to occur over ecological time. Amphibian and reptile species of northern sites (Andrew Experimental Forest, Vienna; Table 13.1) are all wide-ranging species with distributions >1000 km^2, in contrast to tropical sites, which have many species with small distributions. Although individuals of temperate-zone amphibians and reptiles may have limited dispersal abilities, their populations are capable of expanding as their preferred habitats expand. This is evident from the reoccupation of glaciated portions of North America in the last 10–15 thousand years; the current ranges of some species (*Ambystoma laterale, Rana septentrionalis, Elaphe vulpina, Emydoidea blandingii*) are totally within formerly glaciated areas.

Climate Stability and Predictability Climatically stable areas have little seasonal or long-term change in temperature or rainfall. Such locations are limited to a few rain forest areas of the world, for example, Amazonian forest on the eastern slopes of the Andes. These areas generally have relatively high numbers of species of amphibians and reptiles. Santa Cecilia, Ecuador, for example, has 173 species of amphibians and reptiles, and a site near Iquitos, Peru, has about 200 species (Duellman, 1978; Rodriguez and Cadle, 1990). Climatically predictable habitats with regular cycles of wet–dry or hot–cold seasons are far more numerous, but species richness in these habitats varies considerably depending upon latitude. Relative length and harshness of the cold or dry seasons are rarely considered and can be quite influential in limiting the species occurring in a particular habitat. Climatic predictability may be more imagined than real; climate records of this century emphasize the great irregularity in the beginning, end, and length of seasons. Predictability of climate may be no more regular in the tropics than in the temperate zone.

Spatial Heterogeneity Habitats with a greater spatial or structural heterogeneity tend to have more species, within the constraints of climate. A structurally heterogeneous habitat at northern latitudes would not have a high diversity of reptiles because temperature is an overriding limiting factor for ectothermic vertebrates. But a structurally heterogeneous habitat at the same

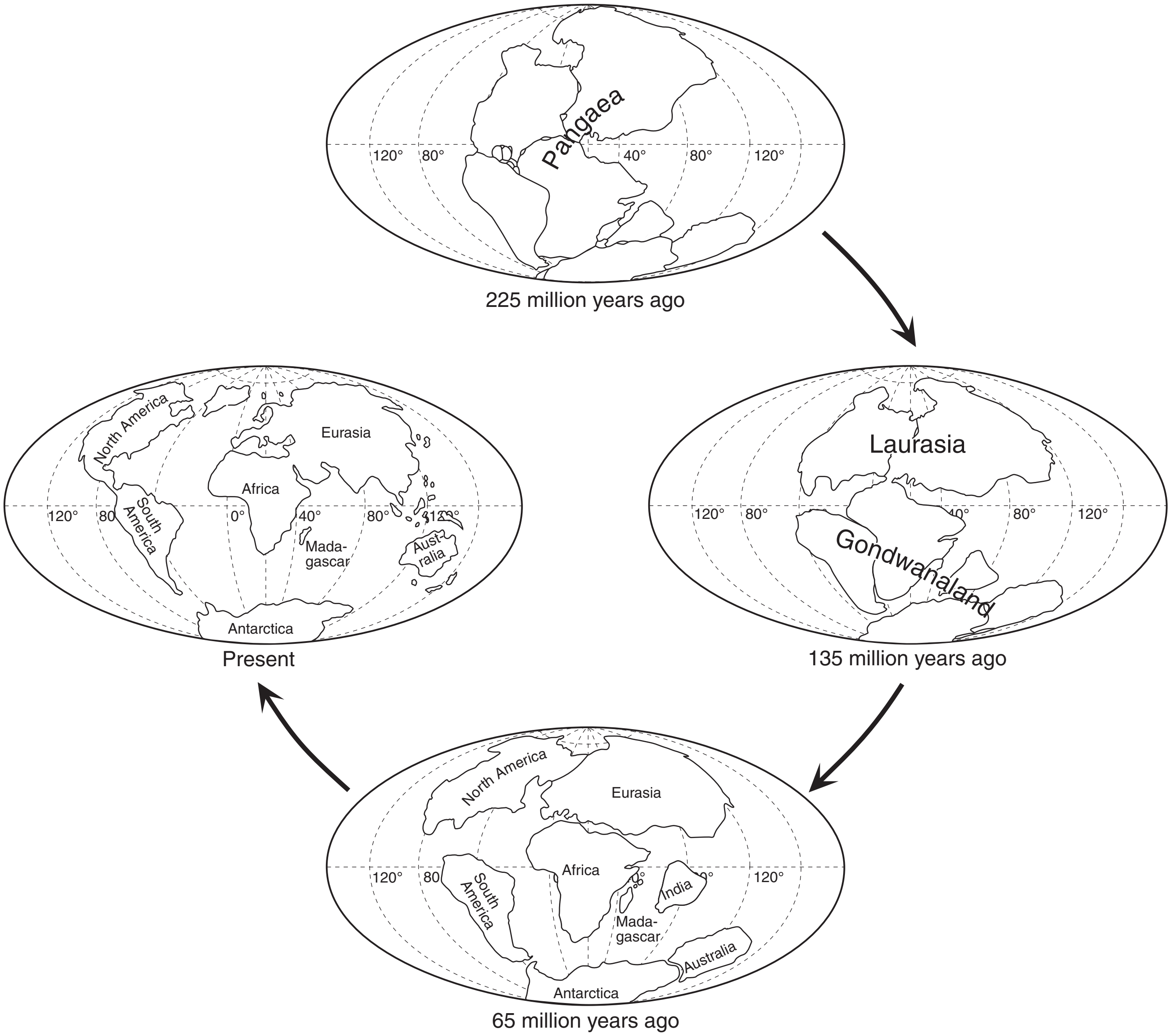


FIGURE 13.16 Diagrammatic reconstruction of the history of continental drift.

latitude as a structurally simple habitat would be expected to contain more species of ectotherms. Structurally complex forest habitats usually have more species than the structurally simpler grassland and desert habitats, but striking exceptions exist. The greatest diversity of lizards, for example, occurs in the Great Victorian Desert of Australia, not in the world's rain forests! Three habitats exist in the Sakaerat area (Table 13.1): gardens and fields, deciduous forest, and evergreen forest. At this locality and elsewhere, herpetofaunal diversity increases proportionately with spatial heterogeneity of the habitat (54, 67, and 77 species, respectively). Productivity is related to spatial heterogeneity. High food availability and high prey diversity allow a greater number and diversity of consumers.

A common assumption is that the abundance of each species is less in a species-rich community than in a species-poor one. This conjecture may be true for tree species in a rain forest compared to a temperate-zone deciduous forest. While probably not true for most herpetological communities, actual comparisons do not exist (see density estimates in Table 12.2). Such comparisons would examine the actual abundance (density) of each member species in the area under consideration. Another abundance comparison would be an examination of the relative abundance (equability or evenness) of each species within the community; however, either manner of comparisons is confounded by several factors: body size, trophic position, seasonal and annual fluctuation in population densities, and widespread lack of accurate population censuses (particularly for tropical populations). Ignoring these difficulties, it is unlikely that all species are equally abundant in any community or assemblage. More likely, one or a few species have high densities, and all other species are at low densities. The Sakaerat skink assemblages show abundance patterns that are likely typical of those between common and rare species in other herpetological assemblages, whether they are from the tropics or a temperate zone (Fig. 13.17).

Exceptions to equal abundance between species-rich and species-poor assemblages occur between mainland and island anole assemblages. Island populations have densities 2 to 10 times higher than mainland populations. A few other lizards also occur at higher densities on islands, but comparisons for other amphibians and reptiles are lacking. These differential densities appear to result from differences in predation; generally, island populations experience relaxed predation rates (see Chapter 5).

Species richness also differs markedly between island and mainland assemblages. Islands have fewer species compared to comparably sized areas on the mainland. Further, a positive relationship exists between island size and species richness, and a negative relationship exists between the distance of an island from a colonizing source (e.g., mainland) and species richness. These species–area relationships led MacArthur and Wilson (1967) to develop an equilibrium theory of island species diversity. The equilibrium theory proposes that a balance exists between the number of species colonizing an island and the number of species going extinct. The colonization or immigration rate is a function of the island distance from a source area, and the extinction rate is a function of island size. Since immigration and extinction are assumed to be continuous processes, species number reaches an equilibrium value and remains constant even though the composition of the species assemblages changes continually.

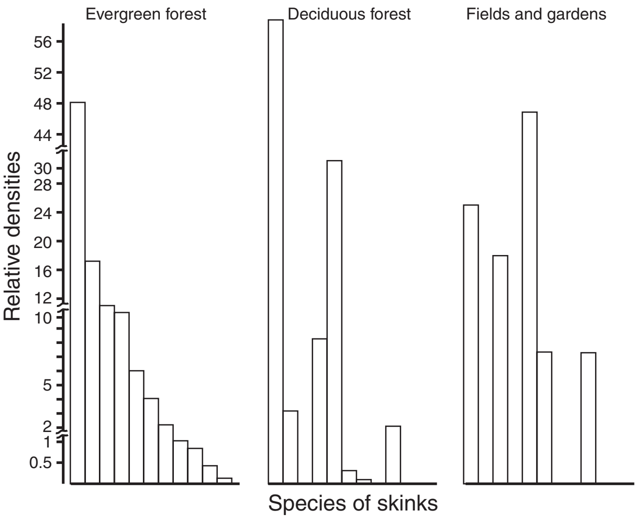


FIGURE 13.17 Relative abundance of skink assemblages in three habitats at Sakaerat, Thailand. Eleven species occur in the evergreen forest, and subsets occur in the deciduous forest and agriculture areas. The species are ranked in order of decreasing abundance for the evergreen forest assemblage, and that order is retained for the two other assemblages. Skink abundance is unequal between habitats; skinks compose 53, 43, and 4% of the total lizards for the three habitats, respectively. Data from Inger and Colwell (1977).

Although a linear relationship between island size and species number exists for lizards (Fig. 13.18), few other herpetological groups have been examined. Island assemblages deviate from several predictions based on theory. Lizard assemblages commonly have a higher species diversity than predicted, suggesting supersaturation, and possess a constant number of species over a wide range of small island sizes. These deviations result from lower dispersal and extinction rates than the birds and insects from which the theory was developed.

A species–area effect has been proposed for peninsulas as well as islands. The peninsula effect predicts a decline in species richness from a peninsula's base to its tip. Its applicability to amphibians and reptiles remains uncertain. Species diversity does decline for some herpetofaunas (peninsular Florida) but not for others. The reptiles of Baja California are as diverse at its tip as at its base.

Historical Biogeography

In historical biogeography, the perspective shifts from the recent past of ecological biogeography to the distant past, the deep time of geological history, and from

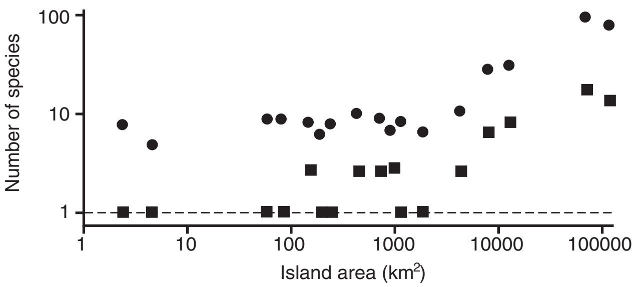


FIGURE 13.18 Relationship between island size and species richness of the *Sphaerodactylus* (squares) and lizard (circles) faunas in the West Indies. Dashed line depicts the islands with only a single species. Data from Schwartz and Henderson (1991).

intracommunity interactions to phylogenetic relationships for reconstruction of species and higher taxa distribution patterns. Current theory and analyses are based either on a dispersal or on a vicariance viewpoint. Many studies fall somewhere between the two extremes. Dispersal was the primary mechanism for explaining current distributional patterns and dominated biogeographic studies, until the early 1970s when the geological worldview shifted from static continents to drifting continents (plate tectonics). A vicariance-based mechanism to explain distributional patterns utilizes cladistic analyses to test distributions against phylogenetic hypotheses.

Dispersal theory rests on two basic assumptions: taxonomic groups have a center of origin and each group dispersed from its origin center across barriers; the resulting communities or biota derive from one to several centers and dispersal events. Vicariance theory rests on the assumptions that taxonomic groups or biotas are geographically static, and that geological events produce barriers and the biota diverges subsequent to isolation. Both theoretical approaches require knowledge of phylogenetic relationships to discern the ancient dispersal routes or the areas occupied by ancient biota. Because allopatric speciation appears to be the dominant mode of speciation and the fragmentation of a biota is more likely than a biota dispersing as a single unit, vicariance interpretations are generally preferred over dispersal explanations. Vicariance explanations are also more amenable to testing. Dispersal explanations are required, however, to account for the evolution of oceanic island biotas, such as those found in the Galapagos and Hawaiian islands.

The geologic history of most areas and their herpetofaunas is so complex that a single theory is inadequate. The Seychelles Islands provide a case study. The herpetofauna of the Seychelles contains several levels of endemicity that strongly indicate multiple origins and suggest that components arrived at different times (Table 13.5). The oldest elements are the sooglossid frogs and caecilians. These groups have only distant (and somewhat uncertain) affinities with African taxa. Both are confined to the high granitic islands of the Seychelles that have been emergent since the Mesozoic. The granitic islands appear to be fragments of the Indian tectonic plate that broke free from the current African plate and moved northward to collide with the Asian plate. Since amphibians are noted for their inability to cross huge saltwater gaps, these amphibians and perhaps the gecko *Ailuronyx* are derived from ancestors living on the original African–Indian plate. The rhacophorid frog *Tachycnemis* and some reptiles also appear to be derived from an early Seychellan herpetofauna, but likely from taxa that arrived via island hopping across narrow water gaps. The day-geckos (*Phelsuma*) and others are more recent arrivals that show closer affinities with Malagasian and African taxa, but presumably arrived prior to human colonization. More recent components have arrived via human transport (*Gehyra*).

TABLE 13.5 Relative Ages of Select Components of the Herpetofauna of the Seychelles

Ancient (>60 mybp)	Near ancient (<60–10 mybp)	Near recent (<10 mybp)	Recent (<1000 years)
Grandisonia			
Sooglossus	*Tachycnemis*	*Ptychadena*	
Ailuronyx	*Urocotyledon*	*Phelsuma*	*Gehyra*
	Janetaescincus	*Mabuya*	
	Lycognathophis	*Boaedon*	*Ramphotyphlops*
	Pelusios seychellensis	*Pelusios subniger*	

Source: Data in part from Nussbaum (1985a).

Note: Taxa are arranged vertically—caecilians, frogs, geckos, skinks, and turtles. The age of each taxon is based on its degree of taxonomic differentiation and endemicity. The ages are arbitrary estimates beginning immediately prior to separation of the Seychelles from Gondwana (Ancient) and mark the islands' progressive isolation from faunal source areas.

A vicariance explanation fits the present-day distribution pattern of chelid turtles (Fig. 13.19). Two cladistic patterns have been proposed for the relationships among the chelid genera. Gaffney's cladogram (1977) suggests *Pseudemydura* as the sister group to all other extant chelids. Further, the Australian *Emydura* group is the sister group of all Neotropical chelids and the Australian long-necked *Chelodina*. This pattern of cladogenetic events would suggest that all modern genera arose from vicariance events in the deep past on the southern continent (Fig. 13.19) or that the ancestor of Neotropical chelids and the Australian chelids, excluding *Chelodina*, arose on the southern continent, and subsequently the ancestral *Chelodina* reached Australia and differentiated there. This latter explanation likely requires a dispersal event. The cladistic relationships proposed by Seddon et al. (1997) offer a simpler evolutionary scenario. The ancestral chelids occurred broadly on the southern continent, and its rifting into the South American and Australian–Antarctica continents was the vicariance event that gave rise to the ancestors for two monophyletic continental clades. While the latter offers a more parsimonious explanation, both explanations and both cladograms are hypotheses and require further testing. The strength of the vicariance model is the ability to test biogeographic hypotheses and reject those that do not match the proposed geologic or other vicariance models.

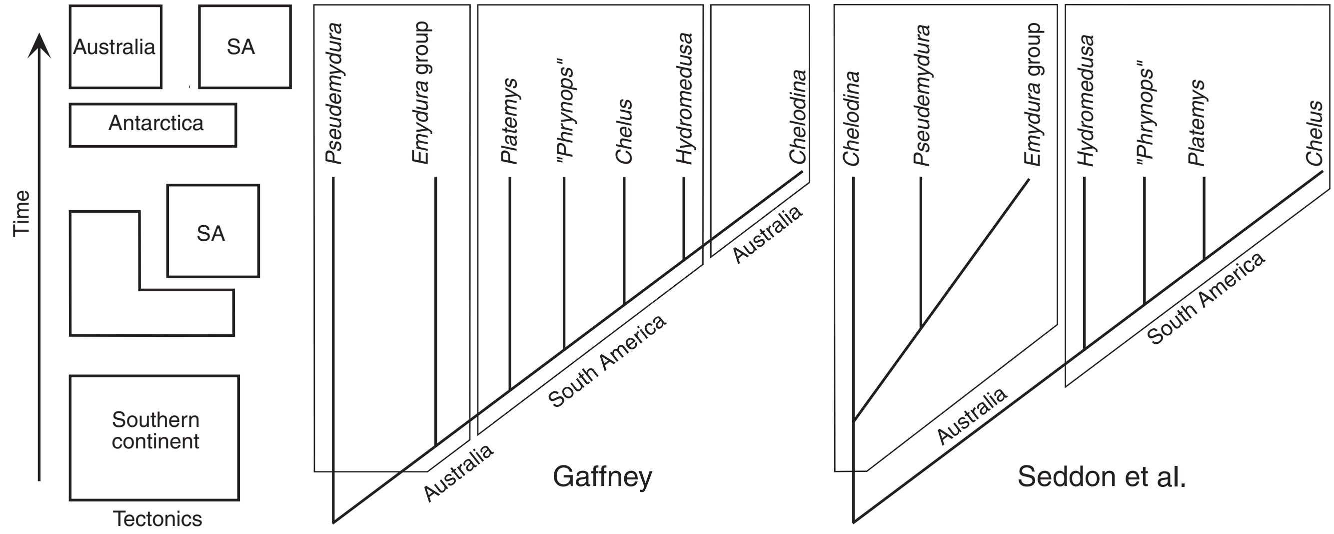


FIGURE 13.19 Comparison of phylogenetic relationships of chelid turtles and their distributions to the tectonics of southern continents. Cladograms adapted from Gaffney (1977) and Seddon et al. (1997).

The Seychelles and chelid examples highlight the necessity of a pluralist approach to biogeographic analysis and of the need to provide explanations (hypotheses) that can be tested. Multiple levels of interpretations are likely required for the patterns of most herpetofaunas and their component species.

ADDITIONAL READING

Cody, M. L. (1996). Introduction to long-term community ecological studies. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 1–15. Academic Press, San Diego.

Pianka, E. R. (1973). The structure of lizard communities. *Ann. Rev. Ecol. Syst.* **4**: 53–74.

Pianka, E. R. (1975). Niche relations of desert lizards. *In* "Ecology and Evolution of Communities" (M. Cody and J. Diamond, Eds.), pp. 292–314. Harvard University Press, Cambridge, MA.

Wilbur, H. M. (1987). Regulation of structure in complex systems: Experimental temporary pond communities. *Ecology* **68**: 1437–1452.

Williams, E. E. (1983). Ecomorphs, faunas, island size, and diverse end points in island radiations of Anolis. *In* "Lizard Ecology. Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 327–370. Harvard University Press, Cambridge, MA.

REFERENCES

Characteristics of Communities: Local Species Assemblages—Factors Influencing Community Structure: Cody, 1996; Pianka, 1973, 1986; Schoener 1974a; Toft, 1985.

Short-Term Studies (Single Sample and Far-Flung): Brockelman, 1969; Caldwell and Vitt, 1999; Inger, 1980; Inger et al., 1986; Morin 1987; Pianka, 1973, 1975, 1985, 1986; Scott, N., 1976; Scott, D., 1990, 1994; Semlitsch et al., 1988; Wilbur, 1972, 1987; Wilbur and Fauth, 1990; Williams, 1972.

Long-Term Studies: Cody, 1996; Congdon and Gibbons, 1996; Dunham, 1980; Ernst, 1971; Hairston, 1996; Likens, 1989; Mitchell, 1988; Pianka, 1992, 1996; Semlitsch et al., 1996; Sexton, 1959; Zweifel, 1989.

Phylogenetic Approaches to Community Ecology: Cadle and Greene, 1993; Vitt et al., 1999.

Ecomorphology: Losos, 1992; Williams, 1972, 1983.

Symbiotic Relationships Among Species: Bjorndal, 1996; Gibbons, 1968; Gradstein and Equihua, 1995; Howland et al., 1990; Hulse, 1976; Iverson, 1982; Nagy, 1982; Troyer, 1991.

Geography of Populations, Determinants of Species Distributions: Fitch, 1985.

Biogeography—Patterns of Distribution: Inger and Colwell, 1977; MacArthur and Wilson, 1967; Seddon et al., 1997.

Chapter

14

Conservation Biology

> *I dreamed I saw the knights in armor coming, saying*
> *something about a queen*
> *There were peasants singing and drummers*
> *drumming and the archers split the tree*
> *There was a fanfare blowin' to the sun, there was*
> *floating on the breeze*
> *Look at Mother Nature on the run in the 1970s*
> *Look at Mother Nature on the run in the 1970s*
> Neil Young, 1970
> "After the Gold Rush."

Conservation biology is a new field of science, arising in the 1970s as a crisis discipline from multiple arenas of established scientific investigation. Of course, neither the recognition of the necessity nor the desire of biologists to conserve natural habitats with their native floras and faunas is new. What is new is the recognition of the urgency of conservation and the application of concepts and tools of biology, no matter how imperfectly known, to real-life conservation issues. The emphasis is now on action. Rather than conducting research for knowledge alone, a critical examination of disappearing biotas and increasingly fragmented and degraded habitats is necessary to develop conservation strategies. New knowledge must be integrated with the old to address issues that impinge directly on human survival in the long term and quality of life in the immediate future (Fig. 14.1).

A primary tenet of conservation biology is that all environmental crises involve people and that the resolution of each crisis must address societal as well as biological issues (Meffe and Carrol, 1994). Problems created by people require the participation of local people in devising solutions and educating themselves to prevent further degradation of their environment.

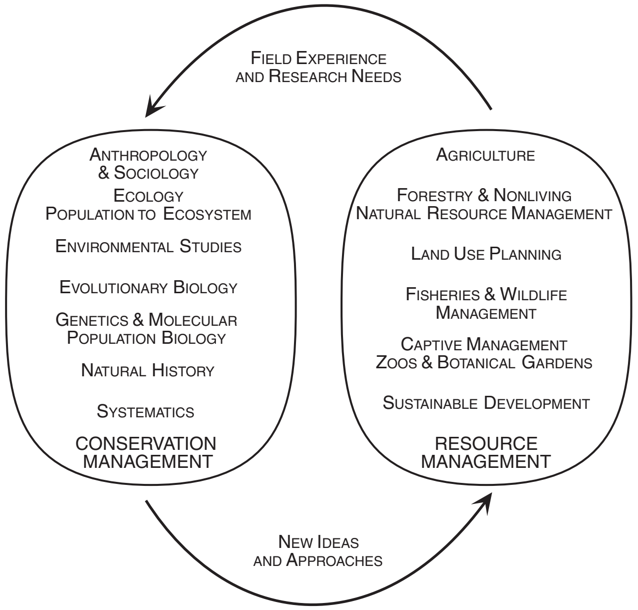


FIGURE 14.1 Conservation biology encompasses a broad range of biological and social studies to address issues and problems arising from, and recognized through, the use and management of natural resources. Adapted from Temple (1991).

GENERAL PRINCIPLES

A major focus of conservation biology is the maintenance of the world's biodiversity. Biological diversity is the product of organic evolution, and biological processes from the molecular level and DNA to the biosphere are not intelligible without reference to organic evolution. Organisms continually interact with their abiotic and biotic environments; intraspecific and interspecific interactions create the numerous local ecological theaters. Nowhere is the ecological play the same; players and conditions constantly change, bringing about a dynamic and evolving ecological world.

Humans have impacted natural landscapes and their living components from the time that they became organized as hunter-gatherers. More recently, human impact has increased dramatically in conjunction with exponential population growth (Fig. 14.2). In the 20th century alone, the world population size has soared from less than 2 billion in the early 1900s to 6 billion in 1999. Because the growth is exponential, the time required to add another billion people to the world is now about 11 years. This tremendous increase in size of the human population has created the biodiversity crisis, as well as many other societal crises for our species. The effect of increased human populations on the biosphere is compounded by the increased rate of technological development, extraction of natural resources for energy production, conversion of natural land, and the resulting pollution from these activities.

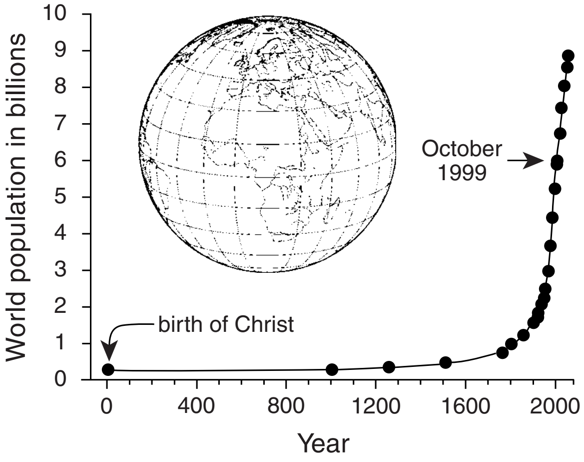


FIGURE 14.2 World population growth during the last 2000 years.

What is biodiversity and how does the biodiversity crisis impact the field of herpetology? At its simplest, biodiversity is the wealth of life throughout the world, including the smallest viruses and microbes to the giant whales and redwoods. Biodiversity includes the genetic diversity embodied in these organisms, and the interactions among them that form unique communities and ecosystems. The history of life on Earth is recorded in the DNA of organisms; this too is an important component of biodiversity. The study of biodiversity and its conservation require addressing diversity at several levels and in several ways (Table 14.1). Species richness, often called species diversity (see Chapter 13), is the easiest to recognize conceptually, simply by noting how many

TABLE 14.1 Types or Levels of Biological Diversity

Genetic diversity	The gene pool or genetic composition of a population or set of populations
Species diversity	The number of species in an area
Alpha diversity	The number of species in a community or habitat
Beta diversity	The difference or change in species number along an environmental gradient
Gamma diversity	The difference or change in species composition among similar communities or habitats in different areas
Community–ecosystem diversity	Number of plant–animal associations or communities throughout an entire naturally or artificially defined region

Sources: Caughley and Gunn (1996) and Primack (1995).

different species exist in a given area. Species diversity is typically reported by taxonomic group. For example, 19 species of snakes occur in the metropolitan Washington area; ±62 species of native frogs occur in the continental United States; and 4200+ frog species occur in the world. These regions are arbitrarily defined, and the numbers offer a sense of a region's diversity but have little biological utility. A biologist or resource manager needs more precise data and asks for species-diversity metrics relative to habitats or natural plant-animal associations. The number of species in a given area is termed alpha diversity (Table 14.1). The biologist may also wish to know how species diversity changes along an environmental gradient (beta diversity) or the differences in number and kinds of species among climatically and structurally similar habitats in different geographic areas (gamma diversity). Such diversity has long fascinated herpetologists. For example, Heyer's study (1967) of herpetofaunal change in an altitudinal gradient represents a study of beta diversity in Costa Rica, and Pianka's studies (1986, 1994a,b) of lizard assemblages in the deserts of Africa, Australia, and North America represent studies of gamma diversity. The fascination, however, extends beyond the number and kinds of species that occur in a region to what these occurrences reveal about the origin and interactions of an assemblage or community and the ecology of the individual species. Subsequently, these studies provide historical "snapshots" by informing us how a locality and its fauna have changed through time. It is the multitude of such biological studies and the presence of voucher specimens in the world's museums that allow scientific assessments of changing diversity and species abundance (Savage, 1995).

Although numerous, these assessments of diversity are few relative to the number of habitats and ecosystems throughout the world. Additionally, many studies may have been scientifically rigorous for their time, but either lack the scope of data or the appropriate sampling regime to rigorously examine current conservation issues. Their proportionately small numbers highlight the necessity of continuing biodiversity inventories in order to obtain an accurate and thorough knowledge of the world's flora and fauna. Another critical aspect of these inventories is the collection of specimens and the prompt study of these voucher specimens. Good science relies on repeating and verifying observations. Verification of species occurrence relies on actual specimens because most plant and animal species cannot be reliably identified "in-hand," from photographs, or from a small set of recorded measurements. Biodiversity inventories regularly identify new species, and these discoveries include amphibians and reptiles. Often these new species are common faunal members, but their uniqueness has not been recognized because they were not carefully examined. Close study of numerous groups of amphibians and reptiles is revealing that the true diversity is masked by not distinguishing among crytic and closely related species. The biodiversity crisis has imposed urgency on the documentation of the world's biota, and the rate of discovery of new organisms seemingly has accelerated. For example, 493 new species of amphibians and 449 new reptiles were recognized between 1991 and 1997 (Bauer, 1999). The known species diversity of the world's amphibian fauna has increased an amazing 349% since 1900.

Conservation biology is also concerned with other types of biotic diversities, including genetic and community–ecosystem diversity (Table 14.1). Genetic diversity is a measure of the breadth of a population's or a species' genetic constitution. Fundamentally, how variable is a population or how many genotypes does it contain? It is easy to recognize the genetic variability of human populations or those of our domestic animals because of our familiarity with them. Most populations of animals and plants are equally variable. The importance of genetic diversity is that it provides a population with broad genetic flexibility to adapt to changing conditions. Without such flexibility, a population cannot adjust to new conditions and may become extinct. Factors affecting genetic diversity include genetic bottlenecks, the founder effect, and genetic drift, which are examined below in the section on extinction.

Community–ecosystem diversity examines the number of habitats or species assemblages throughout a broad region. Whether a community is viewed as a haphazard or an organized assemblage of organisms, the different needs and tolerances of organisms and the heterogeneity of the physical landscape yield structurally similar assemblages of organisms. Species and genetic diversity is directly linked to ecosystem diversity, because more habitat types translate into more kinds of organisms. For each species living in multiple habitats, a broader selective landscape generates greater genetic diversity. Much of the effort of conservation biologists has focused on single species preservation; however, the early preservation of large areas as breeding and hunt-free refuges for game species created the base for the present-day emphasis on community conservation. Within North America, the greatest herpetofaunal diversity and community-segregation occurs in the southeast and southwest United States. For example, the herpetofauna of Florida's sand-ridge communities share only a few species with the pine-flatwood or evergreen-hammock communities. In turn these terrestrial communities have few species in common with marsh to river communities (Carr, 1940). Similar sharp contrasts in species composition exist among the lizard and snake assemblages of the southwestern desert communities in the United States (Papenfuss, 1986).

The biodiversity crisis is characterized by the loss and reduction of diversity within all three levels described above. The most extreme loss is the extinction of a species. Extinction is a natural process and occurs continuously; however, the crisis we now face is occurring because the rate of extinction, that is, the number of species lost per unit time, has greatly exceeded the normal rate. In addition, the breadth of the extinction has broadened, encompassing all sizes and types of organisms. Normally, extinction occurs at a slow pace and the number of species that disappear equals or is slightly fewer than the number of new species that appear. This gradual accumulation of species through time results in increasing diversity. The current phenomenon of rapid decline of the world's biodiversity has characteristics of a geologically ancient mass extinction event, where thousands of species are lost in a short period of time. Mass extinction is a catastrophic event; those documented from the fossil record have losses of more than 30% of the species (Raup, 1991). An estimate of 96% loss of species has been proposed for the mass extinction event at the end of the Permian. Although that estimate may be high, a 50% loss is not. If one of every two species disappears, species interactions and ecosystems change drastically. Conservationists are concerned about the loss of diversity because a high rate of extinction might lead to a cascading extinction event where the loss of one species causes the loss of multiple species. No matter how resourceful we humans are, there is no assurance that the human species will survive a mass extinction because the complex sets of species interactions that support our global food supply are at risk.

In addition to assessing the diversity of amphibians and reptiles, herpetological research contributes broadly to conservation management, both in identifying causes of decline and in developing data on amphibian and reptilian biology, from genetics to natural history. Subsequent sections of this chapter examine major aspects of conservation and offer a few examples of the contribution of herpetological research.

HUMAN IMPACT ON AMPHIBIAN AND REPTILE COMMUNITIES

Humans have modified the environment everywhere. Such a comment may seem to be an exaggeration, but it is not an overstatement (Fig. 14.3). Globally, our activities have resulted in a rising average annual temperature and in a rise in ultraviolet radiation at the earth's surface. These climatic effects are only one facet of our environmental alteration, which ranges from global climatic changes to the local loss of a marsh or a patch of forest. All alterations but those occurring in polar regions affect amphibians and reptiles. Should polar glacial ice melt as the result of human activity (e.g., global warming), the resultant rising sea levels will affect amphibians and reptiles in all coastal and low-lying areas.

Habitat Modification, Fragmentation, and Loss

Habitat alteration and loss is the most visible human-mediated environmental change. Prehistoric human populations began the process by setting fires to catch game, thereby expanding grasslands and savannas at the expense of forest. The rise of agriculture converted grassland and forest into farms and gardens. The conversion of natural landscapes continues. At the end of the previous millennium, the world had 24 megacities, defined as urban areas with populations that exceed 10 million. In addition, all over the world, small cities are rapidly growing and engulfing more and more natural areas. Although everyone is familiar with the environmentalists' plea "to save our rain forests," natural habitats of every type throughout the world are severely threatened.

The direct effect of habitat loss on an amphibian or reptile species or community is obvious: it disappears from that area. The consequences, however, extend beyond the edges of the lost habitat. Clear-cutting of both tropical and temperate forest affects both the abundance and the presence of amphibian species at the remaining forest's edge and at least to 20–30 m inside the forest (Gibbs, 1998). In a wet tropical forest of Amazonian Ecuador, the species richness (i.e., the number of species) of *Eleutherodactylus* frogs increased with increasing distance from the forest opening. Overall, frog diversity had only a weak linear association with distance from the opening because some species of hylid frogs may benefit by the relative openness of the forest (Pearman, 1997). In a deciduous forest in Maine, the edge effect decreased the relative abundance of the native salamanders and frogs; salamanders showed the greatest sensitivity to increased light levels and reduced humidity associated with the forest edge (Demaynadier and Hunter, 1998).

Selective logging within forests has a similar effect on amphibian communities as the edge effect. Totally removing a forest by clear-cutting usually eliminates the entire amphibian community. Removal of all the trees and the associated destruction of the understory vegetation and broad disruption of the litter ground cover expose the soil to direct sunlight. Thereafter, the soil

FIGURE 14.3 Disturbed and fragmented habitats. Clockwise from upper left: tropical clear-cut resulting from slash and burn in Rondônia, Brazil (photograph by L. J. Vitt); desertification in progress due to overgrazing by goats in northern Kenya (C. K. Dodd, Jr.); former Guatemalan cloud forest (ca. 2000 feet elevation) converted to agriculture (C. K. Dodd, Jr.); and a stream (Lost Creek) in Alabama degraded from coal mine runoff where the federally protected flattened musk turtle lived (C. K. Dodd, Jr.).

attains significantly higher temperatures, experiences greater temperature fluctuations, and becomes drier; these microclimatic changes are lethal to amphibians. If the logged areas are left undisturbed, the forest eventually regenerates itself. The speed of the regeneration depends upon numerous factors, including, for example, the size of logged area, presence of small forest stands within the logged area, the species composition of the native forest, soil type and quality, and weather and climate. Temperate and tropical forest naturally develops openings because of storm damage or the death of old trees, but these gaps fill quickly with seedlings from the surrounding forest as well as small trees and herbaceous vegetation regenerated from rootstocks. The same process occurs in logged areas, but larger cleared areas require a longer time for the migration of seeds and seedlings throughout the area. The same principle applies to recolonization of a logged area by the amphibian community (Corn and Bury, 1988). Assuming a relatively rapid regeneration of the forest, the entire amphibian community may reassemble in 20–30 years. Again, local effects as well as logging practices are factors in the reassemblage. Data for Appalachian salamander communities suggest a range of 20 to 50 years for recolonizations (Ash and Bruce, 1994; Petranka et al., 1994); however, in managed forests, site preparation activities drastically alter the soil and other physical aspects of the site and make forest plantations uninhabitable for most species of amphibians and reptiles (Herbeck and Larsen, 1999; Means et al., 1996). Selective logging and other disturbances in tropical rain forests potentially alter community structure by changing species interactions. These activities create hotter forest openings than natural treefalls. The canopy gap attracts large-bodied heliothermic lizards, such as *Ameiva*, and these predators can reduce the population size of smaller lizard and frog species by direct predation and by interference competition for shared prey (Vitt et al., 1998a; Sartorius et al., 1999).

Natural disruptions occur regularly in all ecosystems. Floods, landslides, and fires are the usual agents. While locally devastating, the native flora and fauna have experienced such disturbances over many generations and recovery is relatively quick. Indeed, high species and community diversity of an area may be fostered by the regular occurrence of disturbances. In one sand-ridge site in the Great Victoria Desert of Western Australia, 45+ species of lizards occur; this high diversity is four times the species richness of any desert site in North American and more than double the richness in the African Kalahari. Natural wildfires are frequent but narrowly confined, thereby creating a patchwork of habitats of similar plant composition, each at a different stage of recovery from its most recent exposure to fire (see Chapter 13). Because different assemblages of lizard species are adapted to different habitats, numerous species can occur in the same area, but with a reduction in competition for the same resources (Pianka, 1994a,b).

In rare cases, a natural catastrophe can decimate local populations, or even eliminate entire communities. If a population within one of these communities is the single remaining population of a species, the catastrophe causes extinction. It is this latter aspect that concerns conservationists and becomes increasingly possible because of human-mediated habitat loss and alteration. Several paradigms in conservation biology arise from the problem of habitat destruction and its effects on individual species. The issues of concern are population viability and persistence, and ultimately population size, including both the absolute number of individuals and their density or number of individuals in a unit area. The metapopulation model (see Chapter 11) views a population as consisting of source and sink populations. In the former, sufficient offspring are produced on average to maintain the population and produce an occasional excess of offspring that disperse because one or more critical resources are controlled by other individuals. Sink populations, on average, produce too few offspring for that population to persist and require regular migration of new individuals for their survival. Habitat destruction and alteration fragment the suitable habitat and create dispersal barriers of unsuitable habitat. The barrier may be a road, housing development, new agriculture areas, or any of a number of other disturbances. Regardless of the barrier's size, if it significantly reduces or halts dispersal to sink populations, they soon disappear. Fragmentation can also create problems for source populations and threaten their survival as well. Such factors as demographic stochasticity, inbreeding, and genetic drift can alter the genetic diversity of a population and reduce its survivability. These factors and related ones become increasingly influential in a population's survival in a habitat fragment and are of major concern in establishing reserves and refuges, which are just that—fragments of once larger natural areas.

Determining reserve size depends greatly upon the biology of the species targeted for preservation. "Bigger is better" is true, but it is an overly simplistic solution in today's world where there are many competitors for space. How big does a reserve need to be to maintain genetic diversity and to avoid demographic collapse? The minimum viable population (MVP) size model grew out of this debate. As initially proposed, a minimum viable population is the number of individuals necessary for a population to have a 99% chance of survival for 1000 years and to avoid extinction by natural catastrophes or the effects of demographic, genetic, and environmental stochasticity (Table 14.2; Shaffer, 1981). No one has attempted to derive a precise number for any amphibian or reptilian population, although modeling of turtle populations has identified the demographic features necessary for the survival of populations of these long-lived species populations (e.g., Crouse et al., 1987; Congdon et al., 1994). Some aspects of demographic, genetic, and environmental stochasticity are examined in subsequent sections.

Habitat fragmentation is so common a feature of our present landscapes that we often lose sight of its impact on natural communities and species distributions. A recent study in the Great Central Valley of California is exceptionally revealing, although not exceptional in occurrence (Fisher and Shaffer, 1996). The total number of native amphibian species was not large, only seven species—three salamanders and four frogs, with a maximum of six species in any locality and fewer in some areas (Fig. 14.4). Breeding season surveys of over 1000 aquatic sites in the 28 counties of the Central Valley revealed that only 3 counties still retained populations of their original fauna. Species retention was greatest in hilly areas and least in flatlands, which are now largely agricultural. No county had lost its entire complement of native species but most had lost more than one-half of their species. In some areas, overall diversity had increased by the introduction of exotics; however, in most cases, exotics do not occur with native species and some exotics such as the bullfrog *Rana catesbeiana* are partially to blame for the extirpation of native frogs.

Pollution and Disease

Everyone can recognize industrial pollution with its particle-laden smoke arising from smokestacks and its toxic waste emptying into adjacent waterways; however, pollution is not always so obvious or blatantly toxic but can be lethal nonetheless. The phosphates in laundry detergents

TABLE 14.2 General Threats to the Persistence of Small Populations

Demographic stochasticity	The natural fluctuation in a population's demographic characteristics over generations. It includes:
Changes in population size	A population randomly increases and decreases in size through time. In a random-walk situation, a population fluctuates between highs and lows, and over many generations the declines become more severe. If the population size fluctuates to zero, the population disappears.
Changes in sex ratio	A random distortion of a population's sex ratio can interrupt reproductive behavior and successful juvenile recruitment.
Genetic stochasticity	The loss of genetic diversity through random events in the history of a population. The loss of diversity reduces genetic variation among individuals, hence reducing the adaptive plasticity of a population through time. Genetic stochasticity includes:
Founder's effect	A population that arises from a few individuals contains only the genetic variation of the founding individuals and this variation is likely only a small fraction of the source population.
Genetic drift	Either through random (drift) or selective mating, alleles that occur at low frequencies in a population tend to decrease in frequency and eventually be lost.
Inbreeding depression	Breeding with close relatives increases homozygosity.
Bottleneck	A sudden decrease in population size with a corresponding reduction in genetic variation.
Environmental stochasticity	Unpredictable changes in the abiotic and biotic factors that affect the availability of resources and the equability of the environment. These changes include:
Weather	Exceptional weather patterns may cause floods, droughts, or unseasonably hot or cold periods that disrupt feeding and reproduction or even exceed the physiological tolerance limits of a species.
Climate	Long-term shifts in weather pattern change the seasonal rainfall, insolation, and temperature regime of a locality.
Catastrophes	Major geological disturbances, such as landslides, volcanic eruptions, or meteor impacts, can destroy all life within an area.
Disease and parasites	Appearance of a new disease or parasite or the change in virulence of an existing one.
Predator	Appearance of a new predator or an improved hunting strategy by an existing one.

Sources: Caughly and Gunn (1996), Meffe and Carroll (1994), and Primack (1995).

or the nitrogenous matter from a dairy farm is not toxic when diluted, but add a dozen, a hundred, or a thousand washing machines emptying their wash-water into a lake or the runoff from a dozen dairy farms into a small stream, and it can have serious ecosystem effects. But even the single washing machine or diary farm impacts the local ecosystems by slowly altering microenvironments, making them lethal for native microfauna and microflora. As these organisms change, so does the macrofauna and macroflora. Life persists in many polluted environments, and the diversity of species and their abundance sometimes may be even greater, highlighting one of the dilemmas of conservation—when is action necessary and what action is required?

Unfortunately, action is seldom preventative but occurs with an impending crisis or amid a full-blown one. These crises attract our attention and research efforts. Four of the most visible crises, acid rain, ecoestrogens, seaturtle fibropapillomatosis, and die-offs in frogs, are briefly examined here. These examples highlight the scope and complexity of pollution and its potential fostering or enhancement of disease in amphibians and reptiles. The pollutants or "environmental contaminants" range from solid-waste disposal filling a breeding pool through fragmented waste (e.g., plastic bags, tar balls) to airborne or water-suspended microparticles, such as heavy metals, organic compounds from pesticides and herbicides, and PCB (Grillitsch and Chovanec, 1995). The interactions of these pollutants with life processes are understood only in a few instances and have become a major area of research. Depending upon their concentration and biochemical nature, microparticles can be lethally poisonous, carcinogenic, mutagenic, and, although less well documented, immunosuppressant.

Environmental Acidification

Acid rain has moved out of the forefront of conservation concern, in part because it has been alleviated to some extent in Europe, Canada, and the United States by the enforcement of clean-air legislation. Nevertheless, it remains a pollution problem, perhaps a low-grade one in the preceding areas but certainly a major problem in China, India, and other areas that rely mainly on coal to power their industries but practice little pollution control. Acid rain arises from the combustion of fossil fuels and the release of sulfur and nitrogen oxides in the air. These by-products react with the moisture in the air to produce sulfuric and nitric acids, which in turn are returned to the earth by snow or rainfall. While some acid rain falls locally, much of the acid pollution is carried downwind and dropped hundreds of miles from the pollution source. Normal rain is saturated with carbon

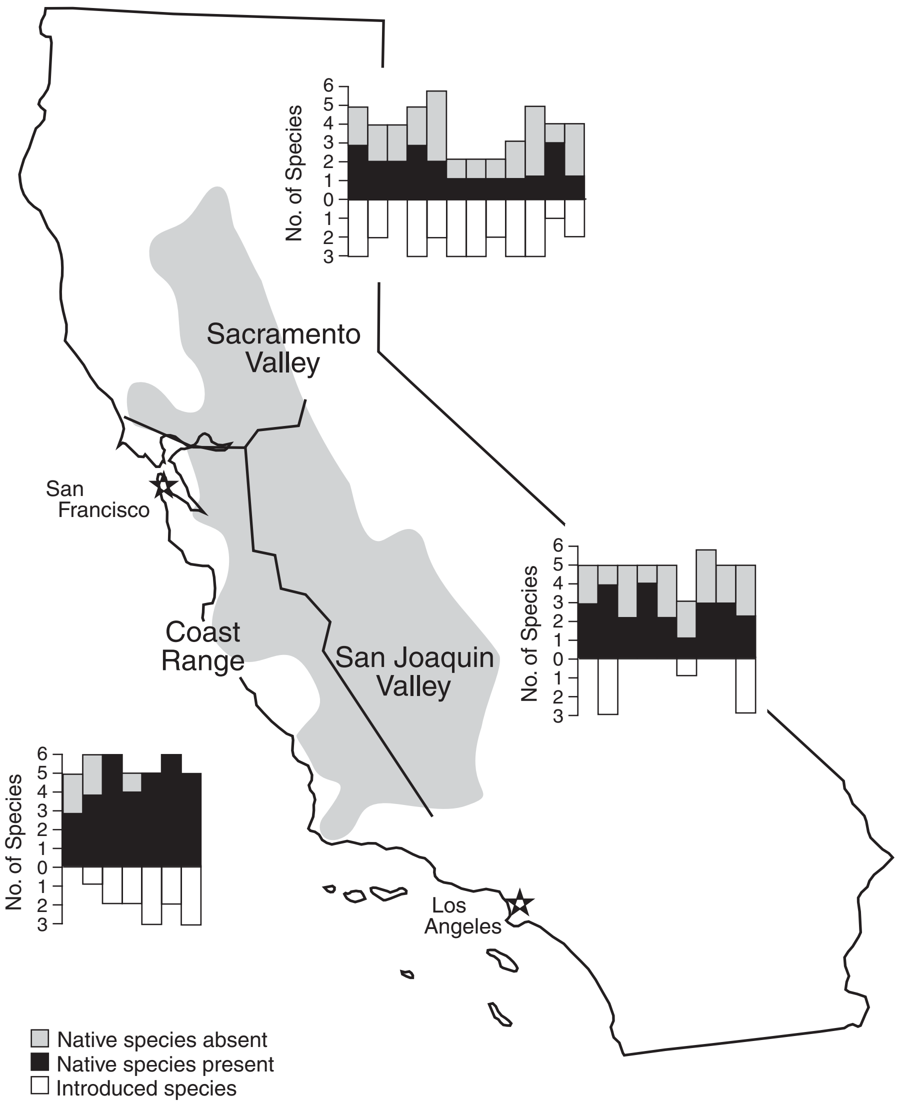


FIGURE 14.4 Amphibian faunas in the Great Central Valley of California. To document the faunal changes during the 20th century, over 1000 aquatic sites were surveyed between 1990 and 1992. The results are summarized in three bar diagrams showing the number of exotic species present, the number of native species lost, and the number still present in each county of the three major valley provinces. Only 4 of the 28 counties surveyed still have all members of their original amphibian fauna. The lightly stippled area denotes the valley oak-grassland habitat; the dark line marks the boundary between the valley provinces. Modified from Fisher and Shaffer (1996).

dioxide and has a pH of about 5.6–5.8; acid rain commonly has a pH of 3.0 to 4.0 and is occasionally even more acidic. The first evidence of the danger of this far-removed pollution was the death of trees on mountaintops. It soon became evident that the effects were far broader, sterilizing life in seemingly unpolluted forest streams and lakes. Acid rain is most destructive when it falls in areas of hard rock and mineral-poor soils, because the soil and water are incapable of neutralizing (buffering) the acid precipitation.

Because many amphibians are aquatic for part of their life, they are highly susceptible to the toxic effects of acid rain; however, their susceptibility is variable (Beebee, 1996; Dunson et al., 1992). Some species, such as *Rana virgatipes* and *Hyla andersonii*, breed in acidic waters (pH <4.0) of cedar bogs, but most amphibian species require water that is less acidic, and their eggs and larvae suffer more than 50% mortality even in water with a pH of 4.5 (Table 14.3). Acidic water affects the survivability of juveniles and adults, but its toxicity focuses on

TABLE 14.3 pH Tolerance Levels of Select Species of Amphibians

Taxon	Critical pH	Lethal pH
Salamanders		
Ambystoma jeffersonianum (field)	4.0–5.0	4.2
Ambystoma jeffersonianum	4.2–4.6	4.2
Ambystoma maculatum (field)	5.5	4.2
Ambystoma maculatum	6.0–7.0	4.0–5.0
Frogs		
Acris gryllus	4.2–4.6	4.0–4.1
Hyla andersonii	3.6–3.8	3.4
Pseudacris crucifer	4.0–4.2	3.8
Hyla versicolor	3.9–4.3	3.8
Hyla andersonii	3.6–3.8	3.4
Xenopus laevis	3.0	3.5
Rana catesbeiana	4.1–4.3	3.9
Rana clamitans	3.8–4.1	3.7–3.8
Rana pipiens	5.5–5.8	—
Rana sylvatica	3.6–3.9	3.5
Rana virgatipes	3.6–3.8	3.4

Source: Tome and Pough (1982), Table 1.

Note: Mortality is presented as critical, denoting 50% mortality of larval sample with exposure throughout the entire development period, and lethal, denoting 100% mortality. pH exposure levels were determined in a laboratory setting unless noted otherwise.

the developmental stages by disrupting the ionic balance within cells and typically killing embryos by the late gastrula stage. Less acidic water that may permit greater than 50% larval survivorship still affects development by slowing growth and morphogenesis; commonly, it produces a high percentage of developmental abnormalities, many of which result in death during metamorphosis. The toxic effect of acid rain is greatest on species that breed in vernal (temporary) ponds. Most of these breeding sites are dry prior to the arrival of the rains and temperatures that stimulate breeding events. The rains not only bring their acid load but also wash acid from the surrounding vegetation and land into the pond, causing pH to drop below even the tolerance levels of the most acid-tolerant species. Species living in permanent waters are buffered from these acid surges simply by the diluting effect of the large volume of water.

If acid levels are not lethal to all species, community structure shifts. For example, the glacial soils of central New York are poorly mineralized and are downwind from the heavy industry of the midwestern United States; thus, all freshwater communities are acidified. Acid precipitation differentially affects two salamanders in the amphibian communities of vernal pools. *Ambystoma jeffersonianum* is an acid-tolerant species, and its larvae can develop and metamorphose in water with a pH of <4.0. Its congener, *Ambystoma maculatum*, is less tolerant and requires water with a pH of >5.0 for successful hatching and metamorphosis. Since snowmelt and spring rainfall commonly produce breeding pools of pH 4.5, more *A. jeffersonianum* larvae metamorphose and eventually return to reproduce, slowly outnumbering the formerly dominant *A. maculatum* (Pough and Wilson, 1977).

Ecoestrogens

Animals, particularly herbivores, have long experienced natural exogenous hormones. Most of these products are produced by plants and fungi as defense mechanisms to stop or reduce consumption by herbivores. Ecoestrogens (estrogen-mimicking chemicals) represent one class of these defense compounds, and interactions across generations (coevolution) result in the consumer's ability to tolerate and neutralize the ecoestrogen or to recognize and avoid its consumption. Human activity inadvertently has introduced numerous new ecoestrogens into the environment, often in excessively high levels. Some industrial pollutants, sewage effluent by-products, and pesticides and their breakdown products act as weak estrogens.

Estrogens are essential components of each animal's reproductive physiology; however, exposure to them at the inappropriate time or in excessive amounts disrupts normal reproductive behavior. Further, larvae and embryos are quite sensitive to estrogens, whose timing or concentration interrupts normal development of the reproductive system and other organ systems (Guillette et al., 1996; Hayes et al., 1997). The potential effects of ecoestrogen still are incompletely known, but evidence from wildlife and laboratory studies increasingly shows their effect in reducing the reproductive potential of individuals, and in causing cancer and immunosuppression.

Studies have demonstrated a striking effect of ecoestrogens on demography and reproduction in the alligator population of Lake Apopka (central Florida). In 1980, this lake suffered a major pesticide spill consisting of dicofol that was contaminated with DDT and its breakdown products. The alligator population showed an immediate demographic loss of its juveniles, probably a direct result of poisoning of these age classes. Adults seemingly were unaffected; however, the population has not yet recovered. Throughout the 1980s, egg viability was 20%, compared to 80% in eggs from a Florida wildlife refuge, and it continues to remain low (Guillette, 1995). The pesticides and their metabolites are persistent, requiring decades to disappear from the environment, and they continue to be present at high levels in alligator eggs. This contamination is directly toxic to many embryos, but a few survive and hatch. However, the hatchlings are not normal. Embryonic exposure to ecoestrogens has disrupted the reproductive system development. For males, this exposure has resulted in feminization of the reproductive organs; penes are smaller and spermatogenesis is lower. In females, ovarian morphology and ovarian follicles are abnormal.

Fibropapillomatosis

Diseases are a natural phenomenon and no plant or animal appears to be free from them (Crawshaw, 1997). Disease becomes a concern to conservationists when it results in sudden die-offs of populations or when its frequency of occurrence increases sharply. The latter has occurred in the endangered and threatened cheloniid seaturtles, especially in the green seaturtle *Chelonia mydas*. In general, neoplasias are uncommon in wild animals and certainly so in reptile populations. However, beginning in the mid-1980s, the incidence of cutaneous papillomas, fibromas, and fibropapillomas has increased markedly in several populations of *C. mydas* (George, 1996). These tissue-proliferation lesions are generically labeled green turtle fibropapillomatosis (GTFP), owing to their presumed origin and highest incidence in that species. Although the lesions are not cancerous, their excessive growth internally and externally is life threatening. Externally, the growths reduce an individual's ability to escape enemies and to find and consume food (Fig. 14.5). Internally, the papillomas enlarge and interfere with the function of the viscera, including blocking the digestive tract and disrupting kidney or lung functions.

GTFP was first reported in 1938 in a captive *C. mydas*, which had been caught 2 years earlier in the Key West area. This occurrence was to prove prophetic, because today, Florida Bay has one of the highest incidences of GTFP. Incidence levels range from 0 to 92% (Kaneohe Bay, Hawaii; Aguirre at al., 1998), and occurrence has been reported pantropically with the exception of east Atlantic coastal Africa. The highest incidence is in lagoons and bays adjacent to dense human populations. Yet, two locations only kilometers apart can have strikingly different incidences. For example, the incidence is 50% in Indian River Lagoon and 0% in the reefs off the central Florida coast. This association with human populations and waters with low circulation suggests that environmental contaminants foster GTFP; however, no matter how strong the association, no evidence presently supports a cause-and-effect association.

The etiology of GTFP remains uncertain, although there is strong support for its transmission via a virus (Herbst, 1994; Herbst and Klein, 1995). The transmission of the virus from individual to individual is less certain; a marine fluke that parasitizes green seaturtles was early suggested as a vector, but evidence is inconclusive. GTFP has a distinct demographic association with juvenile turtles. The papillomas have never been reported in the youngest juveniles of the pelagic phase; however, once returning to near-shore waters, the incidence increases in some populations in the larger size classes (to about 80–90 cm carapace length) before declining. Perhaps there is a natural remission of the disease if infected individuals can survive the debilitating

FIGURE 14.5 Reptiles and amphibians can die from human-induced pollution or disease or as the result of natural events. Left, a subadult green seaturtle (*Chelonia mydas*) from Indian River Lagoon, Florida, with fibropapillomatosis (photograph by C. K. Dodd, Jr.); right, dead and dying tadpoles and metamorphs of *Gastrotheca riobambae* caused by pond drying (S. Ron).

middle years. Fibropapillomas, however, are occasionally seen in nesting females, so adults are not immune to the disease.

GTFP remains a major threat to the survival of populations of *C. mydas*. Throughout the 1980s and 1990s, the incidence in infected populations increased and the number of populations with GTFP individuals increased. The additional threat is that GTFP now occurs in other species, particularly in those resident in habitats with a high incidence in the *C. mydas* population.

Amphibian Die-Offs

Sudden and mass die-offs of frogs are not a recent phenomenon; however, our awareness of the worldwide decline of amphibians (see below) has heightened our attention to such events. The causes of die-offs remain speculative, but a recent die-off in Panama has provided strong evidence that a fungal infection is the cause of death. Nonetheless, other factors including pollution and weather might act synergistically with the primary cause of the die-offs.

One of the first die-offs to be widely reported (although poorly documented) occurred in the late 1960s and early 1970s. The deaths and population crashes of the northern leopard frog *Rana pipiens* were geographically widespread from Vermont, across the Canadian—USA border states, and to Manitoba and Minnesota. This die-off event attracted attention because this species was harvested commercially for the biomedical community, which depended upon acquiring individuals of this frog for experimental research. Collectors found dead and dying frogs in the fall when they typically harvested frogs, and even seemingly healthy frogs died during their laboratory hibernation. "Redleg," a bacterial infection, *Aeromonas hydrophila*, that causes cutaneous hemorrhaging, was a common diagnosis. Although this condition killed some frogs, it remains unknown whether this was the primary cause, the final lethal agent, or perhaps a secondary infection. In subsequent but smaller-scale die-offs, redleg continued to be implicated, but lethal fungi were suggested as well.

Strongest evidence that a highly virulent fungus may be causing amphibian die-offs was provided by independent investigators on opposite sides of the globe. Population studies of numerous species of frogs were initiated in 1991 in an undisturbed cloud forest site in southeastern Costa Rica, where frogs were abundant (Lips, 1998). By the conclusion of the study in 1996, several species of frogs and one salamander had either disappeared or were represented by only a few individuals (Fig. 14.6). Sick and dead adult frogs were found and some tadpoles had mouthpart abnormalities. A bacterial or viral disease, possibly resulting from changing weather patterns and long-distance chemical pollution, was suggested as the cause. Another study was initiated in 1993 to monitor frog populations at a Panamanian site, about 100 km southeast of the Costa Rican site (Lips, 1999). Streamside frogs were initially abundant, but from December 1996 to January 1997, numerous dying frogs were found. Six months later, streamside frogs had been reduced to a few individuals. Necropsies of dead frogs from the December-January sample showed a cutaneous fungal infection in all frogs. At the same time that these studies were being carried out in Central America, amphibian populations were found to be declining rapidly in montane areas in Queensland, Australia (Richards et al., 1993). Like the Central American populations, the Australian populations were in pristine areas that demonstrated no obvious habitat alteration; dead and dying frogs were found at sites that progressed geographically from one adjacent area to another, an indication of the spread of an epidemic caused by a transmissible organism (Laurance, 1996; Laurance et al., 1996).

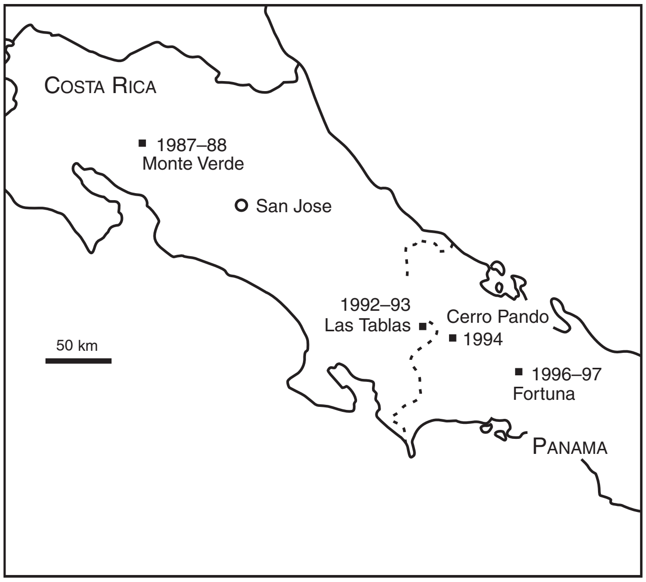


FIGURE 14.6 The timing of amphibian die-offs in Costa Rica and adjacent Panama, suggesting the spread of a virulent pathogen. The dates represent the sudden disappearance of frogs at Monte Verde and the appearance of dead and dying frogs at the other sites. Data from Lips (1998, 1999) and Pound and Crump (1992).

Histological examination of the skin of affected frogs revealed the presence of the same pathogenic organism in both Central America and Australia. The pathogen was identified as an epidermal chytrid (Berger et al., 1998). The fungus primarily infected certain areas of the skin of adult frogs, particularly the digits and the ventral pelvic patch, the highly vascularized area that functions in water uptake. Subsequent study revealed that the fungus specifically attacks keratin in the skin and may interfere with water uptake and osmoregulation, thus leading to death. Tadpoles in affected areas commonly have deformed mouthparts, but because their skin and gills are not keratinized as are their mouthparts, they are not killed by the infection; only adults die as a result of infection. Many questions remain unanswered concerning the distribution, mode of action, and virulence of this fungus. To date, primarily montane populations of frogs are affected, and one hypothesis is that the immune system of frogs in these areas may be weakened by other, as yet undetected, environmental causes.

Harvesting Amphibians and Reptiles

"Apart from habitat destruction and alteration, the biggest threats for wild species of plants and animals are illegal trade and unsustainable consumptive use" (Melisch, 1998). This remark is seemingly an overstatement of human exploitation of the world's biota, yet from Melisch's perspective of a conservationist working in southern Asia, it rings true. Further reflection supports its worldwide applicability if it encompasses all human use—legal or illegal, and intentional or unintentional capture.

Many species and populations of amphibians and reptiles are negatively impacted by human commerce in the broadest sense, and this impact is as great in the developed nations as in developing nations. For example, the European pet trade overharvested native tortoises and those of adjacent Africa and Asia. When *Testudo* populations were decimated, these tortoises were banned from commerce, and the European tortoise trade adopted the North American box turtle, *Terrapene*, as one of the replacement "tortoises," thereby setting in motion the decimation of *Terrapene* populations. The issues of harvesting plants and animals are emotionally loaded, especially concerning regulatory issues and sustainable harvest of living natural resources. Our bias is on the noncommercial, protective side.

Amphibians and reptiles are widely harvested, although the impact is focused on a relatively few species in any locality. Their harvest is largely for consumption (food and folk medicines), luxury trade (leathers, jewelry, and curios), and the pet trade. All three represent commercial exploitation, in which the animals are gathered specifically for sale by the collectors, and each type of harvest represents a worldwide, multimillion-dollar industry. This commercial exploitation regularly leads to overharvesting and is a principal concern of conservationists; however, local family consumption also decimates populations of the targeted species when local human populations are dependent upon wildlife as a major source of protein. The concept of sustainable harvest was developed principally as a management tool for commercially and sport harvested species, but it is useful as well for the conservation of species overharvested for local consumption.

Sustainable use allows the limited harvest of a population, providing that the portion of the population remaining is able to reproduce and maintain itself (Fig. 14.7). Conceptually, sustainable use is easy to establish, but in practice, it is difficult to set and to control harvest limits. The goal is to establish a harvest regime that garners local community support because it is commercially profitable and/or provides the local community with an adequate supply of meat. If the harvest is set too low, the harvest-species population experiences little impact and possibly grows, but the local community receives little benefit and likely will ignore the harvest limits. If the harvest is too high, the harvested population declines toward extinction. The extinction can be the actual disappearance of the population through overharvest or unsustainable-use extinction in which population density is so low that efforts to harvest exceed the benefits to the harvester. Even in the latter situation, the population is likely to disappear because it has fallen below its minimum viable population level (for an explanation of MVP see the previous section in habitat modification section).

Sustainable-use programs have some successes among reptiles. Managed harvest of crocodylians began about three decades ago as a tool to assist the recovery of

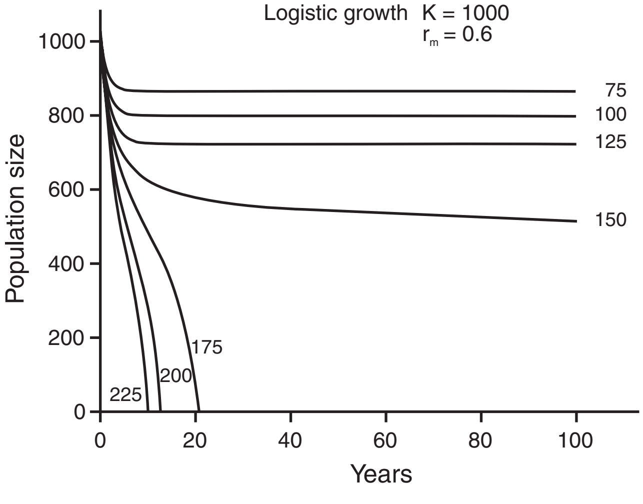


FIGURE 14.7 Hypothetical profiles of populations subjected annually to different levels of constant harvest. The values on the right indicate the number of individuals harvested annually. The profiles demonstrate the potential of sustainable-use harvesting; however, no abiotic or biotic perturbations are incorporated in the population growth model, and natural populations would display fluctuations in population size. Modified from Caughley and Gunn (1996).

species and populations that had been devastated by unregulated hunting for their skins (Brazaitus et al., 1998). The success of managed harvest and captive-rearing in Papua New Guinea, Venezuela, and a few other countries stimulated other governments to begin similar programs. In most countries, the managed species has shown a remarkable resilience, and the populations are no longer endangered. However, with more countries producing skins, supply began to exceed demand and was then followed by a declining popularity for crocodylian leather (Thorbjarnarson, 1999). Ultimately, an economic depression in Asia caused the market for crocodylian skins to collapse. Market fluctuations are common for luxury items such as exotic leathers, and it now seems evident that the conservation management of a species cannot depend solely or even largely on the marketing of products from a particular species. Several other species of large reptiles (e.g., *Tupinambis*, *Varanus*, *Python*, *Naja*) are widely sought for the leather trade and have been examined for sustainable use; harvesting regimes and environmental education have begun in several countries (e.g., Fitzgerald, 1994a,b; Shine et al., 1996d). The fate of these management programs depends upon how accurately biologists have been able to assess the reproductive potential and demography of each population and upon the development of an accurate tracking of the number of individuals captured. These data are required to establish appropriate harvest quotas. Sport wildlife and fisheries depend upon quotas, which have proved to be effective management tools where special interests do not override the recommendation of the fisheries and wildlife biologists.

The commercialization of wildlife has potential negative side effects. The sustainable-use programs for crocodylians have been successful with the commercially valuable species, but the focus on these species has resulted in the neglect of truly endangered species, especially those with small distributions and less flexible demographics, such as *Alligator sinensis* and *Crocodylus mindorensis.* Further, commercialization of one group of species creates a market for all species and becomes a serious threat to endangered species. Even relatively abundant and widespread species can experience overharvesting if managers fail to distinguish between legally harvested skins and illegal ones. This situation probably occurs with the tropical American caimans where the number of imported skins exceeds the number of skins legally exported (Brazaitis et al., 1998). This concern for commercialization fostering the uncontrolled harvest of wild populations is the reason for the seaturtle conservationists' resistance to either the farming or the ranching of seaturtles (Frazer, 1992). By making the marketing of all species from all areas illegal, no legal loopholes remain for the marketing of illegally harvested animals.

Human consumption of reptiles and amphibians, while relatively small compared to fish, birds, and mammals, is still significant. Like the skin trade, it concentrates on larger and long-lived species. Because of delayed maturity and highly variable annual replacement rate, these species lack the demographic resilience to recover quickly from overharvesting. Among the lizards, species of *Varanus*, *Tupinambis*, and certain iguanines are hunted for local consumption and in many areas have experienced sharp population declines because of overhunting. An effort to develop community-based *Iguana* farms for restocking wild populations and providing marketable meat was successful in identifying the proper farming protocols but was unsuccessful in terms of enactment; widespread community support for the program did not occur. Snakes are an important food and source of folk remedies in Asia and their local consumption and capture for distant markets greatly grew during the 1990s. The effect on snake populations has not been documented for most species, but it is likely to become evident by an increase in rodent populations and their devastation of grain crops. The present decline in seaturtle populations had its origins in the butchery of females and/or the harvest of eggs for human consumption (Fig. 14.8). While human consumption remains a significant threat in some regions, the incidental capture and death of seaturtles in the fisheries industry has become the major threat to seaturtle survival. The globalization of the world's economy is strikingly demonstrated by global harvest of freshwater turtles for the Chinese food market. At the end of the 20th century, China had largely eliminated its indigenous populations of turtles, and the trade network has spread throughout the remainder of Asia so that even species from New Guinea regularly appear in local Chinese markets. Much of the harvest of North American turtles, particularly *Chelydra* and *Apalone*, goes to Asia as well. And North American and European markets import tons of frog legs from Asia and elsewhere.

The pet trade also has a significant impact on amphibians and reptile populations. The commerce ranges from local to international, and Japan, North America, and Europe are the principal markets. Common species are exported annually numbering in the tens of thousands. While these numbers clearly impact local populations, the greatest impact is on the less abundant and even endangered species. The rarer a species, the greater its value. The greed for ownership of rare species creates an extraordinary monetary value for individuals of these species. That in turn has created a black market for smuggled animals and the theft of specimens from nature reserves and conservation

FIGURE 14.8 Female green seaturtle being prepared for market in Mexico (photograph by J. P. Caldwell).

captive-propagation programs. Unfortunately, a considerable portion of the trade proceeds under the guise of scientific research.

Exotic Species

The term "exotic species" refers not to excitingly or titillatingly different species but to introduced or nonnative species. Perhaps a chameleon in Hawaii is exciting to some people, but a seemingly innocuous introduction of an exotic species into a new habitat often has major and devastating effects on the native flora and fauna. The innocuous chameleon eats insects. If the insects are exotic also, then the chameleon causes no problem, but if it becomes established in native forests and eats native insects, many of which have small distributions, the chameleon can cause the extinction of native insects and potentially native plants that depend upon the native insects for their pollination. Generally speaking, exotic species are undesirable and negatively impact the native biota. Because humans have so greatly altered their immediate landscapes and bring with them (intentionally and unintentionally) many commensal species of plants and animals, they usually are unaware of the impact of an exotic species until it becomes a "plague." For example, the chestnut blight and the gypsy moth are exotics that have changed the community structure of eastern North American deciduous forests.

Herpetofaunas are impacted by exotic plants and animals and provide exotic species that in turn impact communities (Wilson and Porras, 1983). The impact of exotic and invasive plants on amphibians and reptiles is poorly documented. Most exotic plants accompany human alteration of native floras and habitats, making it difficult to separate the effects of habitat alteration from the dominance of exotics in human-impacted communities. Water hyacinths spread rapidly throughout southeastern United States from a small introduction in the St. Johns River, Florida, in the 1880s. There is no indication that its spread affected any species of amphibian or reptile, and seemingly it provided a new habitat for the dwarf siren (*Pseudobranchus*), whose populations can be incredibly dense in the fibrous root-masses of this floating plant. In turn, dwarf sirens support high densities of their predator, the black swamp snake *Seminatrix pygaea* (Godley, 1980). The preceding statement, however, is strictly anecdotal. There are no estimates of abundance of either the salamander or the snake prior to the introduction of the water hyacinths; similarly, population data on cooter and slider turtles (*Pseudemys*) do not exist, and water hyacinths crowded out many of the native aquatic plants on which these turtles feed. The water hyacinth story illustrates several aspects of the impact of an exotic or invading species. First, most evaluations of an exotic's impact lack preintroduction ecological data on the impacted species; the impact becomes apparent only after the invading species has decimated or eliminated one or more native species. Invading species can benefit some species, and their detrimental effect on other species often is not observed because the impacted species is invisible relative to our knowledge or interest. Our evaluation of the gains or losses from an invading species depends largely on our perception of the value, either economic or aesthetic, of the impacted species. Water hyacinths were introduced for their attractiveness but rapidly became an economic burden because they clogged waterways and slowed or stopped boat traffic. At no time was there any discussion or concern for their impact on the native aquatic communities of the southeast United States. Only recently, as natural communities have declined because of human activities and the rate of invasive-species colonization has increased through the globalization of trade, have both the biological and the business communities recognized the actual and potential cost of exotic species. For the former, exotics threaten the survival of native species and ecosystems; for the latter, exotics increase operation expenses, as when zebra mollusks clog water-pumping equipment or brown tree snakes cause power failures.

The most obvious impacts on native amphibians and reptiles occur on islands to which a vertebrate predator is introduced (Table 14.4). Rats have decimated bird and other reptile populations on almost every island that they have colonized—always with the transport provided by humans—and remain a major threat to many insular populations. The black rat and subsequently the Norway rat were transported worldwide by European explorers and subsequently traders and whalers, although the Polynesian rat (*Rattus exulans*) was the first to be widely introduced, probably intentionally as a food item, by people colonizing the oceanic islands of the Pacific 2000–3000 years ago (Watling, 1986). The Polynesian rat was especially destructive to bird populations but may have had a profound impact on lizard populations as well (Whitaker, 1973), and it may have been responsible for the extinction of the tuatara from the main islands of New Zealand. The black and Norway rats remain major predators of the eggs and small juveniles of the Aldabra and Galapagos tortoises. The mongoose, introduced to control rat populations, proved unsuccessful in that role but highly successful in the elimination of ground-nesting birds and terrestrial lizards, including the skink *Emoia nigra* from Viti Levu, Fiji (Ryan, 1988). House cats, both feral and domestic, are skilled hunters and kill large numbers of amphibians and reptiles in suburban and rural areas of continents (Mitchell and Beck, 1992), and have proved highly devastating to insular populations of lizards. Herbivores, such as goats on the Galapagos or rabbits on the California Channel Islands, change the structure and composition of vegetation, thereby affecting the availability of food for herbivorous reptiles and reducing or eliminating shelter from insolation and predators.

TABLE 14.4 General Requirements for a Successful Invasion by an Exotic Species

- I. Community/ecosystem susceptible to invasion
  - A. Climatically similar to the source ecosystem of the invading species
  - B. Simplified community or one stressed by human or natural disturbance
    - 1. Low species diversity
    - 2. Absence of or few predators
    - 3. Absence of or weak competitor species for the same resources
- II. Successful invader species
  - A. Broad physiological tolerances
    - 1. A habitat generalist
    - 2. Broad dietary requirements
  - B. High reproductive potential
    - 1. Individuals mature quickly and reproduce frequently
    - 2. Each individual produces many offspring during its reproductive life
    - 3. Eggs and juveniles with moderate to high survivorship
  - C. High genetic variability
  - D. Phenotypically plastic

Source: Modified from Meffe et al. (1994b), Table 8.2.

Note: The preceding outline includes many but not all characteristics necessary for a successful invasion. A successful invasion is the colonization and the establishment of a multigenerational and self-reproducing population of a species in an area distant from its area of natural occurrence and in a different community or ecosystem.

But mammals are not the only exotic predators that greatly affect amphibian and reptile populations. The bullfrog *Rana catesbeiana* has been widely introduced in the Northern Hemisphere for human harvest. It is a highly carnivorous species, taking prey ranging from arthropods to mammals, including its own kind and other frogs, in its native habitat. This predaceous behavior has eliminated native frogs from many habitats and has been especially well documented in the western United States, where it has brought about the local extinction of *Rana aurora* throughout much of the latter's original range. The brown tree snake *Boiga irregularis* is widely known for its consumption of the Guam avifauna (Savidge, 1987), but this snake has also greatly reduced lizard density and may have caused the extinction of one or more lizard species (Fig. 14.9). In this case, it appears that the adult snakes are principally bird predators and the juvenile snakes are lizard predators (Fritts, 1988; Rodda and Fritts, 1992).

FIGURE 14.9 The most notorious and successful exotic amphibian (*Bufo marinus*, left) and reptile (*Boiga irregularis*, right). Photographs by G. R. Zug (left) and G. H. Rodda (right).

The marine or giant toad *Bufo marinus* occurs naturally in Central and South America; among amphibians and reptiles, it has the largest exotic distribution (Zug and Zug, 1979). This species now occurs in the West Indies, Oceania, the Philippines, the Solomon Islands, New Guinea, and Australia, although arguably the braminy blind snake *Ramphotyphlops bramineus* might have a larger exotic distribution but is invisible to most people. The marine toad owes its entire exotic distribution to intentional introductions as a biological control agent, mainly for sugarcane beetle control, for which it has never proved effective. Because the marine toad has been most successful in highly disturbed habitats, there is no evidence that it has displaced any native frogs by competition or predation (Crossland, 1998); however, a modicum of evidence from Australia suggests that some mammalian and avian predators experience population declines as the front of toad's expanding distribution passes through new areas. Apparently, the native predators are poisoned by secretions from the toad's parotoid glands, but subsequently, they either avoid the toad or learn how to kill and eat it without being poisoned.

Throughout the tropics, one or more species of geckos are human commensals, living in and on human habitation. Because of this association, they have been unintentionally transported pantropically and widely among oceanic islands. The genus *Hemidactylus* has the largest roster of exotic species, and recently the house gecko *Hemidactylus frenatus* has been spreading eastward through the Pacific Islands. Its spread has occurred at the expense of another commensal gecko, *Lepidodactylus lugubris*. *L. lugubris* is an all-female species that is competitively inferior to *Hemidactylus*. Both females and males of the bisexual *H. frenatus* defend their feeding sites and challenge conspecifics and any other geckos that enter their sites. This behavior drives *L. lugubris* from the prime feeding areas and through time eliminates them from most buildings, thereby providing an example of species displacement via interference competition (Petren et al., 1993).

Extinction

Extinction is the disappearance of a population of organisms. This natural process occurs regularly within a species, but it is much rarer for all populations of a species to become extinct. The extinction rate for sink populations within a metapopulation can be measured in a few generations or years, whereas it may take tens to thousands of generations or years for metapopulations to become extinct, and ten thousands to millions of years for a species to become extinct. The propensity of a population or a species to become extinct usually is associated with its size or number of individuals. A list of species at risk shows the variety of vulnerabilities and their direct association with the number of individuals (Table 14.5). For example, species composed of individuals with large body size or large home ranges typically consist of populations of fewer individuals. Other factors that make species vulnerable to extinction are associated with reproduction or aggregation. Many turtles require 10 or more years to attain sexual maturity; this long interval increases the probability of mortality before an individual can reproduce for the first time. Many frogs and salamanders in seasonal environments, whether tropical wet-dry or temperate hot-cold, form breeding aggregations in temporary pools. The assemblage of most or all breeding adults in a single location at one moment in time increases the probability that a single catastrophic event

TABLE 14.5 Species Potentially at Risk for Extinction: Amphibian and Reptilian Examples

Characteristic	Species
Only one or few populations	*Pseudemydura umbrina*, western swamp turtle
Small population sizes	*Alytes muletensis*, Majorcan midwife toad[3]
Small geographic ranges	*Lepidodactylus gardineri*, Rotuman forest gecko[14]
Populations in decline	*Dermochelys coriacea*, leatherback seaturtle[11]
Low population densities	*Phaeognathus hubrichti*, Red Hills salamander[4]
Low genetic variability	*Clemmys marmorata*, western pond turtle[7]
Adults requiring large home ranges	*Lachesis muta*, bushmaster[8]
Adults of large body size	*Varanus komodoensis*, Komodo dragon[1]
Slow maturity and/or long-lived	*Emydoidea blandingii*, Blanding's turtle[2]
Low reproductive potential	*Clemmys muhlenbergii*, Muhlenberg's turtle[5]
Poor dispersal ability	*Plethodon shenandoah*, Shenandoah salamander[13]
One or more migratory life stages	Cheloniidae, hard-shelled seaturtles[10]
One or more life stages forming temporary or permanent aggregations	*Lepidochelys kempii*, Kemp's ridley seaturtle[10]
Specialized resource requirements	*Hoplocephalus bungaroides*, broad-headed snake[12]
Harvested by people	*Tupinambis nigropunctatus*, tegu[6]

Sources: [1]Auffenberg, 1981; [2]Congdon et al., 1994; [3]Corbett, 1989; [4]Dodd, 1989; [5]Ernst et al., 1994; [6]Fitzgerald, 1994b; [7]Gray, 1995; [8]Greene, 1986; [9]Kuchling, 1998; [10]Natl. Research Council, 1990; [11]Spotila et al., 1998; [12]Webb and Shine, 1998; [13]Witt, 1999; [14]Zug, 1991.

Note: The taxa selected as examples are not necessarily threatened currently but represent the attribute that places them at risk of extinction.

can eliminate the entire population. If the breeding aggregation requires a special habitat, a string of abnormal weather patterns can temporarily eliminate the proper breeding site for the reproductive life of species with short generation times.

One or more species of amphibians and reptiles match each at-risk category (Table 14.5), and in most cases, the species have obtained their at-risk status as a result of human activities. Harvesting and natural habitat reduction and fragmentation are and have been the major factors driving amphibian and reptile species to the brink of extinction. Both factors reduce population size and genetic variation, thereby increasing the likelihood that stochastic events will cause extinction (Table 14.2). Until recently, extinction among amphibians and reptiles has been relatively low or not recognized, but the current biodiversity crisis includes numerous species and herpetofaunas (Table 14.6). Presently, amphibians (especially anurans) and turtles are at greatest risk for mass extinction. Overharvesting threatens turtles, but the cause(s) for the disappearance of frog species is less certain.

Declining Amphibians

Beginning in the 1980s, herpetologists began to note the disappearance of frogs from localities where they had been abundant only a few years earlier. Only when they began to discuss these disappearances with one another did they realize that the phenomenon was occurring globally and frequently in situations in which habitat loss, modification, or fragmentation was not an adequate explanation. In 1989 at an international meeting, numerous scientists presented overwhelming data showing that many populations and some species of amphibians worldwide had disappeared or were in sharp decline. The peculiarity of many of the population declines was their suddenness, their occurrence in areas presumably exposed to a minimum of human influence, and often the disappearances of some species but not others at the same locality (Halliday and Heyer, 1997; Tyler, 1991b). Amphibian populations are known to fluctuate greatly in size (Semlitsch et al., 1996), so some biologists expressed concern that the declines represented natural fluctuations and that by raising a potentially false alarm, the conservation of truly threatened and endangered amphibian species would be hindered.

The initial alarm, unfortunately, has proven real (Pechmann and Wake, 1997). The alarm and the concern about mislabeling natural population fluctuations have focused research on rigorously documenting the status of populations and on determination of the causes of decline. Attention has focused most strongly on anurans because of their greater diversity and worldwide occurrence. Since 1980, at least a dozen frog species and 2 salamanders in North America have experienced significant declines, and about one-half the species of European frogs and salamanders show lower abundance. In the same interval, 3 Australian frogs likely have gone extinct and at least 20 others show significant declines. Three of 18 species of Puerto Rican *Eleutherodactylus* have disappeared in the last 2 decades (Table 14.6) and 9 others are in decline. Similar declines and disappearances have occurred in most other areas where long-term observations are available.

TABLE 14.6 Examples of Amphibian and Reptilian Extinctions during the Last 2000 Years

Amphibians
  Anura
    Bufonidae
      Atelopus oxyrhynchus (Venezuela)[6]
      Bufo periglenes (Costa Rica)[9]
    Discoglossidae
      Discoglossus nigriventris (Israel–Syria)[4]
    Leiopelmatidae
      Leiopelma auroraensis (New Zealand)[5]
      Leiopelma markhami (New Zealand)[5]
      Leiopelma waitomoensis (New Zealand)[5]
    Leptodactylidae
      Eleutherodactylus eneidae (Puerto Rico)[8]
      Eleutherodactylus karlschmidti (Puerto Rico)[8]
      Eleutherodactylus jasperi (Puerto Rico)[8]
    Myobatrachidae
      Rheobatrachus silus (Australia)[11]

Reptiles
  Testudines
    Testudinidae
      Geochelone inepta (Mauritius)[1,4]
      Geochelone abingtonii (Pinta, Galapagos)[7]
  Crocodylia
  Crocodylidae
    Crocodylus raninus (Borneo)[10]
  Squamata
    Anguidae
      Celestus occiduus (Jamiaca)[2,7]
    Gekkonidae
      Aristelliger titan (Jamiaca, West Indies)[2]
      Hoplodactylus delcourti (New Zealand)[2,5]
      Phelsuma edwardnewtonii (Mascarene Islands)[2,7]
    Iguanidae
      Brachylophus sp. (Tonga)[2]
      Cyclura collei (Jamaica)[7]
      Leiocephalus eremitus (Navassa Island, West Indies)[2,7]
      Leiocephalus herminieri (Martinique, West Indies)[2,7]
    Lacertidae
      Gallotia goliath (Canary Islands)[2]
    Scincidae
      Cyclodina northlandi (New Zealand)[2,4]
      Leiolopisma mauritiana (Mascrene Islands)[2]
      Oligosoma gracilicorpus (New Zealand)[2,4]
    Colubridae
      Alsophis santicrucis (St. Croix, West Indies)[7]
      Dromicus cursor (Martinque, West Indies)[7]
    Viperidae
      Vipera bulgardaghica (Turkey)[3]

Sources: [1]Bour, 1984; [2]Case et al., 1992; [3]Corbett, 1989; [4]Day, 1981; [5]Gill and Whitaker, 1996; [5]Halliday and Heyer, 1997; [6]Honegger, 1981; [7]Joglar and Burrowes, 1996; [8]Pound and Crump, 1994; [9]Ross, 1990; [10]Tyler, 1991c.

Note: Extinction is often difficult to verify for amphibians and reptiles. Many instances exist in which a species is described from one or a few voucher specimens and then is not observed for 50 or more years. The absence of observations might indicate a species of small population size, specialized habitat preferences, short or unusual seasonal activity patterns, or similar factors requiring detailed knowledge of the natural history to rediscover the species. Human expansion into and modification of natural habitats, however, increases the probability that many of these "rare" species are already extinct or soon will be.

The causes of extinction and decline vary and often remain uncertain. Habitat loss and modification are major factors in the decline of abundant and uncommon species everywhere. For example, estimates indicate that over 70% of the ponds and marshes of Great Britain have disappeared since the beginning of the 20th century and that frog and toad abundance may have been reduced by more than 90% (Beebee, 1996). Although such drastic population changes might not have occurred elsewhere, habitat loss and modification is a global phenomenon. Natural habitats and their herpetofaunas adjacent to and interspersed among agricultural lands experience a subtle form of poisoning from insecticides and herbicides. These chemicals and their breakdown products have a variety of effects from carcinogenic and mutagenic actions to direct poisoning and hormone mimics, thereby affecting all life stages of amphibians and reducing the survivorship of all species. Environmental acidification (see "Pollution and Disease" above) is also widespread and particularly disruptive of early development. Its effects occur distant from its source. Although it does not appear to have been the direct agent for the disappearance of amphibian populations in western North America (Vertucci and Corn, 1996), acidification may act synergistically with other pollutants, ranging from heavy metals to ecoestrogens, to disrupt the physiology of amphibians and make them more susceptible to bacterial, fungal, and viral diseases. Indeed, disease has become increasingly implicated in amphibian declines, particularly in those declines and disappearances occurring in presumed pristine habitats (Pound et al., 1997). Even though the epidemiology has not been examined for any of the amphibian die-offs, the likely agents appear to have been resident fungi or bacteria, implying that pollutants from distant sources have weakened the immune system of the amphibians. Another possibility is that the widespread introduction of exotic fish has brought new water-borne diseases into the least-disturbed habitats. This facet remains unproved, but studies have demonstrated that introduced predators, such as trout, mosquito-fish, and bullfrogs, strongly impact populations of frogs and salamanders (Lawler et al., 1999; Webb and Joss, 1997). Ultraviolet radiation clearly affects the early development of some amphibians; further, it has been demonstrated that increased UV radiation reacts synergistically with fungus and/or pollutants to increase embryo mortality. The global reduction of the atmospheric ozone layer has resulted in increasing UV radiation in higher elevations and latitudes.

This superficial review demonstrates the numerous factors involved in amphibian declines and highlights the complexity of the problem. Considering that amphibians live at the water–land interface and thus are exposed to environmental contaminants throughout their life history, and considering that amphibians have persisted throughout the entire evolutionary history of terrestrial vertebrates, the rapid declines we see today serve as harbingers of the potential devastating effects of human activity on life on Earth.

PRESERVATION AND MANAGEMENT—IDEALS AND PROBLEMS

As natural areas shrink or are modified, species and ecosystem preservation become increasingly a management task. The ideal situation is retention of large areas of diverse habitats without management, except for their protection from the illegal extraction of natural resources, such as wildlife poaching and logging. Such areas still remain, but for many species and ecosystems, active management is required. Three major management tools are establishment of refuges, the management of animals in captivity, and the reestablishment of populations using reintroductions. None of the three is a panacea.

Reserves and Corridors—Saving Habitats

As noted in the habitat fragmentation section, a key issue in establishing a reserve or refuge is how much area to preserve. Reserve size is absolutely dependent upon the species or assemblage of species to be preserved, and the identification of the necessary area for full protection requires a thorough knowledge of the natural history of the involved species, especially the habitat requirements of all life stages. As with all conservation issues, there is a tug-of-war between the amount of space needed according to biological conservationists and that of the local populace, business interests, and government. Further, ongoing scientific discussions are critical in determining areas in the world that are hot spots—areas of high biodiversity—that require immediate protection, the appropriate size and shape of reserves, the nearness of reserves to one another, and the length and shape of corridors connecting reserves. The issues are complex, so the following review can examine them only superficially.

In addition, a side issue is a philosophical debate on whether conservationists should target species or communities and ecosystems for preservation. Most biologists argue for the latter, but public and political support is required, and game and charismatic species, such as pandas or gorillas, identify the conservation need to a broader audience, thereby gaining the support necessary for reserve establishment. The advantage is that most of these charismatic species are large; hence, they require large areas and often diverse habitats. These requirements protect numerous other species and their communities as well. The major disadvantage is that single-species conservation can become so narrowly focused on the preservation of the target species that it loses sight of the necessity to preserve the entire habitat and ecosystem of the species.

Reserves are established to prevent the extinction of species, so the issues that determine the location, size, shape, and other aspects of a reserve relate to the survival of a population or species; this concept is referred to as the minimum viable population concept (MVP; see also the habitat modification discussion above). The probability of extinction increases as population size decreases and this relationship gave rise to the minimum dynamic area concept (MDA; Tables 14.2 and 14.5). The MDA is the amount of habitat necessary for the maintenance of the MVP for a species. The important aspect of this definition is "amount of habitat." Habitat represents the actual space used by a species and not just the amount of land or water area that theoretically should permit survival. The focus on habitat usage emphasizes the necessity of knowing all the aspects of the natural history of an organism and the need for research into all facets of an organism's biology.

MVPs have been calculated for only a few species, mainly mammals, but not for any species of amphibian or reptile. Some studies have examined aspects of the MVP for turtles and amphibians. These studies examined the conservation value of federal regulations designed to protect USA wetlands and their biota. Within the United States, any wetland larger than 0.4 ha requires protection. One aspect of this protection is a requirement that a terrestrial buffer zone is established around a wetland to prevent development and encroachment into the natural area. Biologists at the Savannah River Ecology Laboratory have had several ponds completely enclosed by drift-fences and pitfall traps for two decades in order to track the inward and outward movement of every individual of each amphibian and reptilian species living in the pond community. These studies have shown that some semiaquatic species spend considerable time in upland sites, both for nesting and for hibernation. Researchers attached radio transmitters to 73 mud turtles (*Kinosternon subrubrum*), 14 Florida cooters (*Pseudemys floridana*), and 6 sliders (*Trachemys scripta*) to map the terrestrial movements of these species. They discovered that the federally mandated terrestrial buffer zone for wetlands protected none of the hibernation or nesting sites of these turtles (Fig. 14.10). Even the strictest state statutes protect less than 50% of these types of terrestrial sites. To encompass the total terrestrial area used by these turtles, the buffer zone must extend about 240 m beyond the outer edge of the federally mandated zone of protection (Burke and Gibbons, 1995).

A similar situation arises when pond-breeding amphibians are examined. Adults of many pond breeders are terrestrial except when breeding; only the larvae are aquatic. Using data from six species of *Ambystoma* salamanders, adults were on the average 125 m from the edge of their breeding ponds (Semlitsch, 1998). This distance is a mean value, and salamanders often were even further from ponds. Assuming that the area within the mean distance contains 50% of the population, a buffer zone would need to extend 164 m beyond the pond's edge to encompass the land-use activities of 95% of the sampled populations.

These studies highlight the difficulty of identifying and providing sufficient space to preserve one or a few

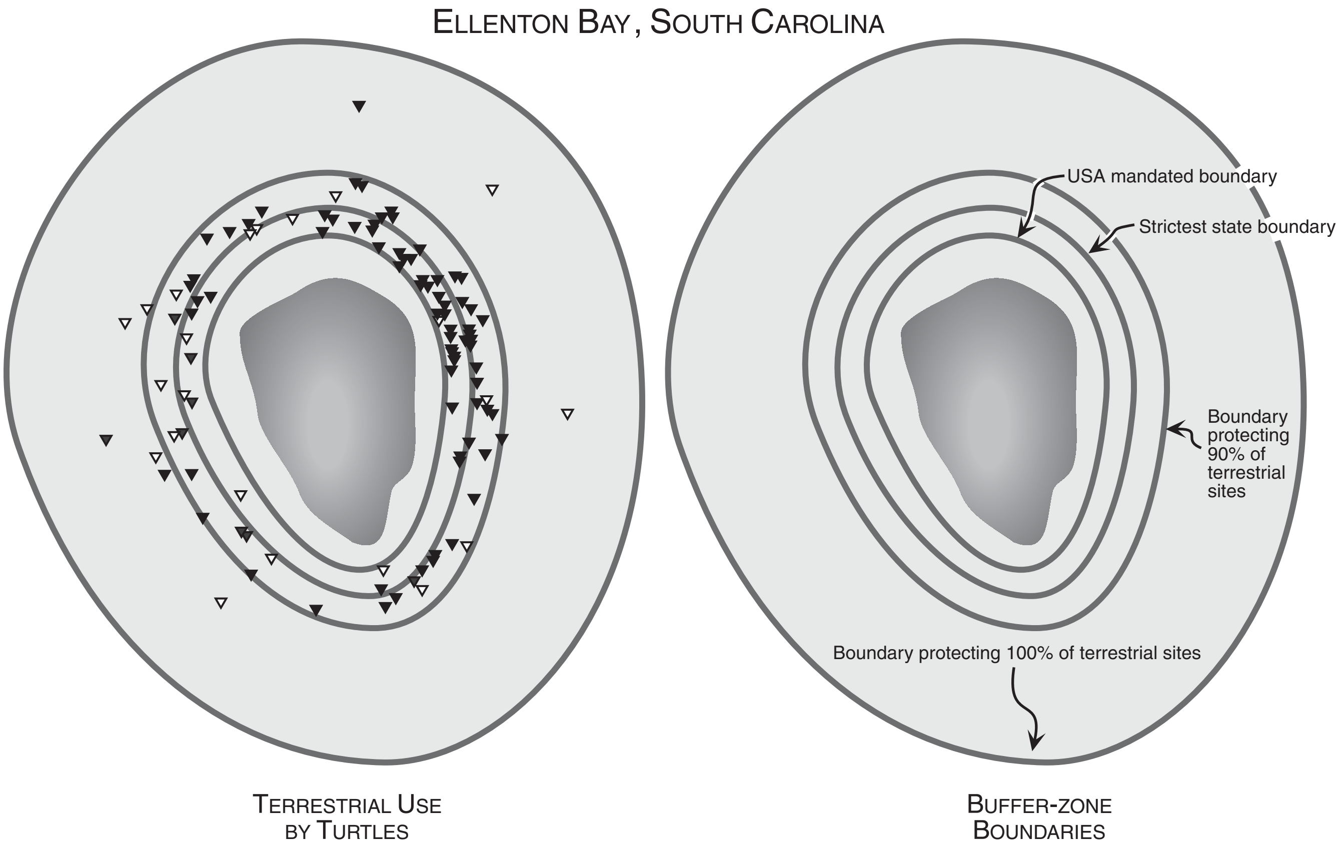


FIGURE 14.10 The inadequacy of the federally mandated terrestrial buffer zones to protect USA wetlands. The schematic diagram shows terrestrial use by three species of semiaquatic turtles living in a 10-ha pond in southeastern South Carolina. The left diagram maps the nesting sites (solid inverted triangles) and hibernation sites (open inverted triangles); the right diagram illustrates various buffer-zone boundaries. Modified from Burke and Gibbons (1995).

components of a single community, and this space would certainly be inadequate to attain MDA requirements of any of the preceding species. Conceptually, the MDA (= minimum reserve size) must encompass at a minimum the distribution of an entire metapopulation, and to expand the MDA concept to community-ecosystem preservation, the MDA must encompass the metapopulation of the species with the largest metapopulation distribution. For small mammals, minimum reserve size is estimated to range between 10,000 and 100,000 ha (100–1000 km^2). Small nonmigratory amphibians and reptiles likely require less area. Using extant species with limited distributions offers one method of estimating potential reserve size. The Shenandoah salamander *Plethodon shenandoah* presently occurs as three isolates in the George Washington National Forest, Virginia. The isolates contain 8 to 10 populations, none of which appears to be a sink population, and in total they occupy about 128 ha. Because of *P. shenandoah*'s close association with talus slopes that lie between 780 and 1150 m, and a known history of recent total defoliation of the forest and of earlier heavy logging and forest fires, we have evidence of the resilience of this species to ecocatastrophes. These data permit an estimate of a 36 km^2 MDA linking all the isolates in a single rectangular forest reserve with a broad buffer zone. A similar process estimates the total land area presently occupied by *Varanus komodoensis* in five islands of the Lesser Sunda group and yields an estimated MDA of roughly 1500 km^2. MDA increases greatly when migratory species are considered. The entire North Atlantic gyre, coastal Florida, and the Greater Antilles would define the MDA for the nesting populations of the green seaturtle *Chelonia mydas* on the Florida east coast.

The preceding MDAs are speculations and illustrate only one of many factors that must be evaluated when establishing a reserve. Among the many factors, the most important one is defining goals for the reserve. Without precise goals, the critical decisions on size, shape, and other aspects of the reserve cannot be made and conservationists will not be able to develop a convincing case to win the support of the local community and the government. Reserves have been established for the protection of amphibians and reptiles. The Archie Carr National Wildlife Refuge was created to protect nesting seaturtles and their nests, and the Komodo National Park was created to protect the Komodo dragon. Both examples represent "single-species" reserves and only the latter is sufficiently large to potentially meet the MDA criteria for the species it is meant to protect. The reserve does serve that function for many smaller lizard and snake species, however. Even though the Archie Carr National Wildlife Refuge does not meet MDA criteria, its establishment is essential to protecting a major nesting beach for two seaturtle species on a coastline that is experiencing rapid and unwise development.

The high potential for extinction of small populations remains a constant threat as the world's natural habitats become increasingly fragmented. The recognition that reserves cannot be as large as conservationists desire and as the populations of many species require led to the biological corridor concept. If single large reserves cannot be established, could numerous small reserves linked by corridors of natural habitat serve as well? Conceptually, biological corridors seem to offer a satisfactory solution, although critics immediately began to identify potential problems, such as increased mortality along the corridors because concentration of predators and the inability of species with low dispersal abilities to find and use narrow corridors. Nonetheless, conservation management groups broadly adopted the corridor concept before the efficacy of corridors was evaluated. Such research is only beginning to test the concept, and, while still limited in scope, the research findings largely support the critics' arguments that corridors are not effective for most species. Two studies of corridor efficacy have used amphibians. In field experiments, *Ensatina eschscholtzii* used disturbed corridors that lacked surface litter and vegetation as frequently as corridors with natural cover (Rosenberg et al., 1997). Salamanders traversing the disturbed corridors moved faster and more frequently than those in the natural corridors, suggesting that the selection of corridors by humans likely will not match the habitat-specific dispersal requirements of many species in the communities being conserved. Similar results and conclusions derive from surveys of species that occur in a river floodplain corridor between two reserves in southern Illinois. The corridor is undisturbed floodplain forest flanked by upland deciduous forest on adjacent bluffs. A 2-year survey of the corridor revealed only 14 species of the 37 amphibian and reptilian species of the upland forest reserves. Even intense surveys do not locate all species, but the occurrence of only 38% of the species suggests that the corridor is not suitable for many species and may act as a sink, potentially reducing population size for some species in the reserves (Gibbs, 1998). Corridors certainly serve some species; however, they cannot be assumed to be effective for all species in a community. Corridors appear to be ineffective for most species of small amphibians and reptiles.

Captive Management

Depending on goals and other factors, animals may be managed in captivity for relatively short periods of time or for much longer periods (Gibbons, 1994). Temporary captivity for short periods may protect one or more life stages in order to increase survivorship during a presumed critical period of life. Temporary captivity includes headstart programs and programs in which eggs are maintained in hatcheries. Long-term captivity for the duration of an individual's life, possibly for several generations, may be for commercial purposes and may eventually result in the death of the animals for their meat, hide, or some other commercially valuable product. Animals in captivity may produce offspring for translocation to replace extinct populations or to augment the size of an existing population with offspring raised in captivity.

Hatcheries and headstart programs are current tools in seaturtle conservation. The effectiveness of these conservation tools remains uncertain because they treat the symptom of population decline (fewer seaturtles) rather than addressing the cause of the decline (Frazer, 1992). These techniques are incorporated into management plans without investigations supporting their efficacy. Both hatchery and headstart programs demonstrate potential dangers of the program in the short- and long-term (Mrosovsky, 1983); however, it is also essential to note that both types of programs appear to have some successes in increasing survivorship to adulthood. Seaturtle hatcheries were begun in the 1970s to protect eggs from terrestrial predators and eroding beaches. Initially, eggs were placed in styrofoam containers filled with local beach sand. Hatching success was comparable to protected nests remaining on the beach; however, temperature-dependent sex determination was as yet unknown. Because the containers were typically maintained in shaded conditions and the boxes were insulated, the nest temperatures were commonly lower than natural nests and the hatcheries produced mainly males. Further, seaturtles are site-specific nesters and adult seaturtles return to their natal beach for nesting. How the hatchlings imprint upon the beach so that they can relocate it as adults remains unknown. Whether disturbing and moving a nest of eggs or hand-releasing hatchlings at water's edge affects the hatchlings' ability to imprint on their future nesting site also remains unknown. The apparent return of some Kemp's ridley seaturtles reared in hatcheries to Padre Island, Texas, indicates that rearing and release techniques allow imprinting in some individuals (but see below).

Headstarting typically involves maintaining hatchlings in captivity for 6 to 12 months and feeding them on a protein-rich diet to increase growth rate. The goal is to enable the young turtles to attain a larger size before releasing them into the sea. Presumably, this enhances survival because the number of potential predators that can kill turtles decreases as the size of turtles increases. The success of such programs remains questionable. Headstart turtles survive for years after release and grow at natural rates; however, headstarting can interfere with the ability of some turtles to locate their parental nesting beaches. This evidence is circumstantial; nonetheless, the nesting attempts by headstart Kemp's ridleys on beaches distant from their natural nesting beach are suggestive.

The most successful examples of long-term captive management are crocodylian farming and ranching (Fig. 14.11). The successes involve both alligators and crocodiles and, in all instances, have been motivated by commercial interest, principally production of hides for the leather trade. Crocodylians have a long history of captive maintenance, but it was only in the late 1960s and early 1970s that crocodylians began to be managed for production of skins as a result of the decline in wild populations from overharvesting. Initially, skin-production programs were done by ranching, in which eggs from wild nests or wild-caught hatchlings are brought into captivity and raised until they attain market size. In addition to the legal protection of large juvenile and adult crocodylians, ranching provides an economic incentive to rural communities to protect large individuals in order to have an annual crop of eggs and juveniles. Recently in some areas a shift from ranching to farming has occurred because of the difficulty of obtaining adequate numbers of eggs and juveniles. Farming involves maintaining breeding adults for production of a sufficient annual volume of eggs and hatchlings. Because of the demands for profitability, ranches and farms have determined the population size necessary to maximize reproduction and growth in the commercially valuable species. Their contribution to conservation is a reduced need to harvest wild animals; however, the attention from the public and government has focused on success in ranching a few of the species. Declines of other species of crocodylians have not received the support necessary to ensure their survival (Thorbjarnarson, 1999).

The captive breeding of pet-trade or hobbyist species became a large-scale commercial enterprise during the 1990s (Fig. 14.12). Aside from aquarium-raised African clawed frogs and the red-eared turtle farms of the south-central United States, amphibians and reptiles in the pet-trade market were taken almost exclusively from wild populations until the mid-1980s. Wild populations remain a major source for this industry; however, captive rearing of hobbyist species now supplies large numbers of amphibians and reptiles to this market. A controversy exists concerning whether hobbyist captive rearing has reduced the demand for wild-caught amphibians and reptiles or has only fueled a demand for the rarer and more threatened species. Hobbyist maintenance has definitely contributed to our knowledge of the biology of many species, and it does provide a pool of amphibian

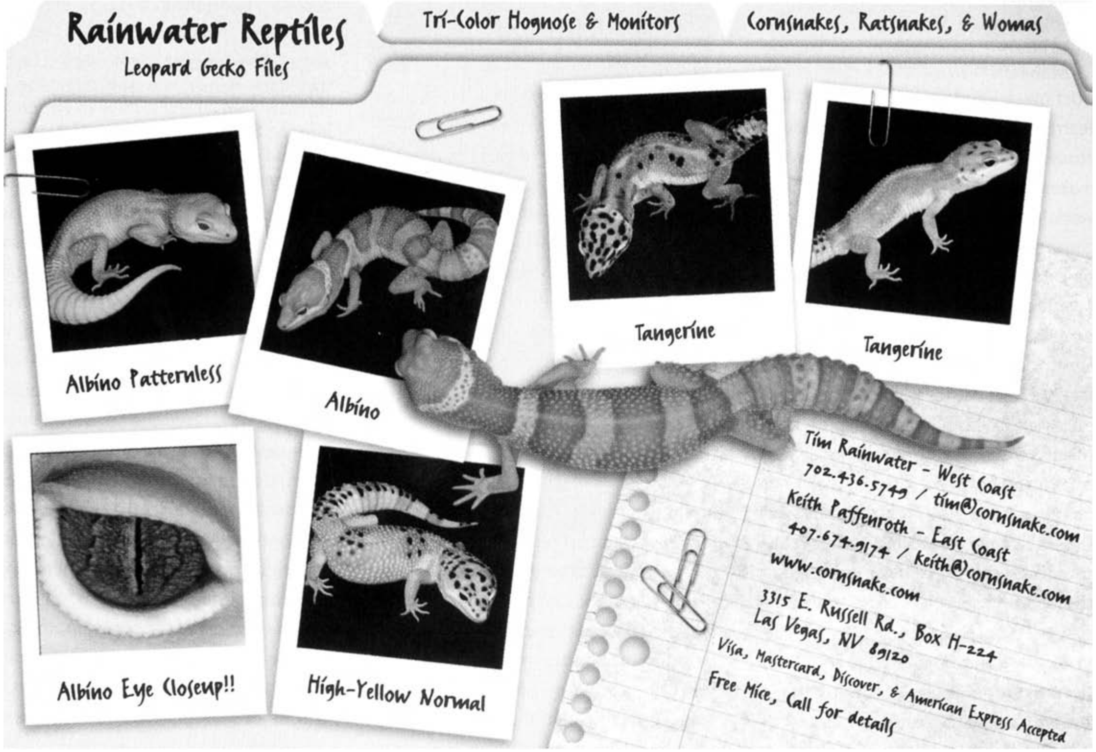
FIGURE 14.11 Clockwise from upper left: egg incubation facility for *Geochelone elephantopus* at the Galapagos tortoise breeding facility (photograph by R. P. Reynolds); juvenile pens at the same facility (R. P. Reynolds); juvenile *Crocodylus porosus* at the Darwin Crocodile Park, Northern Territory, Australia (C. K. Dodd, Jr.); and crocodile farm (P. Ryan).

and reptilian species from which hobbyists can obtain healthy animals that will be long-lived pets. In spite of arguments to the contrary, hobbyist captive rearing does not produce animals for translocation.

We are aware of only a few successful programs of this kind (translocation) for amphibians and reptiles (Table 14.7). A number of zoos and wildlife sanctuaries have successfully maintained and bred threatened or endangered amphibians and reptiles, some for several generations, but few have reported the reestablishment of extirpated populations. Perhaps the most successful program has been the gharial (*Gavialis gangeticus*) program in India. This crocodylian has been reestablished in several river drainages from which it was extirpated. The giant tortoise program in the Galapagos has also reported successful repatriation and augmentation (Fig. 14.11). In contrast to these successes, most programs have failed. A number of reasons may be cited for this lack of success. The primary reason is the difficulty of solving the actual environmental problem that caused the original population decline. Usually the habitat has either disappeared or been drastically modified. Predators, including humans, rats, cats, or others that contributed to the population decline, are still active. Genetic stochasticity and other factors that lead toward extinction of small populations make the maintenance of viable stock in captivity extremely difficult. Conservation-oriented programs actively address this difficulty; commercial and hobbyist programs seldom do. In fact, the latter industry emphasizes genetically aberrant lineages because these designer amphibians and reptiles are commercially more valuable (Fig. 14.12).

Augmentation, Repatriation, and Introduction

Augmentation, repatriation, and introduction fall under the rubric of translocation, defined as the intentional release of individuals to establish or enlarge the population of a target species. The target species is typically a



Rainwater Reptiles
Leopard Gecko Files
Tri-Color Hognose & Monitors
Cornsnakes, Ratsnakes, & Womas

Tim Rainwater - West Coast
702.436.5749 / tim@cornsnake.com
Keith Paffenroth - East Coast
407.674.9174 / keith@cornsnake.com
www.cornsnake.com
3315 E. Russell Rd., Box H-224
Las Vegas, NV 89120
Visa, Mastercard, Discover, & American Express Accepted
Free Mice, Call for details

FIGURE 14.12 Designer amphibians and reptiles are captive-reared species in which attractive color variants are selectively bred for the hobbyist market. This advertisement for designer leopard geckos is taken from the *Reptile and Amphibian Hobbyist*, a magazine for hobbyists who maintain and breed amphibians and reptiles as pets. Reproduced with permission of Tim Rainwater of Rainwater Reptiles.

threatened or endangered species, although introductions include intentional and unintentional release of individuals of nonthreatened species into a locality or habitat foreign to that species. The latter sort of release and colonization was examined above in "Exotic Species." Repatriation is the release of individuals of a species into a locality from which the species was extirpated, and augmentation is the release of individuals of a species into a locality containing the same species. All three types of translocations are widely used conservation tools, although the use of each remains controversial (Burke, 1991; Dodd and Seigel, 1991; Reinert, 1991). They have been used with varying success in the conservation of amphibians and reptiles. The following examples briefly address some positive and negative aspects of translocation conservation.

In 1976, a fire swept thorough an English sand dune nature preserve, largely destroying this isolated patch of heath vegetation. Concern that the plant community would recover but not quickly enough to allow the survival of *Lacerta agilis* led to the capture of all surviving sand lizards. The lizards were maintained in captivity where they prospered, and in 1978, all were transferred to an outdoor vivarium to establish a breeding colony. Sand lizards from the breeding colony were repatriated into the reserve and by 1988, the heath community had completely regenerated and the lizard population was healthy (Corbett, 1988). The breeding colony provided additional lizards for repatriation in other sand dune heath communities in southeastern England and elsewhere, as well as an introduction into the Inner Hebrides (Spellerberg, 1988). Apparently most of the translocations have been successful, although a few populations were destroyed when fires destroyed translocation sites.

A similar success story applies to the Majorcan midwife toad *Alytes muletensis* (Fig. 14.13). This toad was discovered first as a fossil and was considered extinct on the Balearic Islands off the east coast of Spain. A few isolated populations were later discovered in the deep mountain gorges of Majorca. Apparently, many populations of this species were heavily preyed upon and driven extinct by the European water snake *Natrix maura*, which was introduced into the Balearics by the Romans for religious use. Once rediscovered in 1980, the toads were given legal protection, some nature reserves were established, and two zoos established breeding colonies, each from a few individuals. These breeding colonies

TABLE 14.7 Examples of Long-Term Captive Management and Translocation Programs for Amphibians and Reptiles

Taxon	Life stage released	Status	Location
Amphibians			
Alytes muletensis, Majorcan midwife toad[1]	E–A	S	Majorca
Bufo houstonensis, Houston toad[1]	E–J	U	Texas
Peltophryne lemur, Puerto Rican crested toad[5]	L–A	U	Puerto Rico
Reptiles			
Geochelone hoodensis, Española Tortoise[2]	J	I	Española, Galapagos
Gavialis gangeticus, gharial[3]	J	S	Chambal River, India
Lacerta agilis, sand lizard[4]	J–A	S	Southeastern England

Sources: [1]Beebee, 1996; [2]Cayot and Morillo, 1998; [3]Choudhury and Choudhury, 1986; [4]Corbett, 1988; [5]Paine et al., 1989.

Note: These examples include only programs in which the adults have been maintained in captivity for 1 or more years and the released offspring were hatched or born in captivity. A successful translocation requires maturation of juveniles *in situ*, their reproduction, and the survival of their offspring. Abbreviations for life stage released are E, eggs; L, larvae; J, juveniles; and A, adults. Those for success of the translocation are U, unknown; I, indeterminate (some individuals surviving and maturing); and S, successful.

have been used for repatriation; of eight repatriations, three populations now have begun to reproduce, one translocation failed, and the status of the other four is indeterminate (Beebee, 1996).

Captive breeding programs and translocations are not always successful. The endangered Houston toad (*Bufo houstonensis*) is a resident of southeastern Texas in pine flatwoods with sandy soils (Fig. 14.13). Agriculture and other development have eliminated many populations and reduced this species to a few isolated populations. This toad is adaptable to captive breeding, and a breeding program at the local Houston zoo has provided adults and thousands of eggs and metamorphs for translocation. In spite of massive efforts to reestablish the toad at extirpated and new sites, no new populations have become established (Dodd and Seigel, 1991).

A similar lack of success is common in "mitigation" or relocation projects that move animals from sites that are scheduled for destruction because of development. Thousands of gopher tortoises (*Gopherus polyphemus*) have been relocated in central Florida because of development projects. Typically these translocated individuals are placed in existing populations. Of the hundreds of relocations, only a few have included short-term monitoring of the relocated individuals, showing that usually 50% or more of the relocated individuals disappear from the new site within 2 years. Most other relocation projects show similar results. A site in southeast England scheduled for development had a large population of slowworms (*Anguis fragilis*). Slowworms were captured and relocated at a natural site that lacked slowworms but was otherwise ecologically similar. The translocation failed; the slowworms at the relocation sites were clearly less robust than those from nearby populations, and did not become established and reproduce (Platenberg and Griffiths, 1999). In general, relocations largely fail.

FIGURE 14.13 Taxa involved in captive management and/or translocation programs: *Alytes muletensis* (left) and *Bufo houstonensis* (right). The program has been successful for *A. muletensis* but unsuccessful for *B. houstonensis*. Photographs by E. G. Crespo and D. B. Fenolio, respectively.

Further, they mislead the public, developers, and government officials by suggesting that natural populations are conserved. Although these efforts result from good intentions, they lead to poor conservation and should be eliminated as a development trade-off strategy.

Relocation and augmentation programs have real and potential dangers built into them. The introduction of disease into healthy populations is a real danger. For example, a disease of the upper respiratory tract has decimated populations of the desert tortoise (*Gopherus agassizii*) and now appears to be spreading through the gopher tortoise populations of Florida. Another potential danger is outbreeding depression. Small isolated populations are often closely adapted to their local environment, and while subtle to the human eye, microenvironments can be quite different among nearby populations. Augmentation introduces individuals with new genetic constitutions into a genetically stable population, thereby changing the relationship of the resident population to its local environment. Over time the new genetic pool can adapt to the specific local environment, but the initial response of the local population is likely lower survivorship (Templeton, 1986). For a small population, this decline in numbers can push it to extinction. The essential message of translocation conservation is to anticipate failure and to proceed cautiously with intense scrutiny to avoid causing further injury to the species or population that is in need of intervention.

An Afterword

"Values are the key to understanding a conservation system . . . . There are no balances to protect. Rather, nature is protected and promoted because we derive benefits from it, whether the benefit be aesthetic, spiritual, scientific, or economic" (Drury, 1998). Conservation is, indeed, a human endeavor and for human benefit, but the greatest benefit is for the most selfish of selfish reasons, survival. Either we ameliorate the approaching mass extinction event or *Homo sapiens* may be one of the extinctions.

ADDITIONAL READING

Beebee, T. J. C. (1996). "Ecology and Conservation of Amphibians." Chapman & Hall, London.

Drury, W. H., Jr. (1998). "Chance and Change. Ecology for Conservationists." Univ. of California Press, Los Angeles.

Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L.-A. C., and Foster, M. S. (1994). "Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians." Smithsonian Inst. Press, Washington, DC.

Jaffe, M. (1994). "And No Birds Sing. The Story of an Ecological Disaster in a Tropical Paradise." Simon & Schuster, New York.

Mrosovsky, N. (1983). "Conserving Sea Turtles." British Herpetol. Soc., London.

Phillips, K. (1994). "Tracking the Vanishing Frogs." St. Martin's Press, New York.

Primack, R. B. (1995). "A Primer of Conservation Biology." Sinauer Assoc. Inc., Sunderland, MA.

Stebbins, R. C., and Cohen, N. W. (1995). "A Natural History of Amphibians," Chap. 20 (Declining Amphibians). Princeton Univ. Press, Princeton, NJ.

REFERENCES

General Principles: Bauer, 1999; Carr, 1940; Heyer, 1967; Meffe and Carroll, 1994; Pianka, 1986, 1994a,b; Raup, 1991; Savage, 1995; Papenfuss, 1986.

Human Impact on Amphibian and Reptile Communities: Habitat Modification, Fragmentation, and Loss: Ash and Bruce, 1994; Corn and Bury, 1988; Congdon et al., 1994; Crouse et al., 1987; Demaynadier and Hunter, 1998; Fisher and Shaffer, 1996; Gibbs, 1998; Herbeck and Larsen, 1999; Means et al., 1996; Pearman, 1997; Petranka et al., 1994; Pianka, 1994a,b; Sartorius et al., 1999; Shaffer, 1981; Vitt et al., 1998a.

Pollution and Disease: Aguirre et al., 1998; Beebee, 1996; Berger et al., 1998; Crawshaw, 1997; Dunson et. al., 1992; George, 1996; Grillitsch and Chovanec, 1995; Guillette, 1995; Guillette et al., 1996; Hayes et al., 1997; Herbst, 1994; Herbst and Klein, 1995; Laurance, 1996; Laurance et al., 1996; Lips, 1998, 1999; Pough and Wilson, 1977; Richards et al., 1993.

Harvesting Amphibians and Reptiles: Brazaitis et al., 1998; Fitzgerald, 1994a,b; Frazer, 1992; Melisch, 1998; Shine et al., 1996d; Thorbjarnarson, 1999.

Exotic Species: Crossland, 1998; Fritts, 1988; Godley, 1980; Mitchell and Beck, 1992; Petren et al., 1993; Rodda and Fritts, 1992; Ryan, 1988; Savidge, 1987; Watling, 1986; Whitaker, 1973; Wilson and Porras, 1983; Zug and Zug, 1979.

Extinction: Declining Amphibians: Beebee, 1996; Halliday and Heyer, 1997; Lawler et al., 1999; Pechmann and Wake, 1997; Pound et al., 1997; Tyler, 1991b; Vertucci and Corn, 1996; Webb and Joss, 1997.

Preservation and Management: Reserves and Corridors—Saving Habitats: Burke and Gibbons, 1995; Gibbs, 1998; Rosenberg et al., 1997; Semlitsch, 1998.

Captive Management: Frazer, 1992; Gibbons, 1994; Mrosovsky, 1983; Thorbjarnarson, 1999.

Augmentation, Repatriation, and Introduction: Beebee, 1996; Burke, 1991; Corbett, 1988; Dodd and Siegel, 1991; Reinert, 1991; Spellerberg, 1988; Templeton, 1986. Afterword: Drury, 1998.

Part VI

CLASSIFICATION AND DIVERSITY

Chapter

15

Caecilians

OVERVIEW

Caecilians occur worldwide in the tropics, except for Madagascar and Papua–Australia. In spite of their widespread occurrence, there are only about 160 species (Glaw and Köhler, 1998), currently divided into six families. Most caecilians are fossorial, living in moist soils often adjacent to streams, lakes, and swamps; a few species are aquatic. Rarely seen, their biology is largely unknown, and much of our knowledge derives from observations made during capture and from captive or museum specimens.

Caecilians (Gymnophiona; Apoda, stem-based name) are amphibians that look like earthworms. They have blunt, bullet-shaped heads; cylindrical, limbless bodies; and short tails. The bodies of all caecilians are distinctly segmented by encircling primary grooves, and usually each segment (= primary annulus) contains a single vertebrae. In some taxa, the primary annuli are further partitioned into secondary and even tertiary annuli by additional encircling grooves. The blunt heads are digging tools for creating the burrows in which these animals live. Movement through burrows is by a combination of serpentine and internal concertina locomotion, or by serpentine or undulatory locomotion when on the surface. Likely only the heavier-bodied caecilians use internal concertina locomotion. For these caecilians, the muscular body, loosely attached to the skin, bends within the inflexible skin tube and shifts forward, and then the skin tube is contracted, moving the entire animal forward. The slender caecilians use only undulatory locomotion on the surface and in burrowing; hence, they are confined to more friable soils. The aquatic species often have dorsal and ventral fins posteriorly and a somewhat laterally compressed body; undulatory locomotion is used for forward movement.

All caecilians have internal fertilization. Males possess a copulatory organ, the phallodeum; it is an eversible portion of the cloacal floor. Mating is somewhat snakelike. The male lies on or entwines with the female in order that their cloacae are in apposition and that the phallodeum can be everted into the female's cloaca. Offspring may develop internally or externally, and if externally, their development is indirect or direct; however, developmental mode is fixed in each species.

A number of features attest to the monophyly of all living caecilians. Dermal (bony) scales often are present, lying deep within the tissue of the annular grooves. With the head used as a digging ram, the skull is compact and tightly knit to withstand the jarring forces of digging; some elements, such as the maxillary and palatine, are fused as single bones. The eyes are vestigial, represented only by small, darkly pigmented areas, lying beneath the skin and, in some cases, beneath skull bones. External ear openings are absent. The lower jaw is underhung, a position that allows prey capture in narrow spaces yet does not interfere with the head's use in burrowing. The snout bears a retractable sensory tentacle on each side of the head between the nostril and the eye; the tentacles aid in the location and identification of prey. Many structures that are part of the eye in other vertebrates have been preempted for the tentacle in caecilians. The limbs have been completely lost; not even a remnant of the pectoral or pelvic girdles remains in the body wall.

The predominantly subterranean existence of caecilians has effectively hidden them from the attention of most biologists. They existed as seldom mentioned oddities, all lumped in the family Caeciliidae, until Dr. Edward H. Taylor began a survey of these amphibians in the 1960s. In 1968, he published a monograph devoted to caecilians and drew attention to their diversity and how little was known about their systematics and life history. Three decades after their "rediscovery," we know as much about their phylogenetic relationships as we do for salamanders and frogs after a century of study; however, their biology remains little known.

Taylor's 1968 monograph provided no phylogenetic analysis, although his partition of caecilians into 3 families, Caeciliidae, Ichthyophiidae, and Typhlonectidae, is an implicit hypothesis of relationships and monophyly. A year later, he proposed an additional family, Scolecomorphidae, and divided the largest family into 2 subfamilies, Caeciliinae and Dermophiinae, again without phylogenetic analysis. The uniqueness of the genera *Rhinatrema* and *Epicrionops* prompted recognition of the family Rhinatrematidae (Nussbaum, 1977) and, 2 years later, Nussbaum showed *Uraeotyphlus* had closer affinities to the Ichthyophiidae and proposed its transfer from the Caeciliidae to its own subfamily within the Ichthyophiidae. These studies and subsequent ones continued the realignment of genera but without an analysis of all caecilians. In 1986, three phylogenies appeared: Duellman and Trueb's phylogenetic dendrogram based on an explicit cladistic algorithm; Laurent's dendrogram based on an unexplained algorithm; and Lescure and associates' dendrogram erected on cladistic principles. The former two phylogenies recognize 6 families, Caeciliidae, Ichthyophiidae, Rhinatrematidae, Scolecomorphidae, Typhlonectidae, and Uraeotyphlidae; these families continue to be recognized (Figs. 15.1 and 15.2). The Lescure phylogeny and its classificatory interpretation resulted in 10 families and many subfamilies. Two clades and their origins are generally shared by these three phylogenetic hypotheses; that is, the rhinatrematids are primitive and basal, and the Caeciliidae are the most derived.

Nussbaum and Wilkinson (1989), reacting to the analysis and interpretation of Lescure and colleagues (1986), showed that these researchers had misinterpreted the evolutionary direction of some of their key characters. Nussbaum and Wilkinson's phylogenetic analysis demonstrated the uncertainty of relationships among the "higher" caecilians; nonetheless, they proposed the retention of the basic six families. Subsequent studies usually confirmed the basal divergence of rhinatrematids from the main gymnophionan lineage, and then the divergence of ichthyophiids and uraeotyphlids, either independently or as a shared ancestor with their subsequent divergence (Fig. 15.1) from the "higher" caecilians. These confirmations derive from a variety of data sets, including immunological (Hass et al., 1993), RNA sequence (Hedges et al., 1993b), and morphological (Wilkinson, 1989, 1992a, 1997; Wilkinson and Nussbaum, 1996) data. An aspect highlighted by all these studies is the paraphyly of the current Caeciliidae, and the relationships among many smaller clades within the higher caecilians remain unresolved. With fair certainty, the typhlonectids are a monophyletic clade, as are also the three genera of Seychelles Islands caeciliids. Scolecomorphids appear as a clade in some studies but not in others. Generally, the scolecomorphids are a sister group to the African-Seychelles-Asian caeciliids, and the typhlonectids are a sister group to the American caecilians. While these uncertainties remain, a conservative approach recommends the use of Caeciliidae, Scolecomorphidae, and Typhlonectidae without subfamilial partitioning.

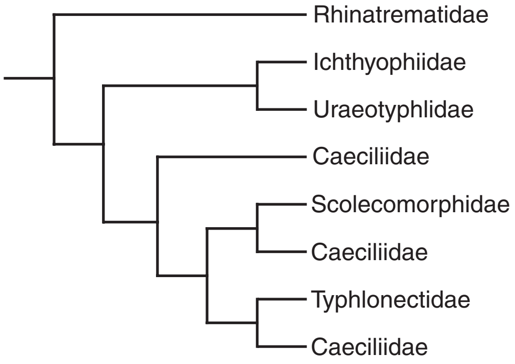


FIGURE 15.1 A cladogram depicting relationships among the families of extant caecilians. The cladogram derives from Wilkinson and Nussbaum (1996, Fig.1b) for the basal taxa and is modified from Wilkinson (1997, Fig. 8) for the "higher" caecilians. Cladogram redrawn from originals for uniformity.

General References Cogger and Zweifel, 1998; Duellman and Trueb, 1986; Halliday and Adler, 1986; Himstedt, 1996; Summers and O'Reilly, 1997; Wake, 1977.

Systematic References Hass et al., 1993a; Hedges et al., 1993a; Laurent, 1986; Lescure, 1986b; Lescure

FIGURE 15.2 Representative caecilians. Clockwise from upper left: ringed tailless caecilian *Siphonops annulatus*, Caeciliidae (photograph by J. P. Caldwell); monochrome tailed caecilian *Ichthyophis monochrous*, Ichthyophiidae (L. L. Grismer); two-colored caecilian *Epicrionops bicolor*, Rhinatrematidae (L. Coloma); African buried-eyed caecilian *Scolecomorphus vittatus*, Scolecomorphidae (L. W. Porras); and water caecilian *Typhlonectes natans*, Typhlonectidae (C. Schwalbe).

et al., 1986; Nussbaum and Wilkinson, 1989; Taylor, 1968; Wake, 1993a; Wilkinson 1989, 1992a, 1997; Wilkinson and Nussbaum, 1996.

TAXONOMIC ACCOUNTS

"Caeciliidae"

Tailless caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon In part and separately, Typhlonectidae and Scolecomorphidae.

Content Twenty-one genera, *Boulengerula*, *Brasilotyphlus*, *Caecilia*, *Dermophis*, *Gegeneophis*, *Geotrypetes*, *Grandisonia*, *Gymnopis*, *Herpele*, *Hypogeophis*, *Idiocranium*, *Indotyphlus*, *Luetkenotyphlus*, *Microcaecilia*, *Mimosiphonops*, *Oscaecilia*, *Parvicaecilia*, *Praslinia*, *Schistometopum*, *Siphonops*, and *Sylvacaecilia*, with ±90 species.

Distribution Tropical America, eastern and western equatorial Africa, Seychelles Islands, and India (Fig. 15.3).

Characteristics All caeciliids have primary annuli, and some species have the primary annuli divided by secondary grooves, but none has tertiary grooves. Scales are present in the annular grooves of some genera and absent in others. The posterior end of the body is capped with a terminal shield but lacks a true tail that has caudal vertebrae and myomeres. Eyes may or may not be visible externally; in some genera, eyes lie in bony sockets beneath the skin, and in others they lie beneath bone. Tentacles are variously positioned; in some taxa, the tentacles are adjacent to the nostrils, whereas in others, they are near the eyes. The middle ear contains a stapes.

Biology Caeciliids range in size from the small *Idiocranium russelli* (98–104 mm adult total length, TL) to the large *Caecilia thompsoni* (1.5 m TL). Adults of most taxa range from 300 to 500 mm TL, although most adult *Oscaecilia* exceed 600 mm TL. All caeciliids are fossorial in moist soils and most live in forests. Caeciliids have a variety of reproductive behaviors. Some are oviparous (e.g., *Grandisonia*, *Hypogeophis*), whereas others are viviparous (*Caecilia*, *Dermophis*). Some oviparous taxa lay eggs in or near water and have free-living larvae. Parents of other species (*Boulengerula taitanus*, *Hypogeophis rostratus*, and *I. russelli*) attend the eggs, which undergo direct development. Current evidence suggests that all direct-developing and many indirect-developing caecilians remain with their eggs until they hatch. The larval period usually extends from 10 to 12 months; metamorphosis occurs shortly before the next reproduction season begins (e.g., *Geotrypetes*). Development is faster in larvae with direct development. Reproduction appears to be seasonal or nearly continuous, depending largely on the climate in a particular area.

References Exbrayat, 1985; Himstedt, 1996; Nussbaum, 1984; Nussbaum and Hinkel, 1994; Wake, 1977.

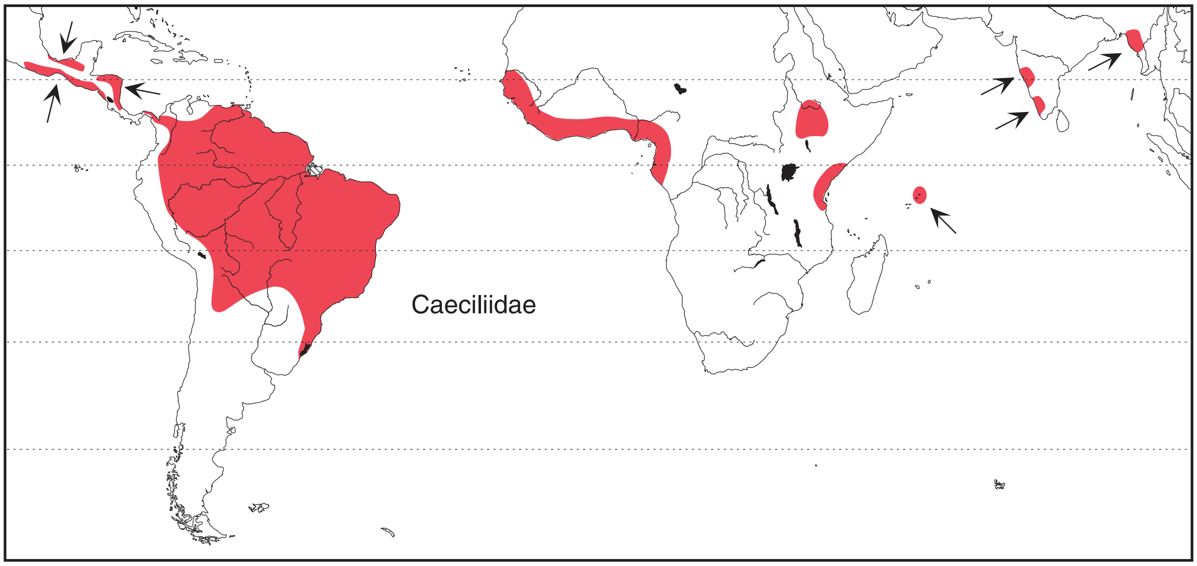


FIGURE 15.3 Geographic distribution of the extant Caeciliidae.

Ichthyophiidae

Asian tailed caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon Uraeotyphlidae.

Content Two genera, *Caudacaecilia* and *Ichthyophis*, with 35+ species.

Distribution India and Southeast Asia (Fig. 15.4).

Characteristics Ichthyopiids have conspicuous primary annuli divided by secondary and tertiary grooves. Scales are present in most annular grooves, but occasionally are absent from the anteriormost grooves. The body ends in a short, true tail that has caudal vertebrae and myomeres. The eyes are visible externally and lie in bony sockets beneath the skin. Each tentacle lies between the eye and the nostril, usually closer to the eye. The middle ear contains a stapes.

Biology Ichthyophiids are moderate-sized caecilians, with adults of most species in the 200- to 300-mm TL size range; a few (e.g., *C. nigroflava*, *I. glutinosus*, *I. malabarensis*) reach total lengths of 400–500 mm. All species in the two genera are oviparous. Development is indirect in the few known examples.

Ichthyophis deposits eggs in its burrows near water. The female remains with the eggs until the larvae hatch. Upon hatching, the gilled larvae exit the burrows and crawl overland to a nearby pond or stream. The entire developmental cycle from egg deposition to metamorphosis is about a year (*I. glutinosus*, *I. kohtaoensis*).

References Breckenridge et al., 1987; Gundappa et al., 1981; Himstedt, 1996; Masood-Parveez and Nadkarni, 1993; Wake, 1977.

Rhinatrematidae

American tailed caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon The clade including all other gymnophionan families.

Content Two genera, *Epicrionops* and *Rhinatrema*, with eight and one species, respectively.

Distribution Northern South America east of the Andes (Fig. 15.4).

Characteristics Rhinatrematid caecilians are strongly annulated. The primary annuli are divided by secondary and tertiary grooves, and numerous scales are present in the primary annular grooves. The body ends in a short tail. The eyes are visible externally and lie beneath the skin in bony sockets. A tentacle arises near

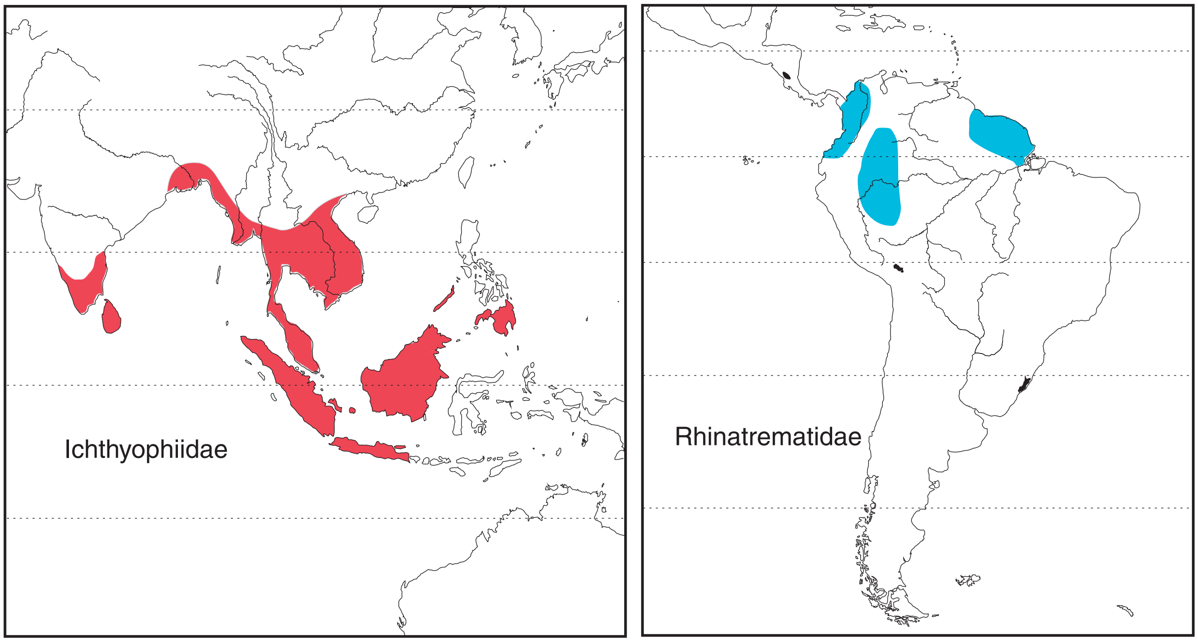


FIGURE 15.4 Geographic distributions of the extant Ichthyophiidae and Rhinatrematidae.

or at the anterior edge of each eye. The middle ear contains a stapes.

Biology Rhinatrematids range from 200 to 330 mm adult TL. Both genera are presumably oviparous. Free-living larvae are known for *Epicrionops*, thereby indicating that this taxon deposits aquatic eggs.

References Nussbaum, 1977; Wilkinson, 1992a.

Scolecomorphidae

Buried-eyed caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon Possibly a clade including Caeciliidae (possibly African) and Typhlonectidae.

Content Two genera, *Crotaphatrema* and *Scolecomorphus*, with two and three species, respectively.

Distribution Eastern and western equatorial Africa (Fig. 15.5); as yet, no caecilians have been found in central Africa (Nussbaum and Hinkel, 1994).

Characteristics Scolecomorphids possess only primary annuli, and only a few vestigial scales occur in the posteriormost annuli. They lack a true tail. Bony orbits are absent, and the eyes lie beneath skull bones; however, because the eyes are attached to the tentacles, they move outward when the tentacles are extended. The middle ear lacks a stapes.

Biology Scolecomorphids range from 150 to 360 mm adult TL, with most adults over 300 mm. They are mountain forest-floor residents, usually inhabiting areas adjacent to streams or other moist habitats. Three species of *Scolecomorphus* give birth to young. Their oviductal eggs are small, yet the developing embryos are many times the mass of the eggs; thus, a maternal–embryo nutrient transfer is likely. C*rotaphatrema* appears to be oviparous, because its oviductal eggs are much larger than those of *Scolecomorphus*.

References Nussbaum, 1985a; Wake, 1998.

Typhlonectidae

Water caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon Caeciliidae or a clade of Neotropical caeciliids.

Content Five genera, including *Atreochoana*, *Chthonerpeton*, *Nectocaecilia*, *Potomotyphlus*, and *Typhlonectes*, with 13 species.

Distribution Northern South American east of the Andes (Fig. 15.5).

Characteristics Typhlonectids have only primary annuli, although in a few species, some primary annuli are partially dissected by false secondary grooves. Dermal

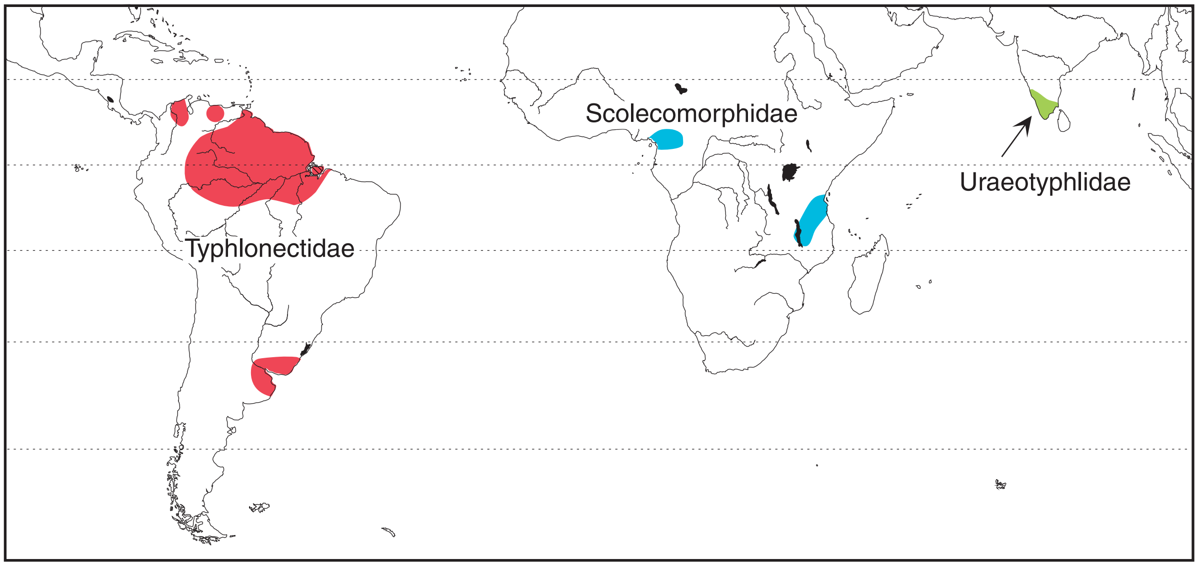


FIGURE 15.5 Geographic distributions of the extant Typhlonectidae, Scolecomorphidae, and Uraeotyphlidae.

scales are absent in the grooves. They lack a true tail. Their eyes are moderately well developed and always visible in bony sockets beneath the skin. The sensory tentacles are small and usually closer to the nostrils than the eyes. Stapes are present.

Biology Typhlonectids are the largest caecilians. Adult *Potomotyphlus* and *Typhlonectes* typically range from 300 to 600 mm adult TL, and *Atreochoana eiselti* reaches 800 mm TL. *Chthonerpeton* and *Nectocaecilia* are generally slender and range from 200 to 400 mm TL, although *C. viviparum* reaches a length of 560 mm. *Atreochoana*, *Potomotyphlus,* and *Typhlonectes* are strongly aquatic, whereas *Chthonerpeton* and *Nectocaecilia* are semiaquatic. The bodies of the aquatic taxa are laterally compressed and bear a middorsal fold or fin, which presumably assists their undulatory swimming. *Atreochoana* is totally lungless, and *Chthonerpeton* has a rudimentary left lung. The other genera have well-developed left and right lungs. *Atreochoana* may have evolved in highly aerated waters, such as mountain streams, but only two specimens are known and they lack locality data. All typhlonectids are viviparous. The embryos' gills fuse into saclike structures that serve as placentas for gas and perhaps waste exchange.

References Billo et al., 1985; Exbrayat, 1984; Exbrayat and Hraoui-Bloquet, 1992; Murphy et al., 1977; Wake, 1977; Wilkinson, 1989, 1996; Wilkinson and Nussbaum, 1997; Wilkinson et al., 1998.

Uraeotyphlidae

Kerala caecilians

Classification Amphibia; Lissamphibia; Gymnophiona.

Sister taxon Ichthyophiidae.

Content One genus, *Uraeotyphlus*, with four species.

Distribution Southwestern India (Fig. 15.5).

Characteristics *Uraeotyphlus* has primary annuli divided by secondary but not tertiary grooves, but none of the annular grooves completely encircles the body. Scales are present in the annular grooves. The body ends in a short tail. The eyes are visible externally and lie in bony sockets beneath the skin. The tentacles are far forward beneath the nostrils. Each middle ear contains a stapes.

Biology *Uraeotyphlus* ranges from 200 to 300 mm adult TL. Few individuals have been observed; hence, their biology is almost entirely unknown. All species are likely oviparous. Larvae of *U. oxyurus* possess a typical caecilian larval morphology; however, the structure of the mouth and throat suggests that the larvae are suction feeders and eat small prey.

References Bhatta, 1998; Nussbaum, 1979; Wilkinson, 1992b; Wilkinson and Nussbaum, 1996.

This Page Intentionally Left Blank

Chapter

16

Salamanders

OVERVIEW

Salamanders, the tailed amphibians, are largely a Northern Hemisphere (Holarctic) group. All except the Plethodontidae are confined to temperate and subtropical areas of North America and/or Eurasia, including North Africa. Most terrestrial salamanders require moist habitats, typically forest, whereas aquatic salamanders may occur in vernal pools, spring seepages, streams, and large lakes and rivers. The only tropical salamanders are plethodontids, occurring mainly in mountains of Central America and a few species in the Amazon basin. These tropical invaders have been highly successful, representing more than one-third of the total extant salamander species, that is, 410+ species (Duellman, 1993; Glaw and Köhler, 1998).

Salamanders (Caudata; Urodela, stem-based name) have well-developed tails; cylindrical, often elongate, bodies; and distinct heads. Most also have well-developed limbs, frequently short relative to body length, although two clades have reduced or lost limbs. Salamander skulls are reduced by the loss of many elements, and other cranial elements are partly or totally cartilaginous (Fig. 2.10). Cartilaginous elements occur in the postcranial skeleton as well. Whether this cartilaginous condition reflects heterochrony is uncertain; however, heterochrony has occurred repeatedly in salamander evolution. Heterochrony (see Chapter 2, "Development and Growth") involving paedomorphosis (interspecific) or paedogenesis (intraspecific) is recognized by the retention of larval traits in adults, such as gill slits and gills, and the absence of eyelids.

Derived lineages of salamanders have internal fertilization, although none has a copulatory organ. The basal lineages Cryptobranchoidea and Sirenidae have external fertilization. Internal fertilization occurs via a male-deposited spermatophore from which the female grasps a packet of sperm with her cloacal lips. With the exception of a few species, development occurs externally, either indirectly via a larval stage or directly into miniature salamanders. Salamanders have varied life histories. Although only 20–25% of known species have terrestrial adults that return to water to mate and deposit their eggs in water to hatch into gilled, aquatic larvae, this biphasic life history is considered the "typical" life history of salamanders. In contrast, most salamander species deposit eggs terrestrially in moist microhabitats, and these eggs hatch directly into fully formed juvenile salamanders. In a very few species, eggs hatch while still in the oviduct of the female (Hairston, 1996).

Living salamanders share a suite of uniquely derived features (Milner, 1988) that demonstrate the monophyly of salamanders. The major synapomorphies include the ossification sequence of the skull, including the late appearance of the maxillae; a remodeling of the palate during metamorphosis; the absence of a middle ear; the origin of the jaw adductor muscle; and the presence of gill slits and external gills in aquatic larvae.

Relationships among the families of living salamanders remain uncertain. Over a century ago, Cope (1889) grouped the nine families then recognized into two groups: Trematodera (Cryptobranchidae) and Amphiumoidea (all other salamanders). He also suggested the derivation of the caecilians from the amphiumas. By the 1930s, Noble had classified the eight families then recognized into five groups: Cryptobranchoidea (Cryptobranchidae, Hynobiidae); Ambystomoidea (Ambystomatidae); Salamandroidea (Amphiumidae, Plethodontidae, Salamandridae); Proteida (Proteidae); and Meantes (Sirenidae). His grouping became the accepted classification, and this consensus persisted into the middle 1960s. Three suprafamilial groups are now recognized, but differences of interpretation on the phylogenetic relationships among salamanders exist. A sampling of cladograms (Fig.16.1) shows the range of differences among investigators. Differences derive from the number of taxa and the particular ones used in producing the cladograms, the type and breadth of the data, and the manner of analysis used in each study. Although no taxa are invariably associated, cryptobranchids and hynobiids regularly appear as sister taxa near the base of the trees. Somewhat less commonly, sirenids are the sister group to all other salamanders. No other pairings occur in more than one-half of the cladograms, thus encouraging the various interpretations of relationships.

The phylogenetic hypothesis of Larson and Dimmick (1993) combines morphological and molecular data; this hypothesis (Fig. 16.1) recognizes salamanders with internal fertilization as monophyletic. This cladogram yields three suprafamilial groups: Meantes (Sirenidae); Cryptobranchoidea (Cryptobranchidae, Hynobiidae); and Salamandroidea (Ambystomatidae, Amphiumidae, Dicamptodontidae, Plethodontidae, Proteidae, Rhyacotritonidae, Salamandridae). Meantes is characterized by presumed external fertilization, a high number of microchromosomes, the absence of hindlimbs and a pelvic girdle, and a derived spinal nerve morphology; Cryptobranchoidea has external fertilization, a high number of microchromosomes, and a presumed primitive spinal nerve morphology; and Salamandroidea has internal fertilization, a reduction in chromosome number, and usually a derived spinal nerve morphology.

General References Cogger and Zweifel, 1992; Dowling and Duellman, 1974–1978; Duellman and Trueb, 1986; Halliday and Adler, 1986; Hairston, 1996; Petranka, 1998.

Systematic References Edwards, 1976; Hay et al., 1995; Hillis, 1991; Larson, 1991; Larson and Dimmick, 1993.

TAXONOMIC ACCOUNTS

Cryptobranchoidea

Cryptobranchidae

Asiatic giant salamanders and hellbenders

Classification Amphibia; Caudata; Cryptobranchoidea.

Sister taxon Hynobiidae.

Content Two genera, *Andrias* and *Cryptobranchus,* with two and one species, respectively.

Distribution East-central China, Japan, and the Appalachian and Ozark Mountains, USA (Fig. 16.2).

Characteristics These giants are the largest living salamanders. The Japanese *Andrias japonicus* reaches 1.4 m TL (total length), the Chinese *Andrias davidianus* 1.5 m TL, and the American *Cryptobranchus alleganiensis* (Fig. 16.3) 750 mm TL. All three are stout-bodied salamanders with four short, well-developed limbs and a heavy, laterally compressed tail. Cryptobranchids have a few paedomorphic traits, including a single pair of gill slits, open in *C. alleganiensis* and closed in *Andrias,* and the absence of eyelids. The lower jaw has separate angular and prearticular bones; the upper jaw has both premaxillae and maxillae, and the lacrimal is absent. Excluding the first spinal nerve, all pre- and postsacral spinal nerves exit intervertebrally. Costal grooves are lacking in the skin above the ribs, and nasolabial grooves are absent. Lungs are present, although vestigial and largely nonfunctional. Fertilization is external, and adult females lack spermathecae in the cloaca; both females and males have only ventral cloacal glands.

Biology Cryptobranchids have extensively folded and wrinkled skin over a depressed body. The skin serves as a nearly exclusive respiratory surface because gills are absent and the small lungs are largely nonfunctional. All

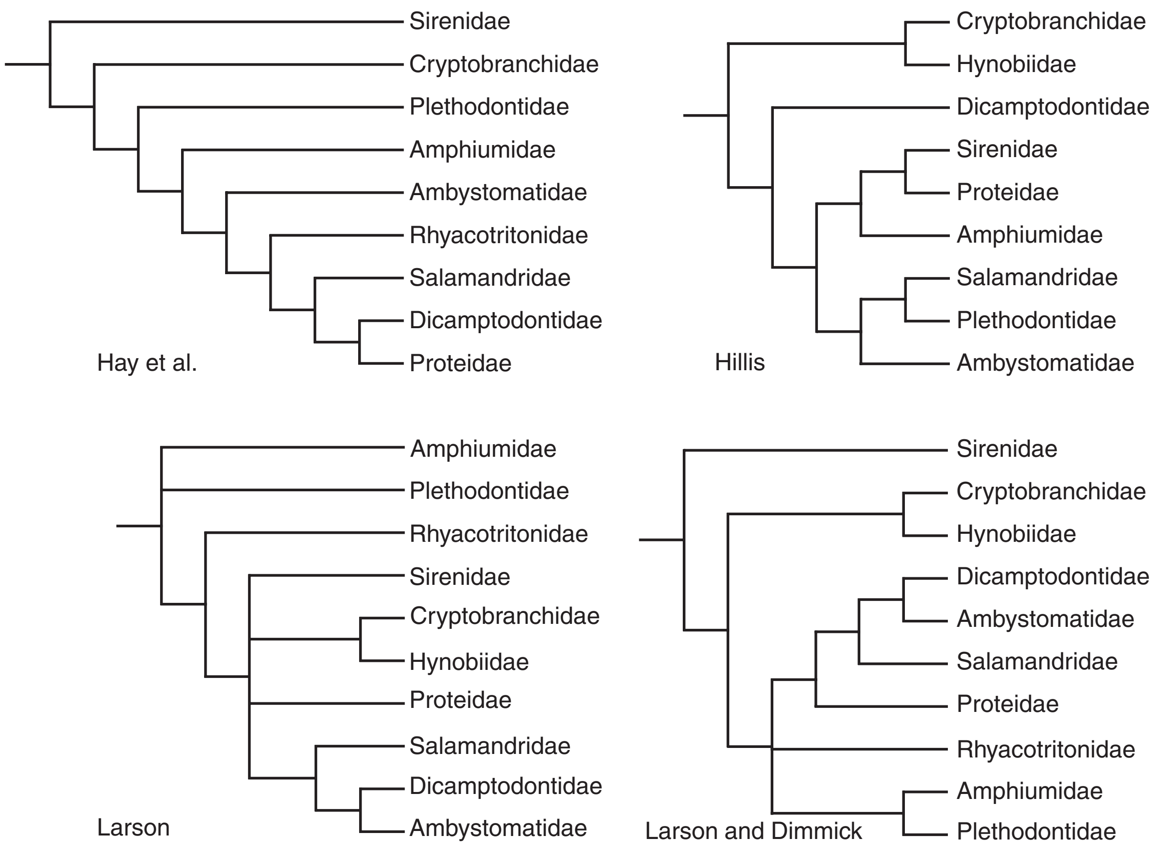


FIGURE 16.1 Cladograms depicting relationships among the families of extant salamanders. Clockwise from upper left: cladogram based on DNA sequence data from mitochondrial and ribosomal RNA sequence data (Hay et al., 1995, Fig. 1, in part); cladogram based on a reanalysis of morphological data of Duellman and Trueb (1986) (Hillis, 1991, Fig.7); cladogram based on combined morphological and ribosomal RNA data (Larson and Dimmick, 1993, Fig. 3); and cladogram based on ribosomal RNA sequence data (Larson, 1991, Fig. 3A). All cladograms redrawn from originals for uniformity.

three species are confined to clear, cold mountain streams. Largely nocturnal, these salamanders hide beneath rocks and sunken logs during the day, sometimes emerging on heavily overcast days to forage or to search for mates during the breeding season. Movement is typically by walking on the stream bottom, but undulatory locomotion is used for short-distance escapes to hiding places. These carnivores feed on a wide

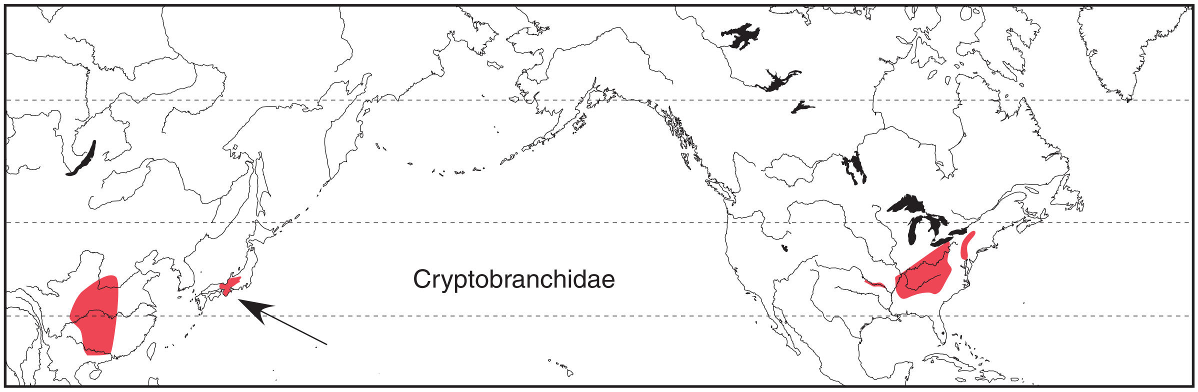


FIGURE 16.2 Geographic distribution of the extant Cryptobranchidae.

variety of invertebrate and vertebrate prey; crayfish are preferred by *C. alleganiensis*. In general, cryptobranchoids lack the stereotypic courtship displays of the salamandroids (see Chapter 9). During the breeding season, *C. alleganiensis* males excavate brooding sites beneath logs and wait for females to appear. When a female approaches, the male guides her into his nest chamber, where she remains until she has oviposited. The eggs, approximately 250 to 400, are laid in two gelatinous strings (one from each oviduct), and the male sheds seminal fluid containing sperm over them. A male may sequentially attract two or more females to his nest chamber, after which he guards the multiple egg clutches. During the entire year, whether breeding or not, adult males and females appear to defend specific rocks, logs, or other sites and drive away other individuals.

References Nickerson and May, 1973; Sever, 1991b.

Hynobiidae

Asiatic giant salamanders

Classification Amphibia; Caudata; Cryptobranchoidea

Sister taxon Cryptobranchidae.

Content Seven genera, *Batrachuperus*, *Hynobius* (Fig. 6.3), *Liua*, *Onychodactylus*, *Pachyhynobius*, *Ranodon*, and *Salamandrella*, with 35+ species.

Distribution Asia, from the Urals to Japan, mainly above 40°N latitude (Fig. 16.4). Hynobiid genera segregate into a temperate group (e.g., *Batrachuperus*, *Liua*) predominantly north of and along the Himalayan axis and a cold–temperate and subarctic group (*Ranodon*, *Salamandrella*).

FIGURE 16.3 Representative salamanders. Clockwise from upper left: hellbender *Cryptobranchus alleganiensis*, Cryptobranchidae (photograph by R. W. Van Devender); Gensan salamander *Hynobius leechi*, Hynobiidae (L. L. Grismer); spotted mole salamander *Ambystoma maculatum*, Ambystomatidae (J. P. Caldwell); and three-toed amphiuma *Amphiuma tridactylum*, Amphiumidae (R. W. Van Devender).

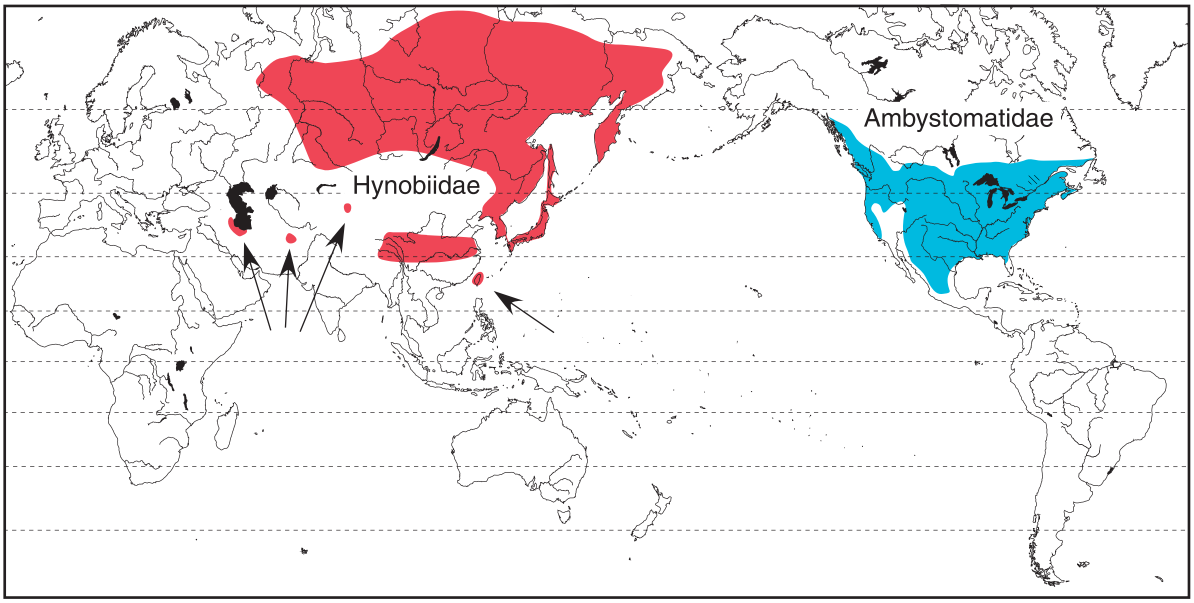


FIGURE 16.4 Geographic distributions of the extant Ambystomatidae and Hynobiidae.

Characteristics Hynobiids are heavy-bodied, thick-tailed salamanders with four short, well-developed limbs. Most hynobiids are small (<100 mm TL), although one species, *Ranodon sibiricus*, may reach 250 mm (TL). The lower jaw has separate angular and prearticular bones; the upper jaw has both premaxillae and maxillae, and the lacrimal is present. Excluding the first spinal nerve, all presacral and postsacral spinal nerves exit intervertebrally. Adults lack gills, gill slits, and nasolabial grooves; they have movable eyelids. Costal grooves are present on the trunk. Lungs are usually well developed, although absent in *Onychodactylus*. Fertilization is external. Females lack spermathecae in the cloaca, and both females and adult males possess only ventral cloacal glands.

Biology Hynobiids display little evidence of courtship. Most species are terrestrial except during the breeding season, when they migrate to breeding ponds or streams. Chemical communication may bring males and females together. The appearance of eggs extruding from females' vents also appears to be a visual signal that stimulates male *Hynobius*. One exception to this pattern is *R. sibiricus*. In this species, males produce a rudimentary spermatophore, and the female lays eggs on the spermatophore instead of taking its sperm packet into her cloaca. In other hynobiids, females deposit eggs in a pair of gelatinous masses, one from each oviduct, and males then shed their sperm directly on these egg masses. Development in all species is indirect with a free-living larval stage. Paedogenesis occurs in *Batrachuperus* and *Hynobius lichenatus*. Overall, the biology of the hynobiids remains poorly studied, with the exception of *Salamandrella*.

References Adler and Zhao, 1990; Kuzmin, 1995; Tanaka, 1989; Vorobyeva, 1994, 1995; Zhao et al., 1988.

Salamandroidea

Ambystomatidae

Mole salamanders

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly Dicamptodontidae.

Content One genus, *Ambystoma,* with 30+ species.

Distribution North America to the southern rim of the Mexican Plateau (Fig. 16.4).

Characteristics Ambystomatids are heavy-bodied, heavy-tailed salamanders with four short, well-developed limbs. Adult size ranges from 80 to 250 mm, usually <160 mm TL. The lower jaw has fused angular and prearticular bones; the upper jaw has both premaxillae and maxillae, and the lacrimal is absent. All presacral spinal nerves, except the second, third, and fourth, and the postsacral spinal nerves exit intravertebrally through foramina in the vertebrae. Most adult ambystomatids lack gills and gill slits and have movable eyelids, but the paedomorphic axolotl (*Ambystoma mexicanum*) and its relatives retain some larval traits. Within some species, for example, *Ambystoma talpoideum*, some individuals retain larval traits such as gills, gill slits, and no eyelids. All ambystomatids have costal grooves on the skin above the ribs, well-developed and functional lungs, and no nasolabial grooves on the snout. Fertilization is internal, and adult females have spermathecae in the cloaca. Adult males possess six sets of cloacal glands.

Biology Most species are terrestrial during adulthood and return to water only for reproduction. Some species and/or populations have paedomorphic or paedotypic traits (see Chapter 2), for example, the *Ambystoma tigrinum* complex (six species), *A. gracile*, and *A. talpoideum*. The *A. tigrinum* complex includes the axolotl (*A. mexicanum*). The ambystomatids occurring in the United States are predominantly winter breeders, migrating to ponds during brief midwinter warm rains, generally when air temperatures are greater than 10°C. The first wave of migrants is males, which await the females on subsequent nights. Courtship occurs in water; the males "dance" and nudge the females (Fig. 9.1), and then deposit numerous spermatophores. Each female picks up one or more sperm packets from the spermatophores and, during the next several days, deposits eggs. The adults leave the ponds and return to their subterranean homes until the following year. *Ambystoma opacum* deviates from this reproductive pattern by reproducing in late autumn. Courtship occurs on land, and eggs are deposited in depressions on the forest floor. When the nests are flooded by midwinter–early spring rains or snow melt water, the larvae hatch and subsequently live an aquatic existence. For most species, larval life lasts 3 to 4 months.

References Jones et al., 1993; Pfingsten and Downs, 1989; Reilly and Brandon, 1994; Sever, 1991a; Shaffer, 1993; Shaffer et al., 1991; Shaffer and McKnight, 1996.

Amphiumidae

Amphiumas

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly Plethodontidae.

Content One genus, *Amphiuma*, with three species.

Distribution Southeastern United States, including the southern half of the Mississippi River valley and along the coastal plain to Virginia (Fig. 16.5).

Characteristics *Amphiuma* are heavy-bodied, eel-like salamanders with four tiny, weakly developed limbs. Adults can be large, depending on species, occasionally exceeding 1 m TL. The lower jaw has angular and prearticular bones fused; the upper jaw has both premaxillae and maxillae, but the lacrimal is absent. Excluding the first spinal nerve, all presacral and all except the distalmost postsacral spinal nerves exit intervertebrally. Amphiumids display some paedomorphic traits; adults have internal gills and a single pair of gill slits, and eyelids and a tongue are absent. They have costal grooves in the

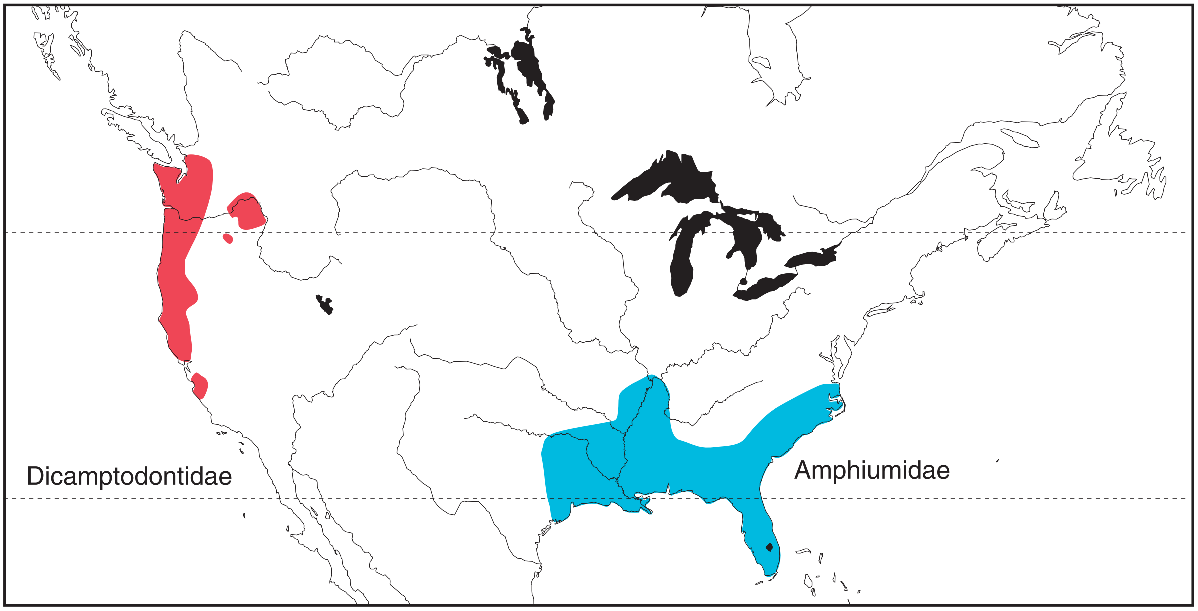


FIGURE 16.5 Geographic distributions of the extant Dicamptodontidae and Amphiumidae.

skin above the ribs and lack nasolabial grooves on the snout. Lungs are present. Fertilization is internal, and adult females have spermathecae in the cloaca. Adult males possess five sets of cloacal glands, of which the posteriormost set has a unique morphology and histology.

Biology Amphiumas lose their external gills during a partial metamorphosis. The limbs are greatly reduced, but the number of toes allows identification of the three species: *Amphiuma tridactylum* (Fig. 16.3) has three toes on each foot, *Amphiuma means* two toes, and *Amphiuma pholeter* one toe. The former two species are large salamanders with adult length exceeding 1 m TL, whereas the latter species is considerably smaller, <300 mm TL. All species are aquatic, although *A. means* has been found active on land during rainy nights. Field observations indicate that males court several females simultaneously or that multiple females contend for the attention of a single male. Since females in other salamandroid genera are passive or even rebuff the male's efforts, these observations require confirmation. Gender is not easily determined and the observations may have consisted of several males vying for a single female. Courtship ends with the male depositing a spermatophore directly into the female's cloaca by means of cloacal apposition. In all species, females stay with and coil around their eggs, usually beneath logs, rocks, and other detritus at the water's edge. For at least *A. tridactylum*, females reproduce every 2 years and produce about 200 eggs each time.

References Fontenot, 1999; Means, 1996; Salthe, 1973a,b.

Dicamptodontidae

Pacific mole salamanders

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly Ambystomatidae.

Content One genus, *Dicamptodon*, with four species.

Distribution Pacific Northwest of North America (Fig. 16.5).

Characteristics *Dicamptodon* are heavy-bodied, heavy-tailed salamanders with four short, well-developed limbs. Adult size ranges from 130 to 350 mm TL. The lower jaw has angular and prearticular bones fused; the upper jaw has both premaxillae and maxillae, and the lacrimal is present. All presacral spinal nerves, except the first, exit intervertebrally, and all postsacral ones exit intravertebrally through foramina in the caudal vertebrae. Adults lack gills and gill slits, except for the permanently aquatic *Dicamptodon copei*, and have movable eyelids. Costal grooves are present on the trunk, but nasolabial grooves are lacking. Small lungs are present. Fertilization is internal, and adult females have spermathecae in the cloaca. Adult males possess six sets of cloacal glands.

Biology All four species (*D. aterrimus* [Fig. 16.6], *D. copei*, *D. ensatus*, and *D. tenebrosus*) live in moist coastal forests. Metamorphosis occurs in all but *D. copei*, which is paedomorphic and permanently aquatic; however, occasional populations of the other species display paedogenesis. Postmetamorphic individuals of the other three species are predominantly terrestrial. Reproduction occurs in forest streams and the terrestrial adults of the metamorphosed populations return to the streams for all reproductive activity. Females typically deposit 50 or more eggs, depending upon body size, in water-filled chambers beneath logs and rocks within or beside streams. Females defend their eggs until they hatch, with incubation often as long as 6 months. *Dicamptodon* larvae forage mainly at night on the bottom of small forest streams, and in many streams; they are the major predator, in abundance and biomass, of invertebrates.

References Good, 1989; Nussbaum 1976; Nussbaum et al., 1983; Parker, 1994.

Plethodontidae

Lungless salamanders

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly Amphiumidae or Rhyacotritonidae (D. Wake, 1993).

Content Two subfamilies, Desmognathinae and Plethodontinae.

Distribution Americas, occurring from southern Canada to southwestern Brazil, and disjunctly, central Mediterranean Europe (Fig.16.7).

Characteristics Plethodontids display a diversity of body shapes, but all have four limbs. Some taxa are stocky and short-limbed, and others are elongate and slender-limbed. Some have tails equal to body length, and in others, the tails are twice the length of the body. Adult body size ranges from 25 to 30 mm TL in the diminutive *Thorius* to 320 mm TL in *Pseudoeurycea belli* (both Mexican bolitoglossines). The lower jaw has the angular and prearticular bones fused; the upper jaw has both premaxillae and maxillae, and the lacrimal is absent. All presacral, except the second, third, and fourth, and

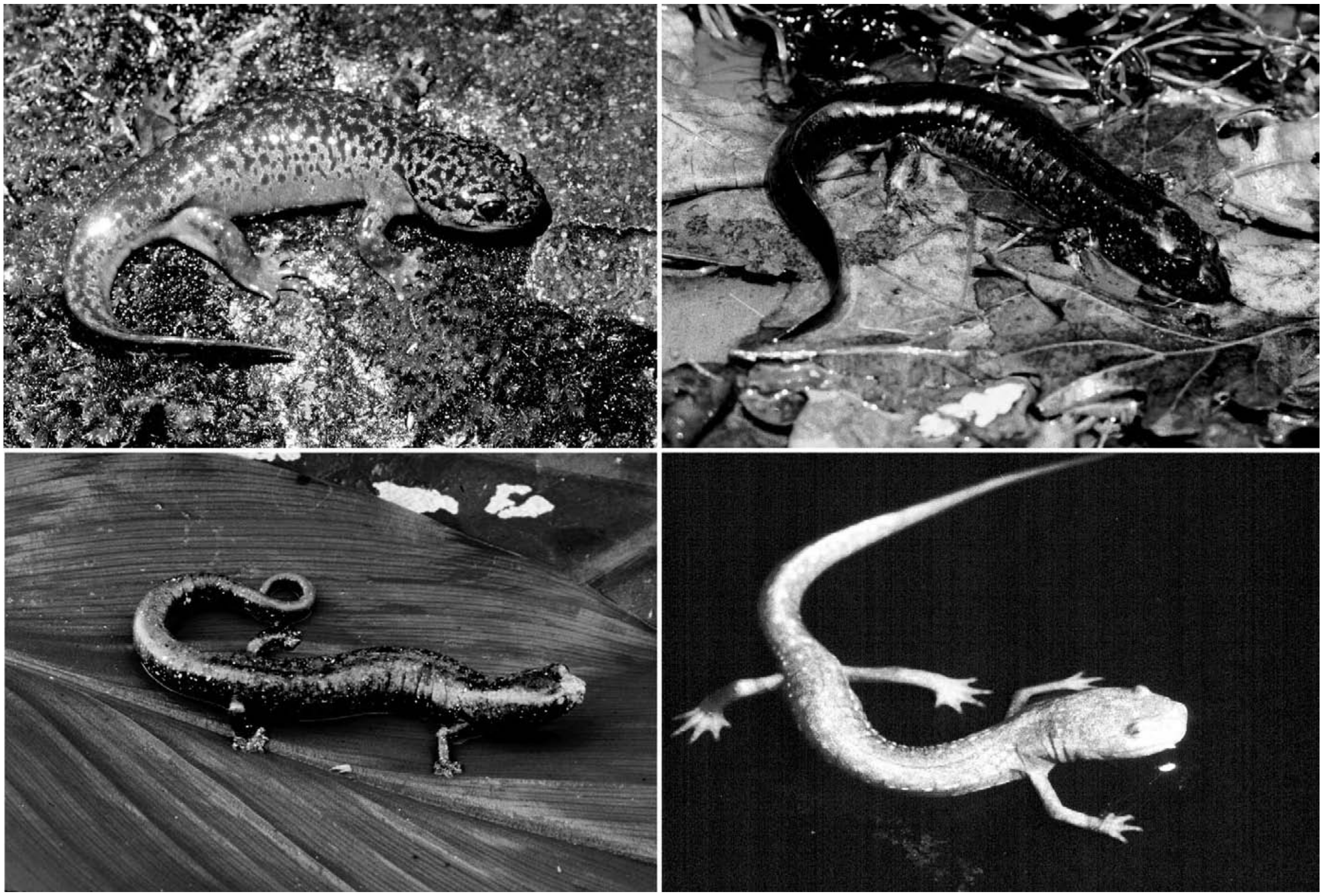


FIGURE 16.6 Representative salamanders. Clockwise from upper left: Idaho giant salamander *Dicamptodon aterrimus*, Dicamptodontidae (photograph by W. Leonard); blackbelly salamander *Desmognathus quadramaculatus*, Desmognathinae (L. J. Vitt); grotto salamander *Typhlotriton spelaeus*, Plethodontinae (R. W. Barbour); and tropical salamander *Bolitoglossa* sp., Plethodontinae (J. P. Caldwell).

postsacral spinal nerves exit intravertebrally through foramina in the vertebrae. Adults lack gills and gill slits, and have movable eyelids except in the paedomorphic taxa, for example, *Haideotriton*. Costal grooves are present on the trunk, and all species possess a pair of nasolabial grooves on the snout. Lungs are absent. Fertilization is internal; adult females have spermathecae in the cloaca, and adult males possess six sets of cloacal glands.

Desmognathinae

Sister taxon Plethodontinae.

Content Two genera, *Desmognathus* and *Phaeognathus*, with 16+ and one species, respectively.

Distribution Eastern half of North America.

Characteristics Desmognathines have a unique jaw-opening mechanism in which the lower jaw is held stationary and the skull swings upward. The cranial and cervical skeleton and musculature have unique features associated with this behavior, including stalked occipital condyles and atlantomandibular ligaments. Embryos and larvae have four pairs of gill slits.

Biology These salamanders are predominantly aquatic, although some species live streamside and forage along the stream or nearby. Other species (e.g., *Desmognathus apalachicolae*, *Desmognathus carolinensis*) are more terrestrial, but surface activity and habitat selection are driven by the requirement for high humidity. The large *Phaeognathus hubrichti* and the smallest desmognathine, *D. wrighti*, are strictly terrestrial. The former lives in burrows and feeds at the burrow mouth, and *D. wrighti* lives under the forest-floor litter. While other taxa lay their eggs in wet situations from spring seepages to beneath rocks and leaf mats in streams, these two species lay their eggs terrestrially, and in both, there is no aquatic larval stage. *Desmognathus aeneus*, another diminutive species, deposits eggs in seepages, and although larvae hatch, they do not feed and quickly metamorphose. Most, if not all, desmognathines show parental care in which females attend their eggs until they hatch.

References Petranka, 1998; Tilley and Bernardo, 1993; Titus and Larson, 1997.

Plethodontinae

Sister taxon Desmognathinae.

Content Three tribes, Hemidactyliini, Bolitoglossini, and Plethodontini, composed of 25 genera: *Aneides*, *Batrachoseps*, *Bolitoglossa*, *Bradytriton*, *Chiropterotriton*, *Dendrotriton*, *Ensatina*, *Eurycea*, *Gyrinophilus*, *Haideotriton*, *Hemidactylium*, *Hydromantes*, *Ixalotriton*, *Lineatriton*, *Nototriton*, *Nyctanolis*, *Oedipina*, *Parvimolge*, *Plethodon*, *Pseudoeurycea*, *Pseudotriton*, *Stereochilus*, *Thorius*, *Typhlomolge*, and *Typhlotriton*, with 250+ species.

Distribution Hemidactyliins (e.g., *Eurycea*, *Gyrinophilus*, *Hemidactylium*, *Pseudotriton*, *Typhlotriton*) occur predominantly in eastern North America with a south-central extension into the Ozarks and the Edwards Plateau; bolitoglossins occur throughout much of tropical America from central Mexico to Brazil (e.g., *Bolitoglossa*, *Oedipina*, *Pseudoeurycea*), western North America (*Batrachoseps*, *Hydromantes*), and central Mediterranean Europe (*Hydromantes*); and plethodontins (*Aneides*, *Ensatina*, *Plethodon*) occur in eastern and western North America.

Characteristics Plethodontines have the typical vertebrate jaw mechanism in which the skull remains rigid and the lower jaw swings downward; the occipital condyles are short and atlantomandibular ligaments are absent. Embryos and larvae have three pairs of gill slits.

Biology The hemidactyliins have indirect development with aquatic, free-living larvae and aquatic to terrestrial adults. The other two tribes, bolitoglossins and plethodontins, have direct development with terrestrial eggs that hatch into a miniature salamander. Paedomorphosis occurs only in the hemidactyliin salamanders, for example, species of *Eurycea* of Edwards Plateau in Texas, *Gyrinophilus palleucus*, *Haideotriton*, and *Typhlomolge*. All these paedomorphs are subterranean aquatic or spring residents. In addition to incomplete metamorphosis and the retention of gills, most paedomorphs are slender-bodied and slender-limbed, and have degenerate eyes and reduced skin pigmentation. The terrestrial bolitoglossins and plethodontins occupy a variety of habitats from forest-floor leaf litter and burrows to rock screes and cliffs; some species are arboreal, occurring high in trees.

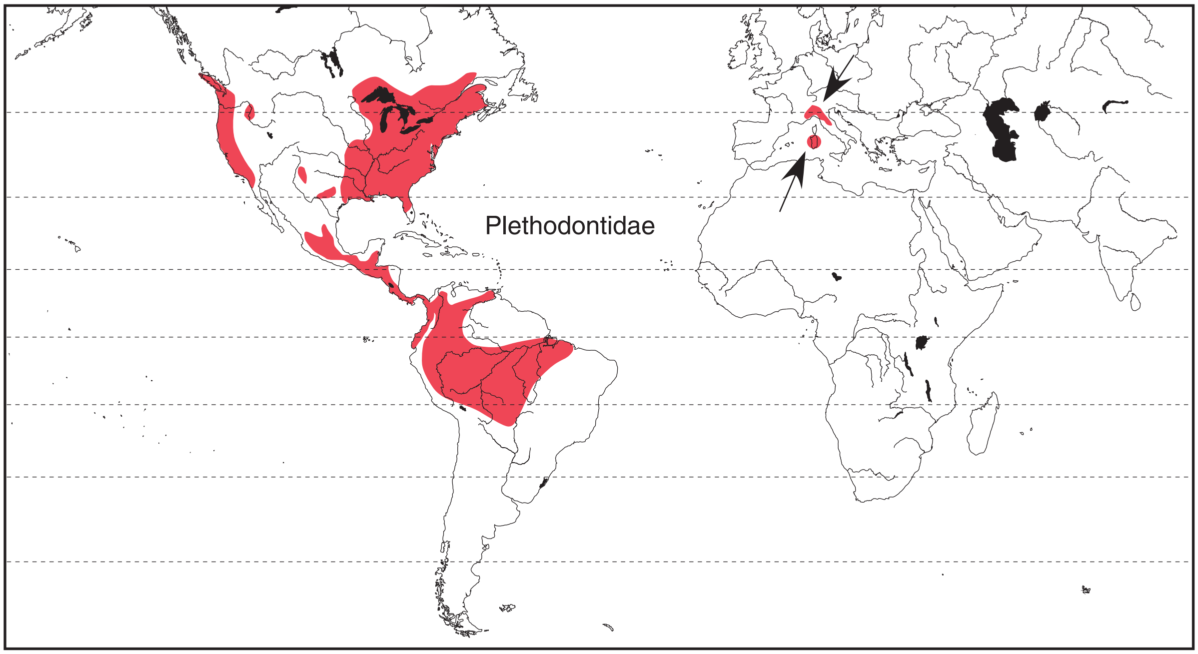


FIGURE 16.7 Geographic distribution of the extant Plethodontidae.

References Houck and Verrell, 1993; Jackman et al., 1997a; Jaeger and Forester, 1993; Lanza et al., 1995; Petranka, 1998.

Proteidae

Olm, mudpuppies, and waterdogs

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly the clade containing the Salamandridae, Ambystomatidae, and Dicamptodontidae.

Content Two genera, *Necturus* and *Proteus*, with five and one species, respectively.

Distribution Eastern half of North America and eastern Adriatic coast of Europe (Fig. 16.8).

Characteristics Proteids are moderately robust salamanders with four short, well-developed limbs and large, laterally compressed tails. Adults of three species of *Necturus* and the more slender *Proteus* are 200 to 250 mm TL. *Necturus punctatus* is <200 mm TL, and *Necturus maculosus* is the largest taxon, 250 to 350 mm TL, and occasionally up to 480 mm TL. The lower jaw of proteids has the angular and prearticular bones fused; the upper jaw has only premaxillae, and the lacrimal is absent. All pre- and postsacral spinal nerves, except the first one, exit intervertebrally. All proteids are paedomorphic; adults have external gills, two pairs of gill slits, and no eyelids. Costal grooves are present on the trunk, and nasolabial grooves are absent. Lungs are present, although small. Fertilization is internal; adult females have spermathecae, and adult males possess six sets of cloacal glands.

Biology Both genera are totally aquatic, but the North American *Necturus* dwells in surface waters, whereas the European *Proteus anguinus* is a cave species. Superficially, *P. anguinus* appears more similar to the paedomorphic hemidactyliins than to the *Necturus* species, because it has a slender body and limbs, reduced eyes beneath the skin, and a pigmentless skin. All species of *Necturus* prefer clear water and rocky, silt-free substrates. They are nocturnal foragers and eat a variety of prey with a preference for crayfish. *N. maculosus* courts in the autumn, but egg-laying does not occur until the subsequent spring. Up to 50 eggs are attached to the roof of the female's shelter, and whether or not they receive active care, they are protected by her presence. *P. anguinus* commonly deposits up to 70 eggs in a season, but apparently warmer water temperatures may induce retention of eggs, resulting in the birth of two fully formed larvae.

References Ashton, 1990; Engelmann et al., 1986; Pfingsten and Downs, 1989.

Rhyacotritonidae

Torrent salamanders

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, but among the salamandroids.

Content One genus, *Rhyacotriton*, with four species.

Distribution Pacific Northwest of the United States (Fig. 16.8).

Characteristics Rhyacotritonids are heavy-bodied, heavy-tailed salamanders with four short, well-developed limbs. Adult size ranges from 90 to 120 mm TL. The lower jaw has angular and prearticular bones fused; the upper jaw has both premaxillae and maxillae, and the lacrimal is present. All except the first presacral spinal

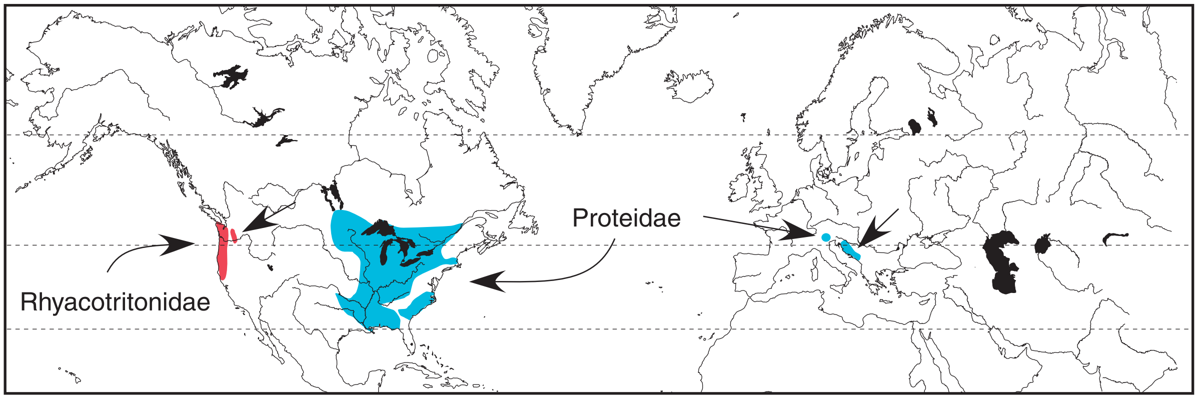


FIGURE 16.8 Geographic distributions of the extant Rhyacotritonidae and Proteidae.

nerve exit intervertebrally, and all postsacral nerves exit intravertebrally. Adults lack gills and gill slits. Eyelids are present and functional. Costal grooves are present on the skin above the ribs, and nasolabial grooves are absent. Small lungs are present. Fertilization is internal; adult females have spermathecae, and adult males possess six sets of cloacal glands and unique enlarged, rectangular vent glands.

Biology These salamanders are semiaquatic residents of humid conifer forest. The larvae and transformed individuals (Fig. 16.9) live in shallow areas of rocky rubble in cold, well-aerated forest streams and spring seepages; occasionally they wander into deeper pools or adults forage on the forest floor during heavy rains. Courtship is presumed to occur on land or in the splash zone of streams. Fertilization is internal via spermatophores. Females deposit 3 to 15 eggs, each attached singly to the underside of rocks. The eggs hatch in 7 to 10 months, and larval development requires 3 to 5 years owing to the cold temperature of the aquatic nesting sites.

References Good and Wake, 1992; Leonard et al., 1993; Nussbaum, 1976; Nussbaum et al., 1983; Sever, 1992; Welsch and Lind, 1996.

Salamandridae

Newts and European salamanders

Classification Amphibia; Caudata; Salamandroidea.

Sister taxon Uncertain, possibly the clade containing Ambystomatidae and Dicamptodontidae.

Content Fifteen genera, *Chioglossa*, *Cynops*, *Echinotriton*, *Euproctus*, *Mertensiella*, *Neurergus*, *Notophthalmus*, *Pachytriton*, *Paramesotriton*, *Pleurodeles*,

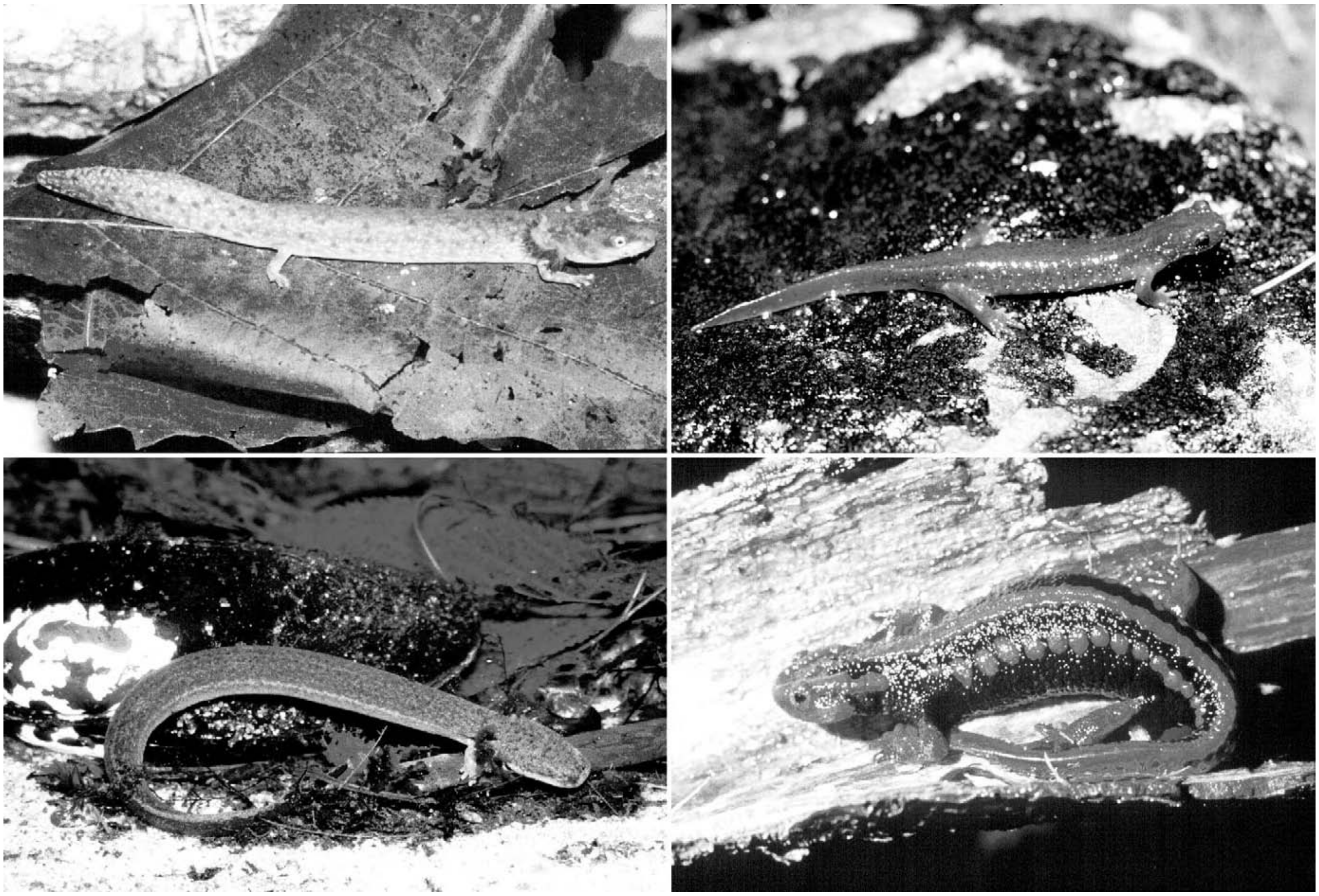


FIGURE 16.9 Representative salamanders. Clockwise from upper left: dwarf waterdog *Necturus punctatus*, Proteidae (photograph by R. W. Van Devender); cascade torrent salamander *Rhyacotriton cascadae*, Rhyacotritonidae (W. Leonard); Himalayan newt *Tylotriton verrucosus*, Salamandridae (K. Nemuras); and lesser siren *Siren intermedia*, Sirenidae (R. W. Van Devender).

Salamandra, *Salamandrina*, *Taricha*, *Triturus*, and *Tylototriton*, with ±55 species.

Distribution Europe eastward to central Russia and southward into northeastern Africa, southeastern China and Japan, and eastern and western North America (Fig. 16.10); different generic groups occur in each region (e.g., *Notophthalmus* and *Taricha* in North America; *Pleurodeles*, *Salamandra*, and *Triturus* in Europe; *Cynops* and *Tylototriton* in Asia).

Characteristics Body morphology of salamandrids ranges from moderately slender to robust; the four limbs are well developed and moderately short. Most adult salamandrids seldom exceed 200 mm TL and even the larger taxa (e.g., European *Pleurodeles* and *Salamandra*) are less than 350 mm TL. The lower jaw has fused angular and prearticular bones; the upper jaw has both premaxillae and maxillae, and the lacrimal is absent. All presacral, except the second and third, and postsacral spinal nerves exit intravertebrally through foramina in the vertebrae. Adults lack gills and gill slits, except in the paedotypic populations of *Notophthalmus* and *Triturus*, and all have movable eyelids. Costal grooves above the ribs and nasolabial grooves are absent. Lungs are present and functional. Fertilization is internal; adult females have spermathecae in the cloaca, and adult males possess five sets of cloacal glands.

Biology Salamandrids typically have a granular or rugose skin because of numerous poison glands, and the secretions of these glands are the most toxic of all salamanders. In association with their high toxicity, many salamandrids are brightly colored, at least ventrally, and advertise their toxicity to potential predators. The bright coloration may be seasonal in appearance. Two salamandrids, *Salamandra atra* and *Mertensiella luschani*, are live-bearers (see Chapter 4, "Reproductive Modes"); a few other species deposit terrestrial eggs, but the majority deposit eggs in the water and have a free-living larval stage. All have courtship displays in which the male circles the female and nudges or rubs her, and in a few species, the male grasps the female and deposits his spermatophore in or near her cloaca. Three life cycles are evident among the taxa with aquatic larvae. In some species, for example, *Cynops* and *Pleurodeles*, the larvae metamorphose into aquatic juveniles and all individuals remain aquatic throughout adult life. Others (*Taricha*, *Triturus*) have aquatic larvae; upon metamorphosis, the salamanders become terrestrial and return to water only to breed. *Notophthalmus* has a triphasic life cycle: aquatic larvae, terrestrial juveniles called efts, and aquatic adults. Paedogenesis occurs in some populations of a few species, including *Notophthalmus viridescens*, *Triturus alpestris*, *Triturus cristatus*, and *Triturus helveticus*.

References Griffiths, 1996; Hayashi and Matsui, 1989; Titus and Larson, 1995; Twitty, 1966; Wake and Özeti, 1969.

Meantes

Sirenidae

Sirens and dwarf sirens

Classification Amphibia; Caudata; Meantes.

Sister taxa Uncertain, likely to the clade containing all other living salamanders.

Content Two genera, *Pseudobranchus* and *Siren*, each with two species.

Distribution Coastal southeastern North America and the Mississippi River valley (Fig. 16.11).

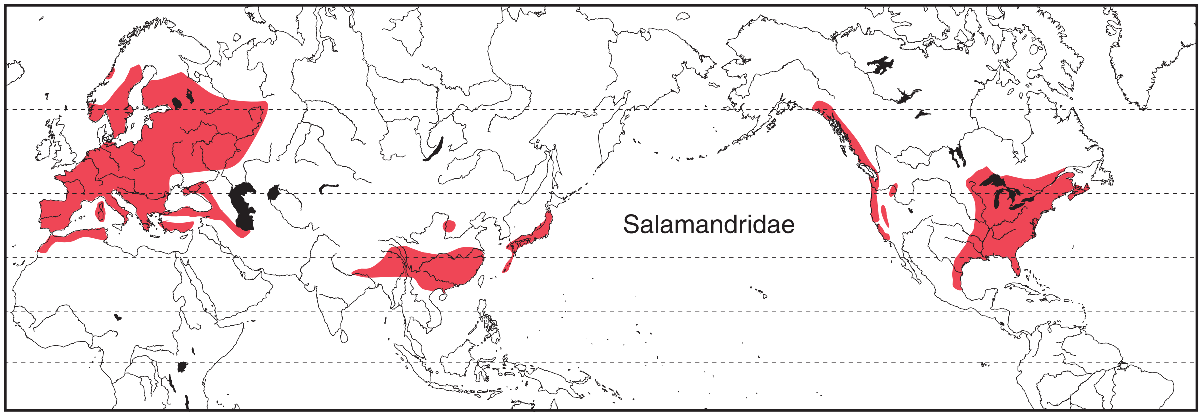


FIGURE 16.10 Geographic distribution of the extant Salamandridae.

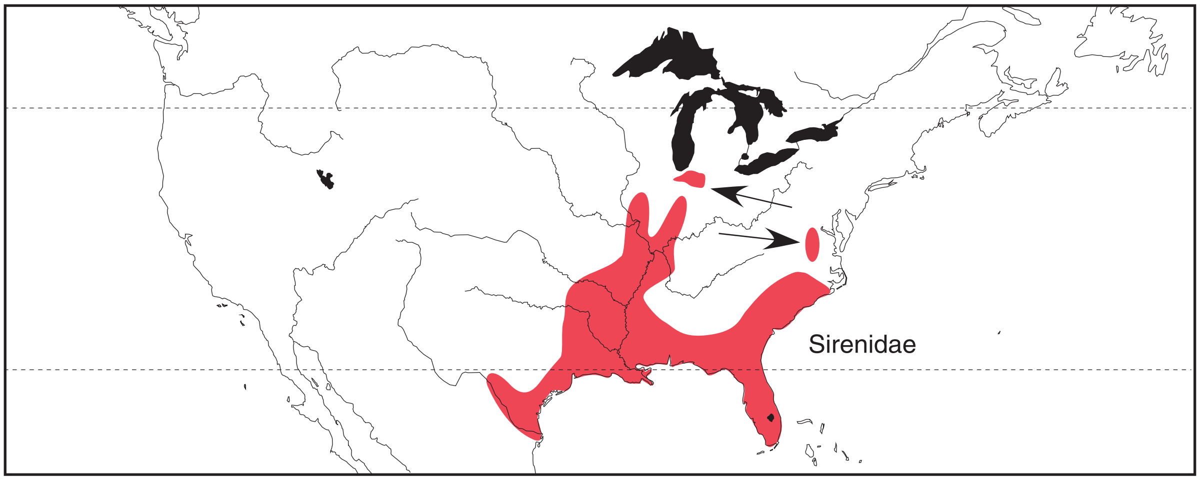


FIGURE 16.11 Geographic distribution of the extant Sirenidae.

Characteristics Sirenids are moderately slender, eel-like salamanders with small forelimbs (Fig. 16.9); the hindlimbs and pelvic girdle are absent. Adult size ranges from 100 to 900 mm TL. The lower jaw has fused angular and prearticular bones; the upper jaw has premaxillae and small, floating maxillae, and the lacrimal is absent. All presacral, except the second and third, and postsacral spinal nerves exit intravertebrally through foramina in the vertebrae. All sirenids are paedomorphic; adults have external gills and one or three pairs of gill slits. They have no eyelids. Costal grooves are present on the skin above the ribs, and nasolabial grooves are absent. Lungs are present, although small. The site of fertilization is unknown and is presumed to be external. Adult females lack spermathecae, and adult males lack reproductive glands in the cloaca. Sirenids are unlike any other salamanders in many aspects. For example, a horny beak replaces premaxillary teeth, and an interventricular septum is present in the heart.

Biology Sirenids typically live in heavily vegetated, slow-moving aquatic habitats, such as lakes, marshes, and swamps. They are active predators, preying on a variety of aquatic invertebrates, which they capture by suction feeding. The larger sirens readily capture crayfish; the dwarf sirens eat principally insect larvae and other small crustaceans and worms. In spite of their locally high abundance and widespread distribution, their biology is poorly known. Courtship behavior has not been observed; the oviductal morphology of *Siren* suggests external fertilization. Eggs are deposited singly or in small clusters attached to vegetation.

References Martof, 1972, 1974; Moler and Kezer, 1993; Sever et al., 1996b.

This Page Intentionally Left Blank

Chapter

17

Frogs

OVERVIEW

Frogs and toads occur worldwide on all continents, except Antarctica, and on most continental islands. They are a diverse group with more than 4200 species (Glaw and Köhler, 1998). Frogs and toads live in most aquatic and terrestrial habitats from lowlands to mountaintops, although their inability to physiologically handle salt water has largely excluded them from estuarine and marine habitats. Their highest diversity is in moist tropical sites; for example, 67+ species of frogs live in the forests of the Manu National Park, southeastern Peru (Morales and McDiarmid, 1996), but even arid or cold–temperate localities commonly have several species of frogs.

Frogs and toads (Anura; Salientia, stem-based name) are unmistakable with their unique short, tailless bodies; broad, flat heads with big mouths; and long muscular hindlimbs. This body form is associated with, and likely evolved as, an adaptation for saltatory (jumping) locomotion. The long hindlimbs extend synchronously and provide the propulsive force to lift and propel the frog forward. The short body provides a compact mass to be hurled forward, and the shortened vertebral column, robust pectoral girdle, and forelimbs readily absorb the shock of landing. Frogs regularly leap 2 to 10 times their body length; a few species are capable of prodigious leaps of 30 to 40 times their body length. Of course, not all frogs move by leaping; instead, some use a typical vertebrate walking gait, and even frogs that normally leap walk when moving slowly or a short distance.

With few exceptions, frogs have external fertilization. Males typically grasp (amplex) females in such a manner that their cloacae are juxtaposed, ensuring fertilization of the eggs as they are deposited. Indirect development of free-living larvae is common, although direct development is widespread. Larval (indirect) development of anurans is strikingly different from that of salamanders and caecilians. The anuran larva or tadpole is structurally, physiologically, ecologically, and behaviorally different from the fully developed froglet or adult. The shift from tadpole to froglet requires a major reorganization of anatomy and physiology as the larva metamorphoses. This contrasting body form and lifestyle may partially explain the lack of paedomorphosis and paedogenesis in anurans.

Living anurans share a suite of unique features attesting to their monophyly (Duellman and Trueb, 1986). All have greatly shortened vertebral columns, consisting of nine or fewer vertebrae; most clades have eight. All presacral vertebrae, except the atlas (first vertebra), have transverse processes, and dorsal ribs are absent (in most clades) or reduced, unicapitate, and usually confined to the second through fourth vertebrae in some primitive clades. The presacral vertebrae are firmly articulated, allowing only moderate lateral and dorsoventral flexure; the postsacral vertebrae are fused into a rod-shaped urostyle lying within an elongated dorsopelvic pocket formed by the uniquely elongated and anteriorly oriented ilia. The epipodial elements of both fore- and hindlimbs are fused, at least at their ends, forming a robust radioulna and tibiofibula in each, respectively. The ankle is elongated and similarly consists of a pair of fused bones (fibulare or astragulus and tibiale or calcaneum) that form a sturdy strut. All frogs lack teeth on the dentary of the lower jaw, except for the hylid *Gastrotheca guentheri* (formerly *Amphignathodon*) and possess large subcutaneous lymph spaces beneath the skin. As noted above, the anuran larva is structurally unlike that of the other extant amphibians; for example, the jaws are toothless, and a keratinous jaw sheaths and labial teeth are usually present as functional substitutes.

Although our current classification of living frogs contains many uncertainties, it does reflect significant progress in the recognition and depiction of phylogenetic relationships. Boulenger's 1882 *Catalogue of Batrachia Salientia* included about 1800 species classified in two suborders: Aglossa, with 2 families, and Phaneroglossa, with 12 families divided into two series, Firmisternia and Arcifera. His classification, as all classifications of that era, was phenetic; nonetheless, some of his contemporaries and successors were broadly surveying anuran anatomy and recognizing character suites that still form the morphological core of present phylogenetic analyses.

Noble (1922) was first to attempt construction of an evolutionary classification of anurans. He examined a large spectrum of characters, drawing on the dentition and pectoral girdle characters of Cope and the vertebral characters of Nicholls, and added his thigh musculature characters to produce a dendrogram of relationships and a classification that was widely accepted into the 1960s. Problems with some of the characters and their interpretation were soon noted (see Griffiths [1963], Lynch [1973], and Ford and Cannatella [1993] for historical reviews), and new character complexes were discovered that offered new insights into phylogenetic relationships. Griffiths (1963) was the first of a new generation of systematists (e.g., Inger, 1967; Kluge and Farris, 1969; Lynch, 1973; Duellman and Trueb, 1986) to provide interpretations based on new analytical protocols, new characters, and character coding. Ford and Cannatella (1993) are the most recent contributors in this chain of investigations and fine-tuning of our knowledge on anuran phylogeny. Their classification is largely adopted here.

The phylogenetic hypothesis (Fig. 17.1, bottom) of Ford and Cannatella recognizes living frogs as a monophyletic group (= clade), but it argues against an early divergence of a primitive frog clade (archaeobatrachians) and the advanced frog clade (neobatrachians). Instead, their cladogram shows independent origins of so-called primitive clades and then a divergence of two highly specialized clades, Mesobatrachia and Neobatrachia. This divergence is an ancient one, likely occurring in the Early Cretaceous or Late Jurassic (see Chapter 3). The uniqueness of the neobatrachians has been recognized since the time of Noble's work, although the composition of the mesobatrachians has varied. DNA evidence supports the Neobatrachia as a clade (Hay et al., 1995; Fig. 17.1, top), but, in contrast, supports the monophyly of the archaeobatrachians and a somewhat different pattern of relationships among the mesobatrachians, although supporting the monophyly of pelobatoid and pipoid clades. The relationships within the Neobatrachia remain controversial. Two groups, the bufonoids (= hyloids; Dubois, 1986) and the ranoids, and their familial membership, are generally accepted (but see Ford and Cannatella's cladogram; Fig. 17.1). For example, the bufonoids includes Bufonidae, Centrolenidae, Hylidae, and Leptodactylidae, and the ranoids includes Hyperoliidae, Ranidae, and Rhacophoridae. When there is clear evidence that a taxonomic group is not monophyletic, the group name is enclosed in quotation marks to indicate that it is not a clade.

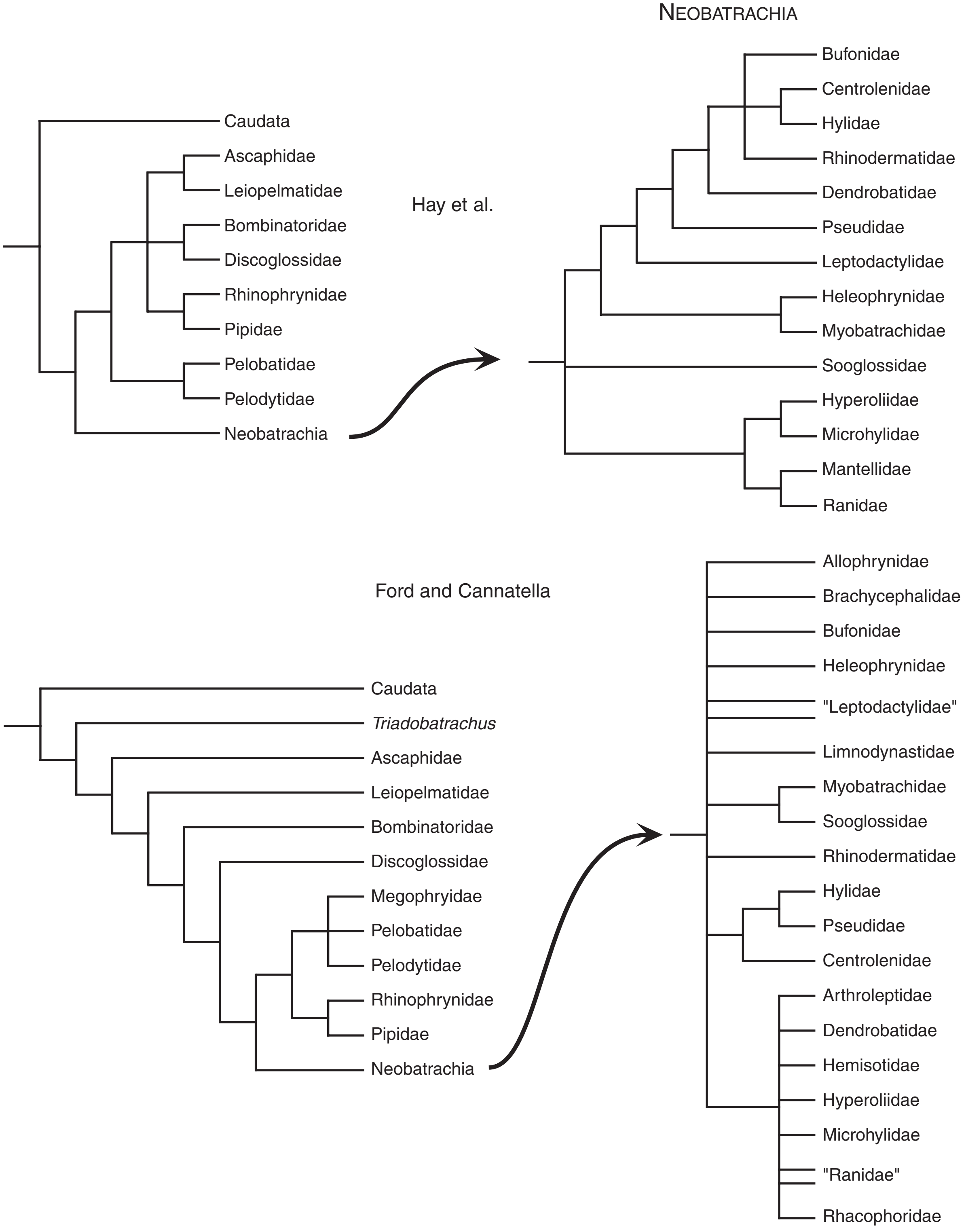


FIGURE 17.1 Cladograms depicting relationships among the families of extant frogs. (Top) Cladogram based on mitochondrial and ribosomal RNA sequence data (Hay et al., 1995, Fig. 1, in part). (Bottom) Cladogram based on morphological data set (Ford and Cannatella, 1993, Figs. 1 and 2). All cladograms redrawn from the originals for uniformity.

General References Cogger and Zweifel, 1998; Duellman and Trueb, 1986; Halliday and Adler, 1986; Laurent, 1986; Stebbins and Cohen, 1995; Vial, 1973.

Systematic References Dubois, 1984, 1986; Duellman, 1993; Ford and Cannatella, 1993; Frost, 1985; Griffiths, 1963; Hay et al., 1995; Lynch, 1973; Noble, 1922; Ruvinsky and Maxson, 1996.

TAXONOMIC ACCOUNTS

Early Frogs

Ascaphidae

Tailed frog

Classification Amphibia; Lissamphibia; Anura.

Sister taxon Clade containing all other living Anura.

Content One genus, *Ascaphus* (Fig. 17.2), with one species.

Distribution Disjunctly in northwestern North America (Fig. 17.3).

Characteristics The single species, *Ascaphus truei*, attains a body size of 35 to 50 mm SVL (snout–vent length). A unique modification of the cloaca and tail muscles produces an intromittent or copulatory organ in males (Fig. 17.2), one of two such structures for internal fertilization in anurans. The skull lacks palatines and has paired frontoparietals. The facial nerve exits through the facial foramen anterior to the auditory capsule; the trigeminal and facial nerve ganglia are separate. The vertebral column consists of nine presacral notochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are slightly expanded, and this vertebra has a cartilaginous connection to the urostyle. Adults have free dorsal ribs on the second through fourth, and occasionally the fifth, presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larva has keratinized mouth parts and two small, fused spiracular tubes with a single anteromedial spiracle.

Biology Tailed frogs are streamside residents of clear, cold, and unsilted mountain streams, living in forest from near sea level to over 2000-m elevations. They are largely nocturnal, active along streams at night or foraging in the forest on rainy evenings. During the day, they hide beneath stones and detritus at or near the stream's edge or in shallow areas within the stream. Courtship occurs in September and October; males are voiceless, and apparently visual cues are used by males and females to find one another. Amplexus is inguinal and copulation commonly occurs underwater. In addition to the rarity of internal fertilization among frogs, the female tailed frog stores sperm in her oviducts for nearly 9 months; fertilization occurs at the time of ovulation and egg deposition in July. Females deposit 40 to 80 unpigmented eggs in small strings attached to undersides of rocks in streams. In the cold water, the eggs take about 6 weeks to hatch into streamlined tadpoles with reduced tail fins and suctorial oral discs. The latter structure permits the tadpoles to simultaneously cling upside down to the undersurface of rocks and feed on the algal crust in rapidly flowing streams. The larval phase lasts 2 to 3 years; metamorphosis usually occurs in late summer.

References Brown, 1975, 1989; Diller and Wallace, 1999; Green and Campbell, 1984; Leonard et al., 1993; Metter, 1968.

Leiopelmatidae

New Zealand frogs

Classification Amphibia; Lissamphibia; Anura.

Sister taxon Clade containing all living taxa of Anura, exclusive of Ascaphidae.

Content One genus, *Leiopelma*, with four species, one presently undescribed.

Distribution North Island, and Stephens and Maud Islands of the Marlborough Sound of New Zealand (Fig. 17.3).

Characteristics Leiopelmatids are moderately small (30–49 mm adult SVL) and are unique among anurans in having ventral inscriptional ribs. The skull lacks palatines and has a pair of frontoparietals. The facial nerve exits through the facial foramen anterior to the auditory capsule; the trigeminal and facial nerve ganglia are separate. The vertebral column possesses nine presacral notochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are slightly expanded, and this vertebra has a cartilaginous connection with the urostyle. Adults have free ribs on the second through fourth, and occasionally the fifth, presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage

FIGURE 17.2 Representative early frogs. Clockwise from upper left: Tailed frog *Ascaphus truei*, Ascaphidae (photograph by W. Leonard); Hamilton's frog *Leiopelma hamiltoni*, Leiopelmatidae (P. Ryan); fire-bellied toad *Bombina bombina*, Bombinatoridae (R. G. Tuck, Jr.); and painted frog *Discoglossus pictus*, Discoglossidae (R. G. Tuck, Jr.).

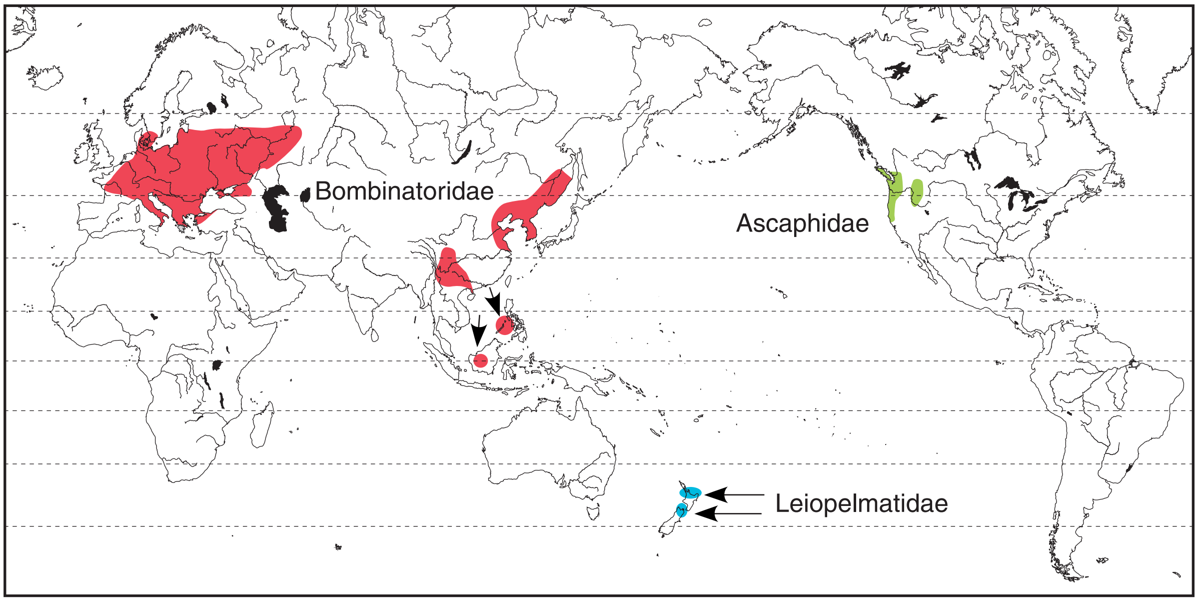


FIGURE 17.3 Geographic distributions of the extant Ascaphidae, Bombinatoridae, and Leiopelmatidae.

occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are generally blunt. The branchial chamber of the larva does not close, so a spiracle does not form.

Biology All species of *Leiopelma* (Fig. 17.2) are secretive frogs that survive in only a few areas along the borders of cool forest creeks and seepage areas. They hide during the day beneath rocks, logs, and other forest litter and emerge at night to feed. Courtship occurs in spring and summer (September–January). Although they lack vocal sacs and tympana, males produce quiet chirping calls during sexual encounters; amplexus is inguinal. The females deposit small clusters of 1 to 22 large, yolky eggs in small depressions beneath rocks or logs, and the males brood the egg clutches, sitting beside them in *Leiopelma hochstetteri* and on them in *Leiopelma archeyi* and *Leiopelma hamiltoni*. Development is best described as incomplete direct. The larvae hatch at a relatively late stage of embryogenesis and are nearly immobile in *L. archeyi* and *L. hamiltoni*. Males continue to attend the larvae, at least in the latter two species. The larvae of *L. hochstetteri* have typical tadpole bodies and are mobile, and males no longer attend the hatched tadpoles.

References Bell, 1978, 1985, 1994; Green, 1994; Green and Cannatella, 1993; Green et al., 1989; Worthy, 1987.

Bombinatoridae

Fire-bellied toads

Classification Amphibia; Lissamphibia; Anura.

Sister taxon Clade containing all living taxa of Anura, exclusive of Ascaphidae and Leiopelmatidae.

Content Two genera, *Barbourula* and *Bombina*, with two and five species, respectively.

Distribution Europe, southern China, Borneo, and Philippine Islands (Fig. 17.3).

Characteristics *Bombina* contains moderate-sized (40–80 mm adult SVL) toadlike frogs; *Barbourula* are somewhat larger (60–100 mm adult SVL). The skull lacks palatines and has paired frontoparietals. The facial nerve exits through the facial foramen anterior to the auditory capsule; the trigeminal and facial nerve ganglia are separate. The vertebral column possesses eight presacral stegochordal vertebrae, and all are opisthocoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have dorsal ribs on the second through fourth presacral vertebrae, articulating with transverse processes in *Barbourula* and fused in *Bombina*. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts and two small, fused spiracular tubes with a single anteromedial spiracle.

Biology The fire-bellied toads, *Bombina* (Fig. 17.2), are mainly diurnal and aquatic, spending much of their time in slow-moving waters of marshes and ponds. Although dark and camouflaged above, they are readily visible because they are active in open areas. Warty, glandular skin with toxic secretions protects them from many predators, and when attacked, they advertise their toxicity by an Unken reflex (Fig. 11.5). This arching reflex displays their bright undersides of black mottling on yellow, orange, or red backgrounds. European *Bombina* breed from late April to midsummer; males call day and night, although most reproductive activity occurs in the early evening. Amplexus is inguinal. Females deposit 60 to 200 eggs in numerous small egg clusters that are attached to either vegetation or the substrate. The embryos hatch within 4 to 10 days, and the tadpoles develop rapidly, usually metamorphosing in 35 to 45 days except in cooler localities. Little is known of the biology of *Barbourula*. They are cryptic and highly, although not exclusively, aquatic frogs. Juveniles and adults live in small, stone-bottomed streams in mountainous areas; juveniles live in shallow pools and seldom emerge, whereas adults occupy rock crevices or sit beneath rocks at the water–air interface. Their hands and feet are fully webbed. Females produce approximately 70 to 80 moderately large, weakly pigmented ova; presumably, the eggs are laid in the water beneath rocks.

References Alcala and Brown, 1987; Barandun, 1995; Engelmann et al., 1986; Grillitsch et al., 1983; Inger, 1954; Iskandar, 1995; M. Lang, 1989a.

Discoglossidae

Midwife toads and painted frogs

Classification Amphibia; Lissamphibia; Anura.

Sister taxon Clade containing all living taxa of Anura, exclusive of Ascaphidae, Bombinatoridae, and Leiopelmatidae.

Content Two genera, *Alytes* and *Discoglossus*, with four and six species, respectively.

Distribution Western and central Europe, and northwestern Africa (Fig. 17.4).

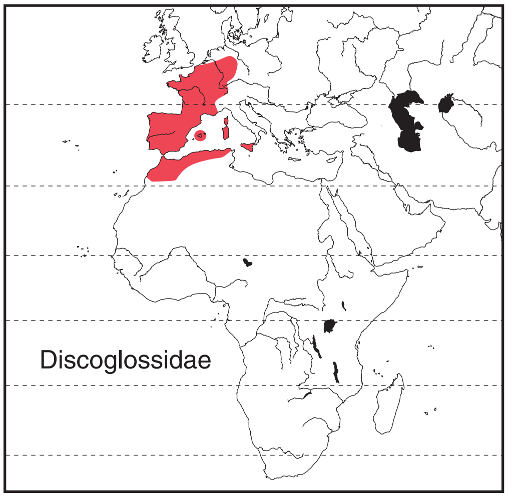


FIGURE 17.4 Geographic distribution of the extant Discoglossidae.

Characteristics Discoglossids are moderate-sized frogs, with adults ranging from 40 to 55 mm SVL in *Alytes* and 60 to 75 mm SVL in *Discoglossus*. The skull lacks palatines and has a pair of frontoparietals. The facial nerve exits through the facial foramen anterior to the auditory capsule; the trigeminal and facial nerve ganglia are separate. The vertebral column possesses eight presacral stegochordal vertebrae, and all are opisthocoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have dorsal ribs on the second through fourth presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts and two small, fused spiracular tubes with a single anteromedial spiracle.

Biology The species of *Alytes* are terrestrial frogs that live in wooded areas as well as more open habitats near ponds and streams. They are strongly nocturnal, and during the day hide beneath rocks and logs. They dig their own burrows, constructing a system of tunnels underground, using primarily their forelimbs; they sometimes do push-ups to pack the substrate against the tunnel with their heads. *Discoglossus* is more aquatic and occurs mainly at the edge of fast flowing streams with rocky substrates. Males of both genera have voices, and amplexus is inguinal. During one season, females of *Discoglossus pictus* (Fig. 17.2) deposit about 500 to 1000 eggs singly on vegetation or in small clusters on the stream bottom. Development to metamorphosis occurs in 3 to 8 weeks, depending on water temperature. In *Alytes*, males fertilize a clutch of 20 to 100 egg strings during amplexus, which are then wrapped around their legs. The eggs are carried by the male until the larvae are about to hatch (3 weeks in *Alytes cisternasii*; 4 to 5 weeks in *Alytes obstetricans*), and then the male returns to water, allowing the tadpoles to swim free. The tadpoles overwinter and metamorphose in late spring and early summer.

References Arntzen and García-París, 1995; Berger and Michalowski, 1973; Engelmann et al., 1986; Hemmer and Alcover, 1984; Márquez, 1992, 1995; Salvador, 1985.

Mesobatrachia

Megophryidae

Asian toadfrogs

Classification Amphibia; Lissamphibia; Anura; Mesobatrachia; Pelobatoidea.

Sister taxon Pelobatidae.

Content Six genera, *Leptobrachella*, *Leptobrachium*, *Leptolalax*, *Megophrys* (Fig. 17.5), *Ophryophryne*, and *Scutiger*, with 80+ species.

Distribution Subtropical and tropical Asia from Nepal to the Philippines (Fig. 17.6).

Characteristics Megophryids are small to large frogs (15–120 mm adult SVL). The skull lacks palatines and has paired frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral stegochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a single condylar articulation or is fused with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology *Scutiger* are principally high-elevation frogs occurring above 1000 m; one specimen of *Scutiger boulengeri* was found at 5030 m. Other megophrynids

FIGURE 17.5 Representative pelobatoid frogs. Clockwise from upper left: long-footed toadfrog *Megophrys longipes*, Megophryidae (photograph by L. L. Grismer); smallmouth toadfrog *Ophryophryne microstoma*, Megophryidae (A. Lathrop); eastern spadefoot *Scaphiopus holbrookii*, Pelobatidae (J. P. Caldwell); and Parsley frog *Pelodytes punctatus*, Pelodytidae (C. Raxworthy).

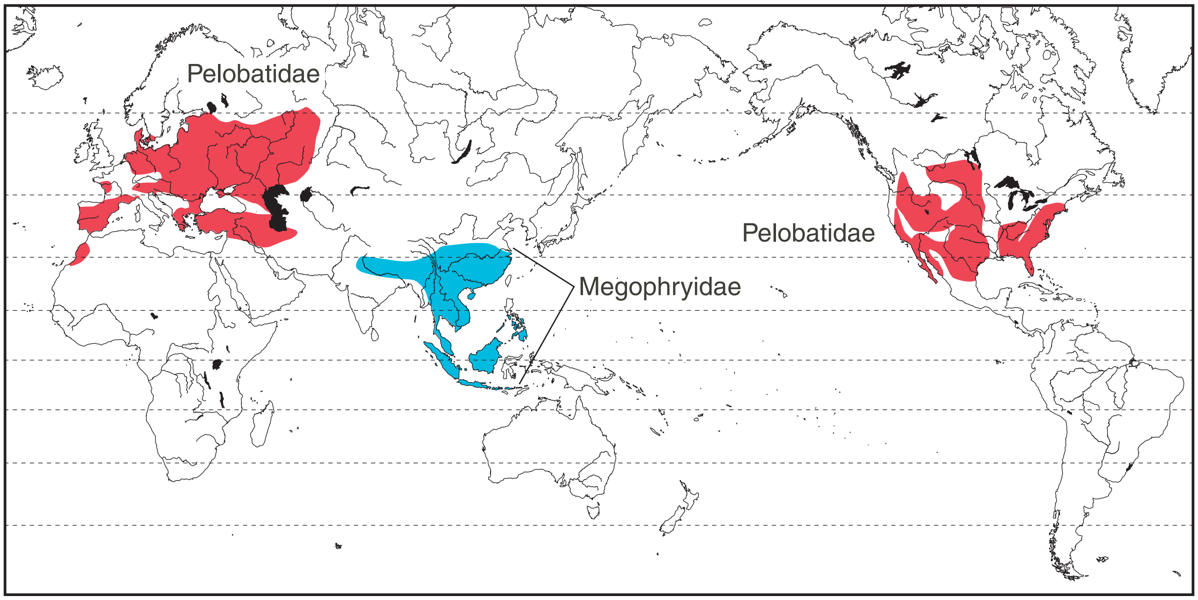


FIGURE 17.6 Geographic distributions of the extant Pelobatidae and Megophryidae.

are predominantly low montane or lowland frogs. Most are forest floor inhabitants, and many species are strictly streamside residents. The reproductive biology is inadequately known. Amplexus is inguinal; eggs are laid in water and hatch into free-living larvae. Because many species live or breed in small, rapidly flowing streams, their larvae are streamlined and some are torrent-adapted. Direct development has been suggested for *Megophrys longipes*.

References Berry, 1975; Henrici, 1994; Inger, 1966; Lathrop 1997; Rao and Yang, 1997.

Pelobatidae

Spadefoot toads

Classification Amphibia; Lissamphibia; Anura; Mesobatrachia; Pelobatoidea.

Sister taxon Megophryidae.

Content Three genera, *Pelobates*, *Scaphiopus* (Fig. 17.5), and *Spea*, with four, three, and four species, respectively.

Distribution North America and Europe to Central Asia (Fig. 17.6).

Characteristics Pelobatids are moderate-sized frogs (50–80 mm adult SVL) with squat toadlike bodies and warty, although soft, skin. The colloquial name is derived from the large, keratinous-edged, crescentic tubercle on the outer edge of each hindfoot. The pelobatid skull lacks palatines and has a pair of frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral stegochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology All spadefoots are fossorial (subterranean) and burrow backward with an alternating shuffling movement of the hindlimbs. Spadefoots spend much of their lives in burrows, but contrary to the general misconception that Nearctic species emerge only for reproduction, they regularly forage on the surface during damp evening hours. This misconception arises from the explosive reproductive habitats of *Scaphiopus* and *Spea*, and their generally drier habitat preference. In these species, reproduction can occur on any warm evening with heavy rains from early spring to late summer. As temporary ponds form, the males establish a raucous chorus and are soon joined by the females; inguinal amplexus and egg deposition soon follow. Most often, a local population's annual reproduction is completed in a single short period; individuals may call and breed even during the day after the first heavy rains of the season. The larval period can be as rapid as 6 to 8 days in *Scaphiopus couchii* but is usually 24 to 32 days. In contrast, the species of *Pelobates* breed in spring and have a 2- to 3-month larval period (*Pelobates syriacus*) or have slower development and overwinter for 1 to 3 years, depending on the local climate (*Pelobates fuscus*). This extended larval period results in large tadpoles (to 180 mm total length)—the largest tadpoles among European anurans. These reproductive traits, coupled with morphological differences, lead some systematists to question whether the Nearctic and Palearctic genera are closely related, but other data suggest only that their divergence is ancient (Sage et al., 1982; Maglia, 1998).

References Bragg, 1965; Engelmann et al., 1986; Justus et al., 1977; Maglia, 1998; Nöllert, 1990; Sage et al., 1982; Salvador, 1985; Wiens and Titus, 1991.

Pelodytidae

Parsley frogs

Classification Amphibia; Lissamphibia; Anura; Mesobatrachia; Pelobatoidea.

Sister taxon Clade containing Megophryidae and Pelobatidae.

Content One genus, *Pelodytes*, with two species.

Distribution Southwestern Europe and the Caucasus Mountains in southwestern Asia (Fig. 17.7).

Characteristics The two species of *Pelodytes* (Fig. 17.5) are moderately small frogs, 45 to 55 mm SVL. The skull lacks palatines and has a pair of frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral stegochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a

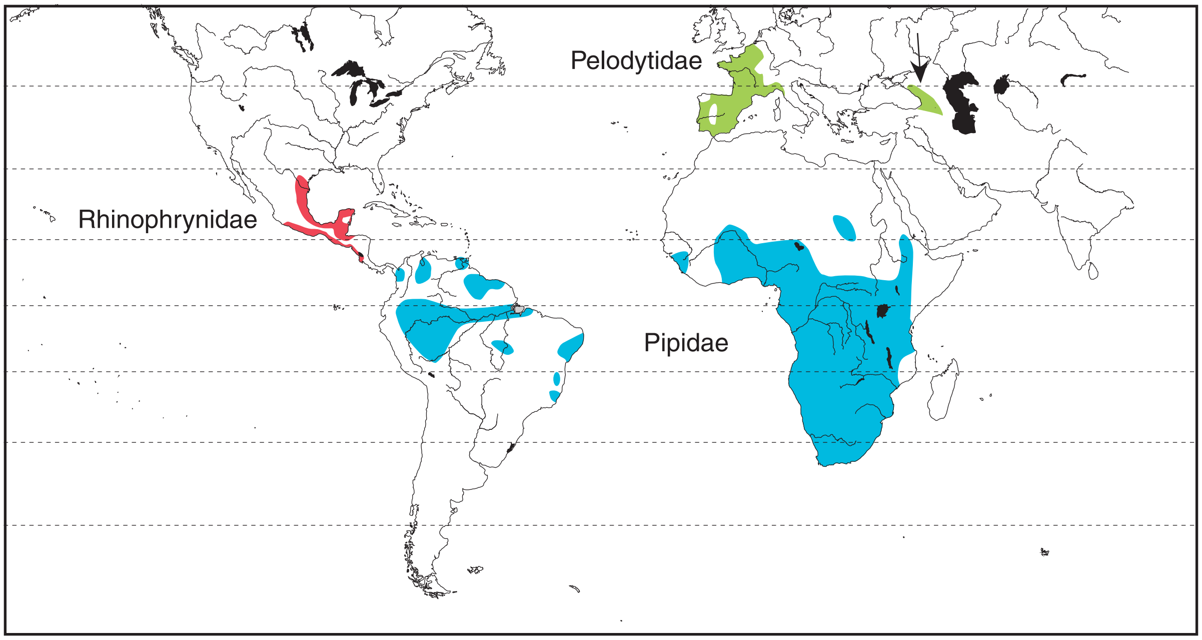


FIGURE 17.7 Geographic distributions of the extant Rhinophrynidae, Pipidae, and Pelodytidae.

distinct sternum. The fibulare and tibiale are fused along their entire lengths. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology The two pelodytids are terrestrial, living in moist habitats from sea level to midmountain elevations (2300 m). They are nocturnal until the breeding season, when reproductive activity occurs throughout the day and night. *Pelodytes punctatus* males call primarily from submerged positions. Amplexus is inguinal and occurs in the water. Females of *P. punctatus* lay 1000 to 1600 eggs, whereas females of *Pelodytes caucasicus* deposit about 40 eggs. In both, the eggs hatch quickly, and metamorphosis occurs in 75 to 80 days.

References Borkin and Anissimova, 1987; Henrici, 1994; Malkmus, 1995; Salvador, 1985.

Pipidae

Platannas, African clawed frogs, and Surinam toads

Classification Amphibia; Lissamphibia; Anura; Mesobatrachia; Pipoidea.

Sister taxon Rhinophrynidae or extinct Paleobatrachidae.

Content Two subfamilies, Pipinae and Xenopodinae, with ±30 species.

Distribution Sub-Saharan Africa and tropical South America (Fig. 17.7).

Characteristics Adult size is variable, ranging from the small *Pipa parva* (27–44 mm adult SVL) and *Hymenochirus* (25–33 mm SVL) to the larger *Xenopus laevis* (60–130 mm SVL) and *Pipa pipa* (105–170 mm SVL). All pipids are highly aquatic and possess dorsoventrally depressed bodies and large muscular hindlimbs and webbed feet. All lack tongues but retain the lateral line organs as adults. The pipid skull lacks palatines and has a single frontoparietal. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses six to eight presacral stegochordal vertebrae, and all are opisthocoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have dorsal ribs fused to the second through fourth presacral vertebrae. The pectoral girdle is arciferal—pseudofirmisternal in *Hymenochirus*—with a small sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are pointed. The larvae lack keratinized mouth parts, and the left and right branchial chambers are emptied by separate spiracles.

Comments Báez and Trueb (1997) reanalyzed the relationships of extant and extinct pipids. Their results support the recognition of the two extant clades or subfamilies and reveal a sister-group relationship between the xenopines and the Brazilian fossil "*Xenopus*" *romeri.*

References Báez and Trueb, 1997; Cannatella and de Sá, 1993; Cannatella and Trueb, 1988a.

Pipinae

Sister taxon Xenopodinae.

Content Three genera, *Hymenochirus*, *Pipa,* and *Pseudhymenochirus*, with four, seven, and one species, respectively.

Distribution Tropical South America and West Central Africa.

Characteristics Pipinae lack palpebral membranes (= nictitating membranes), nasolacrimal or subocular tentacles, and an epipubis. The larvae do not have a sensory barbel at each corner of the mouth.

Biology Pipines are aquatic frogs, occurring in a variety of habitats, usually still or slow-moving water among vegetation. Both adults and larvae are carnivorous. Elaborate courtship rituals are more fishlike than froglike, and amplexus is inguinal. Males lack vocal cords and vocal sacs, yet they still attract females by sound, producing a series of sharp clicking notes by snapping the hyoid apparatus. During amplexus, the pair performs a series of aquatic somersaults that allow the male to fertilize the eggs prior to their rolling on to the female's back in *Pipa* (Fig. 4.11) or being deposited on the water surface in *Hymenochirus.* In *Pipa*, amplexus lasts longer than 12 hours to allow morphological and physiological changes of dorsal skin. When the eggs roll onto the female's back, they sink into the skin and eventually become fully embedded. In *Pipa pipa* (Fig. 17.8) and *Pipa arrabali* development is direct and toadlets "hatch" from their skin pockets; it is indirect in *Pipa carvalhoi*, *Pipa myersi*, and *Pipa parva,* with larvae emerging and completing their development as free-living tadpoles.

References Cannatella and Trueb, 1988b; Rabb and Rabb, 1960, 1963a,b; Rabb and Snediger, 1960; Trueb and Cannatella, 1986; Weygoldt, 1976.

Xenopodinae

Sister taxon Pipinae.

Content Two genera, *Silurana* and *Xenopus*, with ±15 species.

Distribution Sub-Saharan Africa.

Characteristics Xenopinae have palpebral membranes, nasolacrimal or subocular tentacles, and an epipubis. The larvae have long, thin sensory barbels at the corners of the mouth.

Biology *Xenopus* are immensely successful aquatic frogs, seemingly occurring in every freshwater habitat south of the Sahara, including roadside puddles. This broad distribution is largely that of the *Xenopus laevis* complex, which occupies this entire area, and encompasses the much smaller distributions of *Silurana* and the other species of *Xenopus.* The genetic diversity of *Xenopus* is polyploid-derived and all or most extant species likely arose from interspecific hybridization events. Like the pipines, male *Xenopus* and *Silurana* attract females by underwater sound production via the hyoid apparatus. Reproductive activity appears to be stimulated by heavy rains that wash high nutrient loads into the water. Amplexus (inguinal) and egg deposition are relatively quick. Eggs hatch within a few days and the larvae begin feeding on suspended matter. The larvae are positively buoyant and swim head down, typically in schools. They are suspension feeders, efficiently filtering the phytoplankton from the water. Apparently owing to the specializations of their branchial apparatus for this mode of feeding, the tadpoles are obligate air-breathers and must regularly rise to the surface for air.

References Graf, 1996; Kobel et al., 1996; Tinsley et al., 1996; Wassersug, 1996.

Rhinophrynidae

Mesoamerican burrowing toad

Classification Amphibia; Lissamphibia; Anura; Mesobatrachia; Pipoidea.

Sister taxon Pipidae.

Content Monotypic, *Rhinophrynus dorsalis.*

Distribution Lowlands of extreme southern Texas to Costa Rica (Fig. 17.7).

Characteristics *Rhinophrynus dorsalis* (Fig. 17.8) is a peculiar frog with a tiny, cone-shaped head and four short but robust limbs projecting from a large, somewhat flattened, globular body (75–85 mm SVL). Its skull lacks palatines and has a single frontoparietal. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral notochordal vertebrae, and all are opisthocoelous. The transverse processes of the sacral vertebra are broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal and lacks a sternum. The

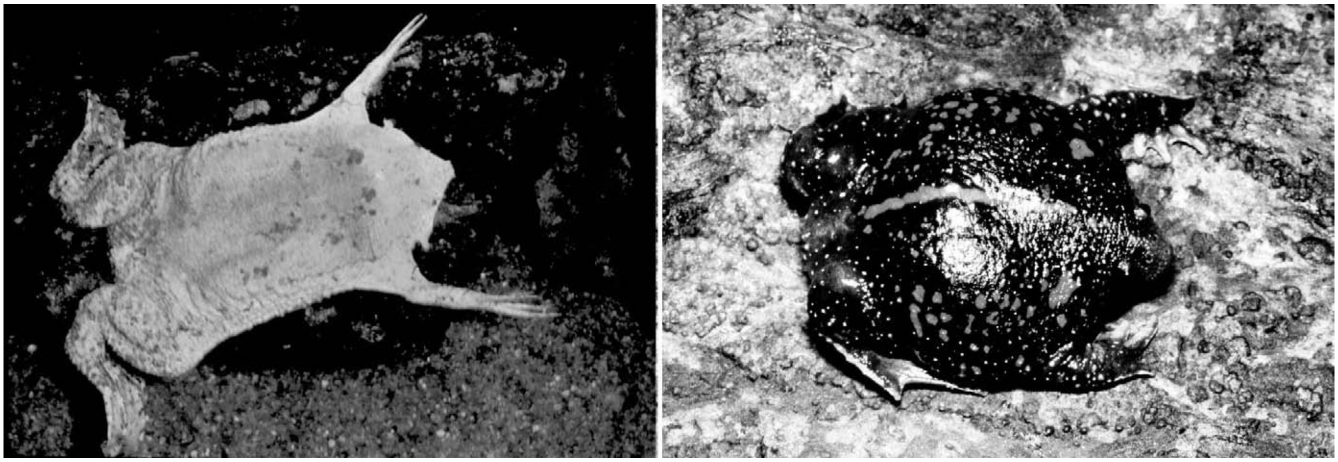


FIGURE 17.8 Representative pipoid frogs. (Left) Surinam toad *Pipa pipa*, Pipidae (photograph by R. W. McDiarmid). (Right) Mesoamerican burrowing toad *Rhinophrynus dorsalis*, Rhinophrynidae (J. A. Campbell).

fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt. The larva lacks keratinized mouth parts, and the left and right branchial chambers are emptied by separate spiracles.

Biology The globular microcephalic habitus of *R. dorsalis* denotes a fossorial existence and a diet of soft-bodied, subterranean arthropods, such as termites and ant larvae. A highly specialized feeding apparatus allows this frog to project its tongue straight out from the mouth, rather than flip it outward in the typical frog fashion. It digs with the hindlimbs; its spades are on the inside edge of each hindfoot. How *R. dorsalis* penetrates termite and ant nests to feed is unknown, but it is unlikely that it backs into these nests, which are guarded by big-jawed workers. It breeds in temporary pools, where the males call from floating postures. Amplexus is inguinal, and a female deposits several thousand eggs that sink to the bottom. Duration of the tadpole stages is unknown; tadpoles swim in schools of 50 to several hundred individuals.

References Foster and McDiarmid, 1983; Fouquette, 1969; Lee, 1996.

Neobatrachia

“bufonoids”

Allophrynidae

Ruthven’s frog

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content Monotypic, *Allophryne ruthveni.*

Distribution Northern South America, including the Amazon Basin (Fig. 17.9).

Characteristics *Allophryne ruthveni* (Fig. 17.10) is a small species, 26 to 31 mm adult SVL. Its skull is strongly ossified dorsally, and has paired palatines and frontoparietals, and toothless maxillae. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded (dilated), and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are T-shaped. The larvae of *A. ruthveni* are unknown.

Biology This species occurs in rain forest; individuals congregate in large breeding aggregations in trees and low vegetation along rivers as the water begins to rise, flooding the forest during the wet season. Smaller choruses also occur in trees and shrubs at the edge of small ponds and flooded depressions in the forest.

References Duellman, 1975; Caldwell, 1996b; Hoogmoed, 1969; Caldwell and Hoogmoed, 1998.

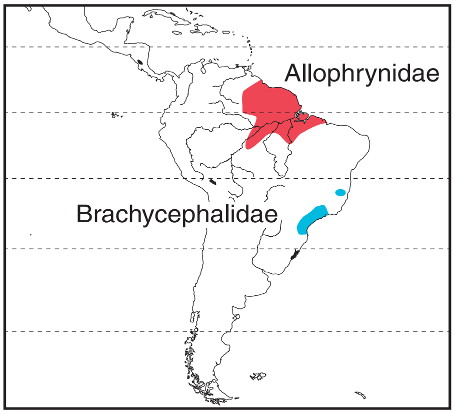


FIGURE 17.9 Geographic distributions of the extant Allophrynidae and Brachycephalidae.

Brachycephalidae

Three-toed toadlets

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content Two genera, *Brachycephalus* and *Psyllophryne*, with three and two species, respectively.

Distribution Atlantic Forest of southeastern Brazil (Fig. 17.9).

Characteristics Brachycephalids are tiny frogs, 12 to 18 mm adult SVL. Aside from their small size, they have reduced numbers of digits: two or three functional fingers on each forefoot and three toes on the hindfoot. The skull has a pair of palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses seven presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal and lacks a sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt to pointed. As far as is known, there is no free-living larval stage.

Biology *Brachycephalus ephippium* (Fig. 17.10) is a bright orange or yellow frog that lives in leaf litter of seasonal rain forests. The bright color is likely an aposematic warning of its toxic skin secretions, a tetrodotoxin-like compound. Males give a low buzzlike call from future nest sites beneath cover. Amplexus is initially inguinal in *B. ephippium* but shifts to a more axillary position as the female deposits the eggs, which she later coats with soil particles, perhaps for camouflage or to reduce desiccation. Development is direct. Little is known of *Brachycephalus nodoterga* and *Psyllophryne didactyla* other than they are cryptically colored.

References Heyer et al., 1990; Pombal et al., 1994, 1998.

Bufonidae

True toads, harlequin frogs, and relatives

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content Thirty-one genera, *Altiphrynoides*, *Andinophryne*, *Ansonia*, *Atelophryniscus*, *Atelopus*, *Bufo*, *Bufoides*, *Capensibufo, Crepidophryne, Dendrophryniscus*, *Didynamipus*, *Frostius, Laurentophryne, Leptophyne, Melanophryniscus, Mertensophryne*, *Nectophryne, Nectophrynoides*, *Nimbaphrynoides, Oreophrynella, Osornophryne*, *Pedostibes*, *Pelophryne*, *Peltophryne*, *Pseudobufo*, *Rhamphophryne*, *Schismaderma*, *Spinophrynoides*, *Stephopaedes*, *Werneria,* and *Wolterstorffina*, with ±400 species.

Distribution Worldwide on all continents except Antarctica and Australia (Fig. 17.11). *Bufo marinus* has been introduced widely in the Caribbean, Oceania, Philippines, and Australia.

Characteristics Bufonids vary greatly in size, ranging from the tiny *Dendrophryniscus carvalhoi, Mertensophryne micranotis,* and *Pelophryne brevipes* (< 20 mm adult SVL) to giants, such as *Bufo marinus*, which has a maximum length to 230 mm SVL. Bufonids are the only anurans to possess a Bidder's organ in male tadpoles, and this organ persists in most adult males. All adults lack teeth in the upper jaw; thus bufonids are toothless amphibians. The bufonid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses five to eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar

FIGURE 17.10 Representative bufonoid anurans. Clockwise from upper left: Ruthven's frog *Allophryne ruthveni*, Allophrynidae (photograph by J. P. Caldwell); three-toed toadlet *Brachycephalus ephippium*, Brachycephalidae (C. Haddad); beautiful harlequin frog *Atelopus andinus*, Bufonidae (R. W. McDiarmid); Mitre toad *Bufo typhonius*, Bufonidae (J. P. Caldwell); and red-bellied toadlet *Melanophryniscus rubriventris*, Bufonidae (M. Vaira).

articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is ariciferal, rarely pseudofirmisternal, with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

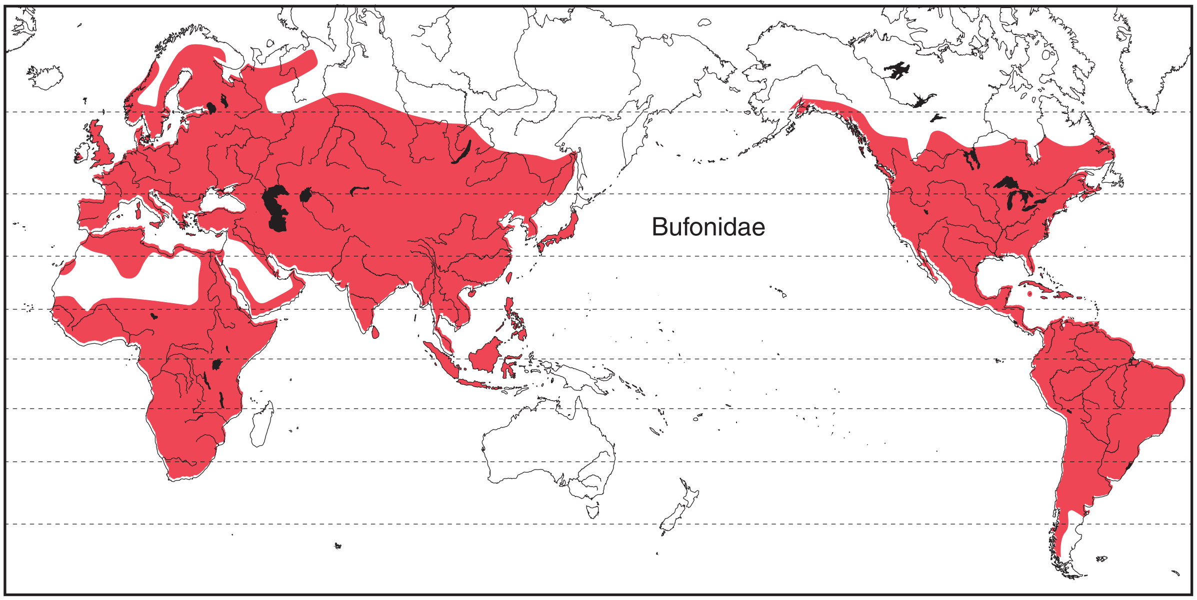


FIGURE 17.11 Geographic distribution of the extant Bufonidae.

Biology The bufonids have a diverse array of life histories. Although the majority are terrestrial to semifossorial, some (*Pseudobufo*) are aquatic and others (*Pedostibes*) are arboreal. Most have prominent skin glands, often with highly toxic skin secretions. *Bufo* has a thick, warty, often spiny skin and enlarged concentrations of glands in the temporal–neck area forming prominent parotoid glands. *Atelopus* (Fig. 17.10) lacks the prominent glandular swellings, but its skin secretions are more readily lethal to predators; its bright aposematic coloration of red, yellow, or orange markings on a black background advertizes its toxicity to predators. *Bufo* and many other bufonids reproduce using axillary amplexus (rarely inguinal, e.g., *Osornophryne*, *Bufo fastidiosus*); they typically deposit strings of pigmented eggs in water, and these hatch into free-living tadpoles. The tadpoles develop quickly and generally metamorphose within 2 to 10 weeks of hatching. Other bufonids have terrestrial eggs and direct development (e.g., *Osornophryne*), and even internal fertilization and viviparity. *Nectophrynoides* has five species that show the total spectrum from typical external fertilization and external development of free-living larvae (*Nectophrynoides osgoodi*) to external fertilization and direct development (*Nectophrynoides malcolmi*), and internal fertilization and internal development (three species). In two of the live-bearing species (*Nectophrynoides tornieri*, *Nectophrynoides viviparus*), the embryos develop fully in the females' oviducts, and their nourishment apparently derives entirely from their yolk, although they are totally dependent upon the females for gaseous exchange. In *Nectophrynoides occidentalis*, the developing embryos receive their nutrients from secretions of the oviductal mucosa for about the last 3 months of their 8- to 9-month gestation. In all three live-bearing *Nectophrynoides*, internal fertilization occurs by cloacal apposition. In another bufonid live-bearer, *Mertensophryne*, the cloaca is modified into an intromittent organ for internal fertilization.

Comments More than one-half of the bufonid species is placed in the genus *Bufo*, a generally morphologically, ecologically, and behaviorally conservative group. The remaining species usually are specialized and divided into small species groups, some of which are probably monophyletic (see Graybeal and Cannatella, 1995); however, in spite of the diversity of morphology and lifestyles, our knowledge of phylogenetic relationships within the clade is limited.

References Berry, 1975; Blair, 1972; Grandison and Ashe, 1983; Graybeal, 1997; Graybeal and Cannatella, 1995; Inger, 1966; Izecksohn, 1993; Lötters, 1996; Poynton, 1996; Poynton and Broadley, 1988; Tihen, 1965; Wake, 1993b; Xavier, 1986.

Centrolenidae

Glass frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Clade containing Hylidae and Pseudidae.

Content Three genera, *Centrolene*, *Cochranella,* and *Hyalinobatrachium*, with ±120 species.

Distribution Central and South America (Fig. 17.12).

Characteristics Centrolenids (Fig. 17.13) are moderately small species (18–40 mm adult SVL) although a few are larger (to 77 mm SVL in *Centrolene geckoideum*). The colloquial name refers to the transparent abdominal peritoneum and skin through which the heart and other internal organs are visible. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused along their entire lengths. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology Centrolenids are tropical forest residents that spend their lives largely in the trees, except for the aquatic larval stage. Males typically call from vegetation over small to large streams and rivers. Unlike many arboreal frogs, the female does not descend to water after amplexing with the male but deposits her eggs on the leaf on which the male is calling. Parental care is common, and a male guards one to several clutches of 2 to 30 eggs (Fig. 4.22). Major predators of the eggs are various "frogflies" of the families Ephydridae and Drosophilidae that deposit their eggs on the frog egg mass and whose larvae will then consume the frog embryos. Centrolenid development is indirect, and hatched tadpoles fall into the water below. There, the elongate tadpoles complete their development, commonly living within the leaf litter on the stream bottom. Tadpoles of some species burrow into the mud on the banks of streams or rivers; these tadpoles are bright red because of dense capillary beds in the skin, which function in respiration in this low-oxygen environment. The large *C. geckoideum* is an exception to the arboreal breeding. It lives along small forest streams and attaches its eggs to rocks behind waterfalls; subsequently, the male parent attends the eggs.

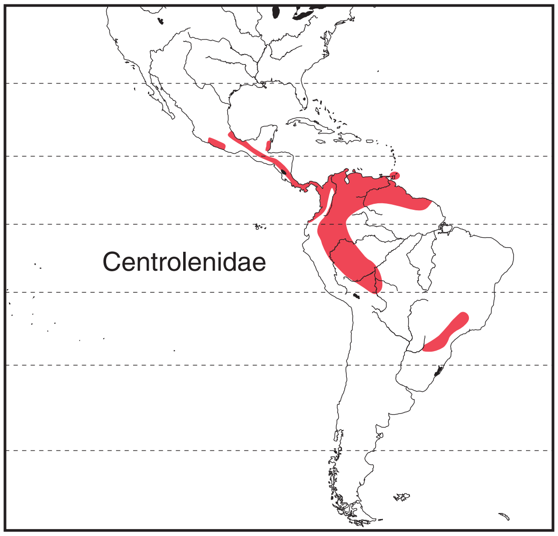


FIGURE 17.12 Geographic distribution of the extant Centrolenidae.

References Lynch et al., 1983; McDiarmid, 1978; Ruiz-Carrnaza and Lynch, 1991; Villa, 1984.

Heleophrynidae

Ghost frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain, possibly the clade containing Myobatrachidae and Sooglossidae.

Content One genus, *Heleophryne*, with five species.

Distribution Cape area of southern Africa (Fig. 17.14).

Characteristics Heleophrynids are moderately small (35–65 mm adult SVL) treefrog-like anurans with expanded digit tips. Their skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral notochordal vertebrae, and all are amphicoelous. The transverse processes of the sacral vertebra are moderately expanded (dilated), and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to slightly flared. The larvae have keratinized mouth parts, but lack a beak, and the left and right branchial chambers fuse behind the

FIGURE 17.13 Representative bufonoid anurans. Clockwise from upper left: undescribed glass frog *Centrolene* sp., Centrolenidae (photograph by J. P. Caldwell); Valerio's glass frog *Hyalinobatrachium valerioi*, Centrolenidae (R. W. McDiarmid); Cape ghost frog *Heleophryne purcelli*, Heleophrynidae (J. Visser, courtesy of the Natural History Museum, The University of Kansas); and back-breeder *Hemiphractus scutatus*, Hemiphractinae (J. P. Caldwell).

heart and are emptied by a spiracle on the left side at midbody.

Biology The five species of heleophrynids occur only in swift-flowing, rocky streams in isolated mountain gorges in the Cape area. This area is being converted to housing developments, thus threatening the frogs' habitats and survival. Adults (Fig. 17.13) are active mainly at night as sit-and-wait predators in the splash zone of the streams. Their expanded digital pads allow them to move easily and quickly over the slippery rocks. The reproductive biology is largely unknown. Unlike many torrent-inhabiting frogs, the males call (*Heleophryne purcelli*) and inguinal amplexus is preceded by an elaborate courtship that includes tactile behavior between the male and the female. A few large unpigmented eggs are attached beneath rocks in the streams. The tadpoles have a large oral disc, permitting them to cling to rock surfaces while feeding. Development is prolonged and metamorphosis may occur 1 to 2 years after hatching.

References Boycott, 1988; Boycott and de Villiers, 1986; Passmore and Carruthers, 1995; Poynton, 1964; Wager, 1986.

Hylidae

Amero-Australian treefrogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.
Sister taxon Pseudidae.

Content Four subfamilies, Hemiphractinae, Hylinae, Pelodryadinae, and Phyllomedusinae, with 720+ species.

Distribution Americas, disjunctly in Eurasia, and Australia (Fig. 17.14).

Characteristics Hylids range in size from tiny frogs (12–20 mm adult SVL; e.g., *Litoria microbelos*,

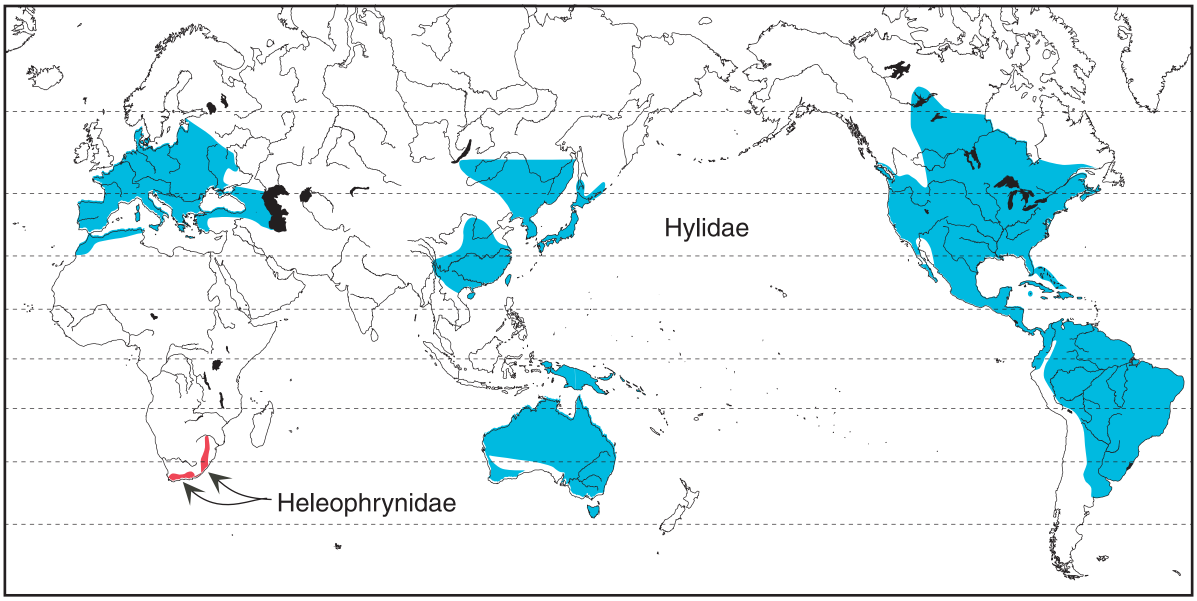


FIGURE 17.14 Geographic distribution of the extant Heleophrynidae and Hylidae.

Pseudacris ocularis) to giants (135–140 mm adult SVL; e.g., *Litoria infrafrenata*, *Hyla vasta*). Most have a treefrog habitus. The hylid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are slightly to moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are pointed, and occasionally claw-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody. All hylids have axillary amplexus.

References Duellman, 1970; Duellman and Trueb, 1986; Schwartz and Henderson, 1991; Tyler and Davies, 1993.

Hemiphractinae

Sister taxon Uncertain, possibly the clade containing all other hylid subfamilies.

Content Five genera, *Cryptobatrachus*, *Flectonotus*, *Gastrotheca*, *Hemiphractus*, and *Stefania*, with 65+ species.

Distribution Tropical America from Panama to Peru and northern Argentina.

Characteristics The skull is strongly ossified, with or without the skin (dermis) co-ossified to the roofing bones. The pupils are horizontal. Of the superficial mandibular musculature, the interhyoideus lies within the lower jaw, and the intermandibular muscle has variable development of accessory slips.

Biology The hemiphractines are known as marsupial frogs because many, but not all, have a specialized dorsal pouch in which eggs are carried. The pouch is present in *Flectonotus* and *Gastrotheca* (Fig. 17.15); the other three genera carry the eggs exposed on the back (Fig. 4.22). In all species with exposed eggs, including *Flectonotus* and some *Gastrotheca*, development follows the typical anuran pattern with a free-living tadpole stage. In other *Gastrotheca*, the eggs are held in the pouch throughout the entire developmental period, and froglets hatch and emerge from the pouch after several months. In these direct-developing species, the embryo develops an extensive capillary net that acts as a placenta for the maternal transfer of gases, water, and nutrients.

References del Pino, 1989; Duellman et al., 1988; Tyler and Duellman, 1995; Weygoldt and de Carvalho e Silva, 1991.

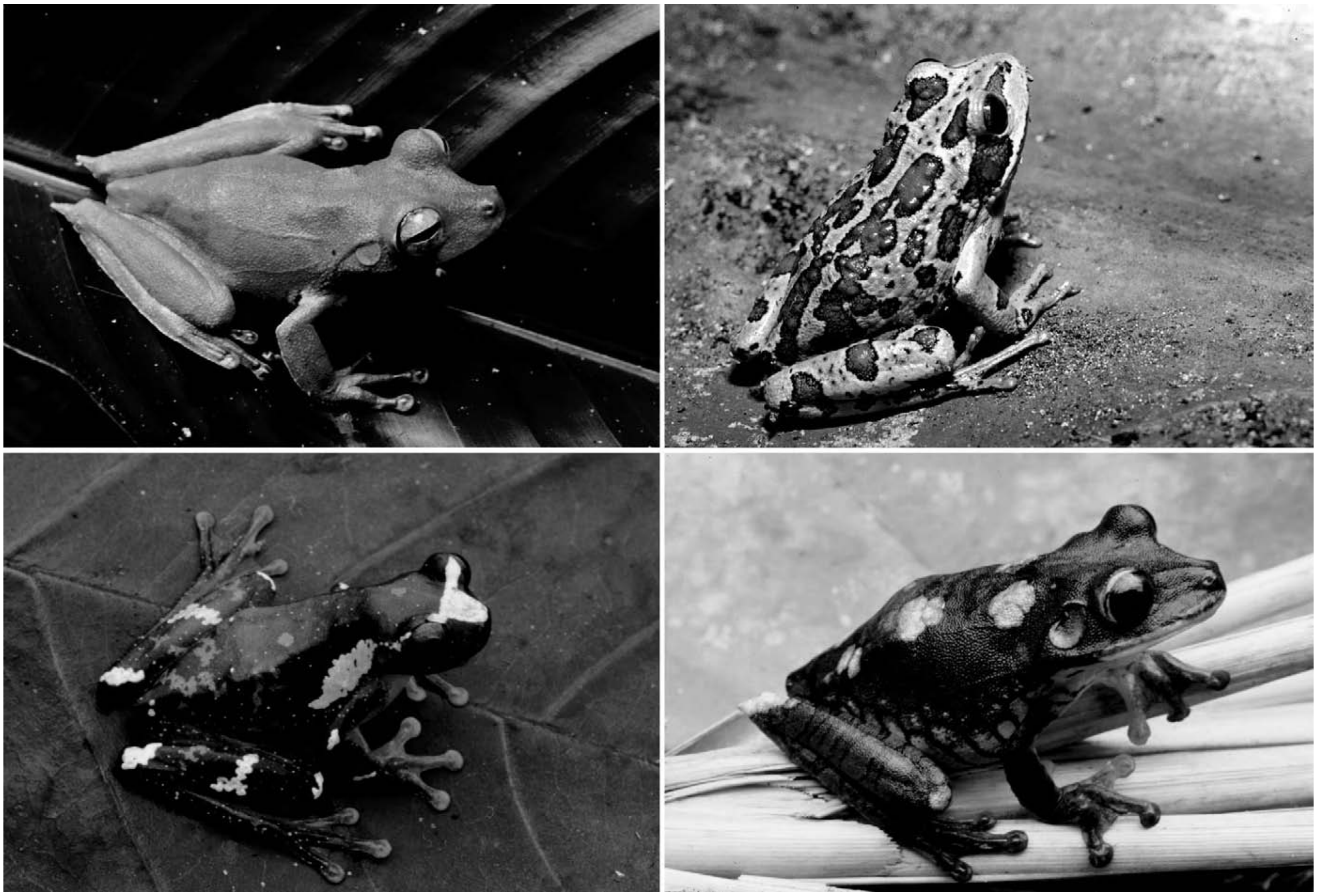


FIGURE 17.15 Representative hylids. Clockwise from upper left: treefrog *Hyla calcarata*, Hylinae (photograph by J. P. Caldwell); Peruvian marsupial frog *Gastrotheca peruana*, Hemiphractinae (R. D. Bartlett); map treefrog *Hyla geographica*, Hylinae (J. P. Caldwell); and Sarayacu treefrog *Hyla sarayacuensis*, Hylinae (J. P. Caldwell).

Hylinae

Sister taxon Uncertain, possibly a paraphyletic group.

Content Twenty-four genera, *Acris*, *Anotheca*, *Aparasphenodon*, *Aplastodiscus*, *Argenteohyla*, *Calyptahyla*, *Corythomantis*, *Duellmanohyla*, *Hyla*, *Nyctimantis*, *Osteocephalus*, *Osteopilus*, *Phrynohyas*, *Phyllodytes*, *Plectrohyla*, *Pseudacris*, *Pternohyla*, *Ptychohyla*, *Scarthyla*, *Scinax* [formerly *Ololygon*], *Smilisca*, *Sphaenorhynchus*, *Trachycephalus,* and *Triprion,* with 470+ species.

Distribution Disjunctly across Eurasia and throughout the Americas.

Characteristics Ossification of the skull is variable, commonly lacking extensive fusion. The skin usually is not fused to roofing bones, although it is fused in the casque-headed taxa (e.g., *Osteopilus*, *Triprion*). The pupils are horizontal. Of the superficial mandibular musculature, the interhyoideus extends posteriorly beyond the lower jaw, and the intermandibular muscle usually is undifferentiated.

Biology Hylines are predominantly arboreal frogs, although a few such as *Acris* (Fig. 17.16) and *Pseudacris* are terrestrial or live close to the ground on grasses and forbs; *Pternohyla* and *Triprion* are burrowers. Reproductive behavior includes male vocalization to attract females, and axillary amplexus stimulated by female contact with male. Egg deposition occurs in water in sites ranging from tree holes and bromeliads to streams and lakes. Eggs hatch into free-swimming tadpoles that eventually metamorphose into froglets. Parental care is uncommon but occurs in the gladiator frogs (e.g., *Hyla boans*, *Hyla faber*, *Hyla rosenbergi*). In these species, the males build nests in or adjacent to streams by pivoting around in sand or mud and pushing substrate with their feet. Males call to attract females to their nest for egg deposition and then guard the eggs and tadpoles. *Osteopilus brunneus* and some species of *Osteocephalus* deposit unfertilized eggs in bromeliads or tree holes to

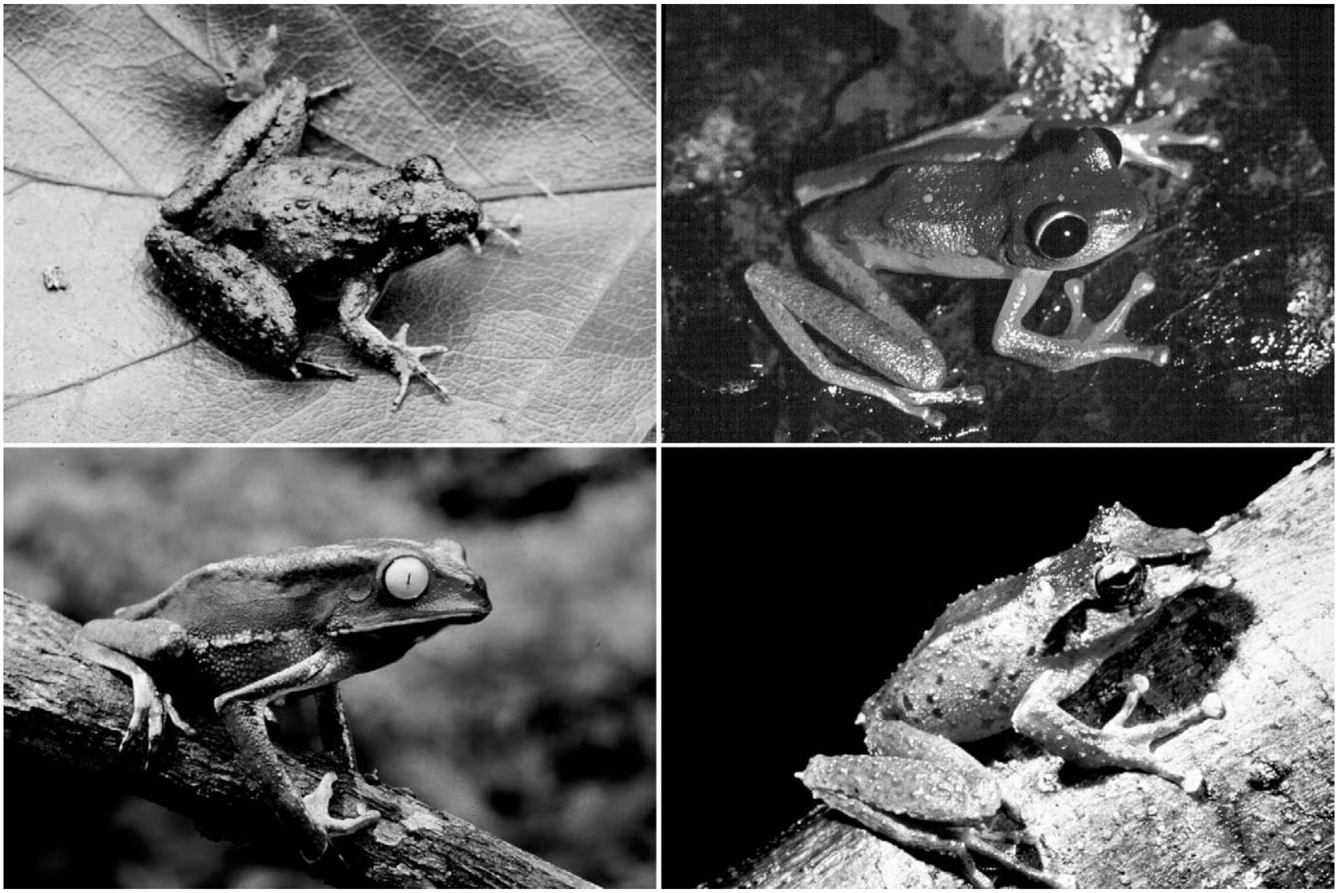


FIGURE 17.16 Representative hylids. Clockwise from upper left: northern cricket frog, *Acris crepitans*, Hylinae (photograph by J. P. Caldwell); lacelid treefrog *Nyctimystes trachydermis*, Pelodryadinae (E. Lindgren); Arfak treefrog *Litoria arfakiana*, Pelodryadinae (J. W. Lang); and Vaillant's leaf frog *Phyllomedusa vaillanti*, Phyllomedusinae (J. P. Caldwell).

feed tadpoles developed from eggs previously deposited by the same parents.

References Cei, 1980; Cocroft, 1994; Duellman, 1970; Duellman and Wiens, 1992; Geiger, 1995; Hedges, 1986; Heyer et al., 1990; Jungfer and Weygoldt, 1999; Kluge, 1981; Maeda and Matsui, 1989.

Pelodryadinae

Sister taxon Uncertain, possibly Phyllomedusinae.

Content Four genera, *Cyclorana*, *Litoria, Nyctimystes,* and *Pelodryas*, with 145+ species.

Distribution Mainly Australia and New Guinea, although present on a few southern Indonesian islands and with scattered introductions on Southwest Pacific islands.

Characteristics Ossification of the skull is variable, commonly lacking extensive fusion, and the skin usually is not fused to roofing bones. The pupils are horizontal. Of the superficial mandibular musculature, the interhyoideus extends posteriorly beyond the lower jaw, and the intermandibular muscle has a separate apical element.

Biology Pelodryadines are terrestrial to arboreal frogs (Fig. 17.16). *Cyclorana* are strictly terrestrial frogs, and a few are even semifossorial. Species of the other three genera are mainly arboreal, but a few are terrestrial, such as *Litoria nasuta*, which is known to Australian children as the rocket frog because of its prodigious jumps of over 1 m. Reproductive behavior and development follow the typical anuran pattern. The male vocalizes to attract females, although a few species of *Litoria* and *Nyctimystes* lack vocal sacs and are either voiceless or produce quiet calls. Amplexus is axillary and is stimulated by female contact with the male. Eggs are deposited mainly in ephemeral pools or streams and lakes and hatch into free-swimming tadpoles. Parental care is unknown in pelodryadines.

References Barker et al., 1995; Pyke and Osborne, 1996; Tyler, 1985; Tyler and Davies, 1978, 1993.

Phyllomedusinae

Sister taxon Uncertain, possibly Pelodryadinae.

Content Six genera, *Agalychnis*, *Hylomantis*, *Pachymedusa*, *Phasmahyla*, *Phrynomedusa*, and *Phyllomedusa*, with ±50 species.

Distribution Central and South America.

Characteristics Ossification of the skull is variable, commonly lacking extensive fusion, and the skin usually is not fused to roofing bones. The pupils are vertical. Of the superficial mandibular musculature, the interhyoideus extends posteriorly beyond the lower jaw, and the intermandibular muscle has lateral accessory slips.

Biology Most phyllomedusines are highly arboreal frogs (Fig. 17.16). Although capable jumpers, they usually walk slowly and methodically among branches to forage or search for resting sites. Some phyllomedusines (e.g., *Phyllomedusa hypochondrialis* and *Phyllomedusa sauvagii*) are uricotelic, having developed the ability to excrete uric acid rather than urea as a water-saving mechanism. Further, most species appear to have a lipid skin secretion that permits them to reduce water loss from the skin. *P. sauvagii* uses its hindlimbs in a contortionist-like manner to wipe its entire body with the secretion. This species is also able to tolerate excess heat loads without resorting to increased skin evaporation loss to shed the excess heat. Phyllomedusines derive their colloquial name, leaf frogs, from their egg-laying behavior. Egg deposition typically occurs on leaves or branches overhanging water. While in amplexus with a male, the female selects a deposition site and deposits 100 to 150 eggs, which the male fertilizes. The female and male, still in amplexus, descend to the water so that the female can absorb water before returning to the original egg site to deposit more eggs. This sequence may be repeated several times. Not all leaf frogs deposit eggs in this manner; *Phrynomedusa marginata* hides its eggs in crevices.

References Bagnara and Rastogi, 1992; Cruz, 1990; Shoemaker et al., 1989; Shoemaker and McClanahan, 1982; Weygoldt, 1991.

"Leptodactylidae"

Rain frogs, white-lipped frogs, American horned frogs, and relatives

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain; present taxa content makes Leptodactylidae paraphyletic.

Content Four subfamilies, Ceratophryinae, Hylodinae, Leptodactylinae, and Telmatobiinae; see Heyer (1975) for a different subfamilial paradigm.

Distribution Americas from southwestern North America through Central and South America and the West Indies (Fig. 17.17).

Characteristics Leptodactylids range from tiny frogs (e.g., 13–14 mm adult SVL, *Eleutherodactylus cubanus*) to giant ones (e.g., 145–185 mm adult SVL, *Leptodactylus pentadactylus*). The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal, rarely pseudofirmisternal, with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are variable, blunt, pointed, or T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

References Heyer, 1975, 1979; Lynch, 1971.

FIGURE 17.17 Geographic distribution of the extant Leptodactylidae.

Ceratophryinae

Sister taxon Uncertain, possibly the clade containing all other leptodactylid subfamilies.

Content Three genera, *Ceratophrys*, *Chacophrys,* and *Lepidobatrachus*, with 10+ species.

Distribution South America east of the Andes, including Pacific Ecuador and northern Peru.

Characteristics The sternum is cartilaginous. A bony shield lies over the presacral vertebrae and fuses with the dermis; the transverse processes of the anterior presacral vertebrae are long and distally expanded. The tips of the terminal phalanges are knobbed. Amplexus is axillary.

Biology Ceratophryines are best known for the voracious predatory behavior of *Ceratophrys calcarata* and *Ceratophrys cornuta* (Fig. 17.18). Their big mouths and fanglike teeth in the upper jaws enable them to capture and consume large prey, including lizards, other frogs, and small mammals, typically from ambush. The other two genera share the same habitus and the same feeding behavior. All ceratophryines are seasonal breeders, laying numerous small eggs in aquatic habitats; the eggs hatch into free-living tadpoles. *Chacophrys* and *Lepidobatrachus* are fossorial and inhabit arid areas, and all species possess well-developed metatarsal spades. *C. ornata* produces a keratinous cocoon and remains in torpor during the driest part of the year; perhaps the other aridland species do also.

References Cei, 1980; Maxson and Ruibal, 1988.

Hylodinae

Sister taxon Uncertain, possibly telmatobiines.

Content Three genera, *Crossodactylus*, *Hylodes,* and *Megaelosia*, with ±25 species.

Distribution Southeastern Brazil and adjacent Argentina.

Characteristics The sternum is cartilaginous, and occasionally calcified in old adults. The presacral vertebrae lack a bony or cartilaginous shield; the transverse processes of the anterior presacral vertebrae are short and not expanded. The tips of the terminal phalanges are variable. Amplexus is axillary.

Biology These streamside frogs are usually small (<35 mm adult SVL), although adult *Megaelosia* may attain lengths of 120 mm. All are diurnal predators. *Crossodactylus* spends much of its time in the water, even as adults; the other taxa occur on rocks and vegetation along streams. All species deposit eggs in water and possess a typical tadpole stage.

References Cei, 1980; Heyer et al., 1990.

Leptodactylinae

Sister taxon Uncertain, possibly the clade containing hylodines and telmatobiines.

Content Eleven genera, *Adenomera*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus*, *Limnomedusa*, *Lithodytes*, *Paratelmatobius*, *Physalaemus*, *Pleurodema*, *Pseudopaludicola,* and *Vanzolinius* (Fig. 17.18), with 120+ species.

Distribution Southwestern North America, Central and South America, and most Greater Antilles islands.

Characteristics The sternum has a medial ossified element. The presacral vertebrae lack a bony or cartilaginous shield; the transverse processes of the anterior presacral vertebrae are long and not expanded. The tips of the terminal phalanges are variable. Amplexus is axillary.

Biology Leptodactylines are less diverse in morphology, ecology, and behavior than the telmatobiines. These frogs range in size from small to large. None is totally aquatic, although many are obligate streamside dwellers; many species are terrestrial (most commonly in moist forest-floor situations), and a few are semiarboreal. Reproduction ranges from egg deposition in water with a free-living tadpole stage (e.g., *Pseudopaludicola*) to terrestrial egg deposition in a nest chamber with nonfeeding, largely immobile larvae (e.g., *Adenomera marmorata*). Eggs are deposited in a foam nest produced from cloacal secretions in all *Physalaemus* and *Leptodactylus* (Figs. 4.9 and 4.10); within the *Leptodactylus*, nest location ranges from on the water surface to hidden in a soil chamber.

References Cei, 1980; Heyer, 1969; Heyer et al., 1990; Ryan, 1985.

Telmatobiinae

Sister taxon Uncertain, possibly hylodines.

Content Thirty-three genera, *Adelophryne*, *Alsodes*, *Atelognathus*, *Atopophrynus*, *Barycholos*, *Batrachophrynus*, *Batrachyla*, *Caudiverbera*, *Crossodactylodes*, *Cycloramphus*, *Dischidodactylus*, *Eleutherodactylus*, *Euparkella*, *Eupsophus*, *Geobatrachus*, *Holoaden*, *Hylorina*, *Insuetophrynus*, *Ischnocnema* (Fig. 17.18), *Lynchophrys*, *Macrogenioglottus*, *Odontophrynus*, *Phrynopus*, *Phyllonastes*, *Phyzelaphryne*, *Proceratophrys*, *Scythrophrys*, *Somuncuria*, *Telmalsodes*, *Telmatobius*, *Telmatobufo*, *Thoropa,* and *Zachaenus*, with nearly 700 species.

FIGURE 17.18 Representative leptodactylids. Clockwise from upper left: horned frog *Ceratophrys cornuta*, Ceratophryinae (photograph by J. P. Caldwell); Humboldt tree toad *Hylodes perplicatus*, Hylodinae (C. Haddad); Vanzolini's frog *Vanzolinius discodactylus*, Leptodactylinae (J. P. Caldwell); and common bighead frog *Ischnocnema quixensis*, Telmatobiinae (J. P. Caldwell).

Distribution Southwestern North America, Central and South America, and most islands of the West Indies.

Characteristics The sternum is cartilaginous. The presacral vertebrae lack a bony or cartilaginous shield; the transverse processes of the anterior presacral vertebrae are long and not expanded. The tips of the terminal phalanges are blunt, pointed, or T-shaped. Amplexus is axillary in most genera, but inguinal in a few, for example, *Batrachyla*.

Biology Telmatobiines are an extremely diverse group of frogs morphologically, behaviorally, and ecologically. Taxa span the entire spectrum from entirely aquatic (e.g., *Telmatobius culeus*) to strictly arboreal (e.g., *Eleutherodactylus orphnolaimus*). They occur in arid areas to rain forest, and from sea level to high montane forest and paramo. Some taxa (e.g., *Cycloramphus*) lay eggs in water and have free-living tadpoles; others (e.g., *Eleutherodactylus*) lay terrestrial eggs and have direct development. Viviparity has evolved within the *Eleutherodactylus* (*E. jasperi*), and this Puerto Rican species and another one (*E. coqui*) have internal fertilization. Presumably sperm transfer occurs via cloacal apposition.

References Cei, 1980; Duellman, 1975; Gallardo, 1987; Hutchison, 1982; Schwartz and Henderson, 1991; Townsend et al., 1981; Wake, 1993b.

Limnodynastidae

Australian ground frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain, possibly the clade containing Myobatrachidae and Sooglossidae.

Content Ten genera, *Adelotus*, *Heleioporus*, *Kyarranus*, *Lechriodus*, *Limnodynastes*, *Megistolotis*, *Mixophyes*, *Neobatrachus*, *Notaden*, and *Philoria*, with 40+ species.

Distribution *Limnodynastes* (Fig. 17.22) and *Lechriodus* occur in both Australia and New Guinea (Fig. 17.19); all other genera are strictly Australian, and *Kyarranus* and *Philoria* occur only in the montane forest of southeastern Australia.

Characteristics Limnodynastids range from small (*Kyarranus*, 22–35 mm adult SVL) to moderately large (*Mixophyes*, 60–100 mm adult SVL) frogs, whose habitus is mainly toad- and spadefootlike. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology Limnodynastids live in a variety of habitats from dry scrub and savannas to marshes, stream or lake shores, and the floor of the rain forest. All species are terrestrial, although individuals occasionally forage near the ground in the foliage of shrubs. The species living in the drier habitats use burrows to escape the heat and aridity of daytime and drought conditions. In the latter situation, the burrow is plugged and the frog estivates until rains arrive. In wet periods, the frogs emerge in the evening to feed. Reproduction is associated usually with heavy rains. Males attract females by vocalizing; *Heleioporus* and *Neobatrachus* lack vocal sacs, yet produce loud calls. Amplexus is inguinal in all except *Mixophyes* which has axillary amplexus. *Mixophyes*, *Neobatrachus*, and *Notaden* produce typical egg masses that are laid as clusters in leaf litter along streams in the former and as strings of eggs in the water in the latter two taxa. The remainder of the limnodynastids deposit eggs in foam nests that are produced by cloacal secretions from the male and female. The foam nests, depending upon the species, are deposited in burrows, on shorelines, or floating on the water.

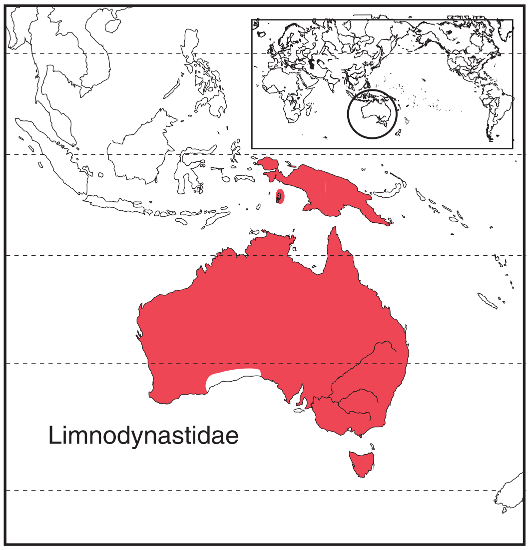


FIGURE 17.19 Geographic distribution of the extant Limnodynastidae.

References Barker et al., 1995; Heyer and Liem, 1976; Littlejohn et al., 1993; Tyler, 1985, 1989.

Myobatrachidae

Australian toadlets and turtlefrog

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Sooglossidae.

Content Twelve genera, *Arenophryne*, *Assa*, *Crinia*, *Geocrinia*, *Metacrinia*, *Myobatrachus*, *Paracrinia*, *Pseudophyrne*, *Rheobatrachus*, *Spicospina*, *Taudactylus*, and *Uperoleia*, with 65+ species.

Distribution Australia (Fig. 17.20).

Characteristics Myobatrachids consist predominantly of small frogs (13–36 mm adult SVL), with the exception of *Myobatrachus* (34–50 mm SVL) and the enigmatic *Rheobatrachus* (33–79 mm), of uncertain relationship. Among the small taxa, habitus is either typical frog or toadlike, in contrast to the obese, molelike *Myobatrachus*. The myobatrachid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare

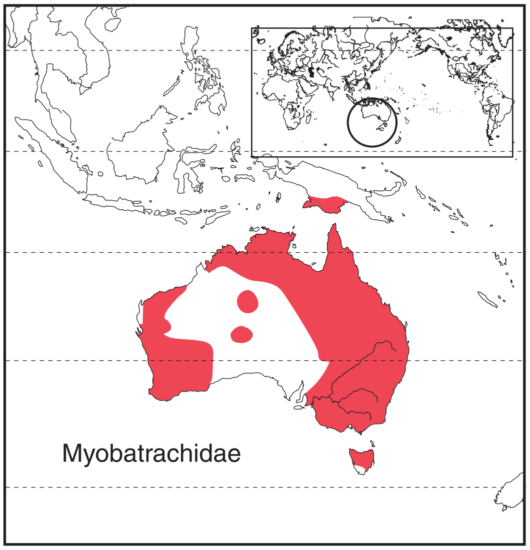


FIGURE 17.20 Geographic distribution of the extant Myobatrachidae.

and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are usually blunt. The larvae have keratinized tooth rows only, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology Like the limnodynastids, all myobatrachids are terrestrial frogs that occupy a diverse set of habitats from dry grassland, scrub, and savannas to marshes, stream or lake shores, and the floor of rain forests. *Uperoleia* is the most speciose taxon with ±25 species and occurs in grassland and dry forest habitats around the periphery of Australia, although individual species have small geographic ranges. Reproductive data are unknown for most species but presumably all deposit eggs in water and have indirect development. Presumably all myobatrachids have inguinal amplexus. *Crinia* is also speciose and broadly distributed but occurs mainly in moist habitats. Some of the unorthodox reproductive behaviors of Australian anurans occur among the myobatrachids. For example, *Arenophryne* and *Myobatrachus* burrow headfirst in sandy soils distant from water; both lay a few, large eggs, buried deep in the soil, which undergo direct development and metamorphose into burrowing froglets. *Assa* lays 10 to 11 eggs in terrestrial but boggy situations; the male attends the developing egg mass. When the larvae hatch, the male sits in the egg mass and the larvae wriggle onto him and into his inguinal tadpole pockets, emerging about 2 months later as froglets. Perhaps the strangest of all are the stomach- or gastric-brooding *Rheobatrachus*. After the eggs are fertilized, the female swallows the eggs or tadpoles (which stage remains unknown!). The eggs or embryos produce prostaglandin E_2, which blocks the production of stomach acids. The embryos develop in the female's stomach and froglets emerge from the female's mouth in about 2 months.

References Barker et al., 1995; Littlejohn et al., 1993; Roberts et al., 1997; Tyler, 1985, 1989.

Pseudidae

Paradox frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Hylidae.

Content Two genera, *Lysapsus* and *Pseudis*, with one and two species, respectively.

Distribution South America east of the Andes (Fig. 17.21).

Characteristics These frogs are small (18–40 mm adult SVL, *Lysapsus*) to moderate sized (40–60 mm, *Pseudis*) with a ranidlike habitus. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are pointed to claw-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody. Amplexus is axillary.

Biology Pseudid frogs (Fig. 17.22) are highly aquatic, and most live in permanent bodies of water, usually slow-moving portions of streams or in lakes, marshes, or large ponds. In the Chaco region where streams and lakes dry up, *Pseudis paradoxus* estivates in burrows in dry mud. *Pseudis* is paradoxical because they have giant tadpoles that metamorphose into strikingly smaller froglets. *P. paradoxa* has tadpoles to 220 mm total length and 98 g mass, yet the tadpoles metamorphose into froglets one-third or less than the length of the tadpole.

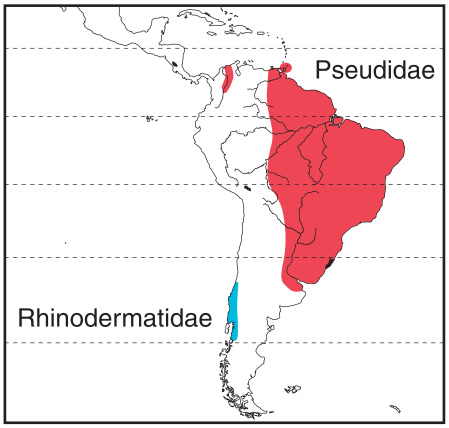


FIGURE 17.21 Geographic distributions of the extant Rhinodermatidae and Pseudidae.

References Cei, 1980; Emerson, 1988; Gallardo, 1987.

Rhinodermatidae

Mouth-brooding frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content One genus, *Rhinoderma*, with two species.

Distribution Southern South America (Fig. 17.21).

Characteristics Both species are moderately small (25–30 mm adult SVL). The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is arciferal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology The behavior of male *Rhinoderma* of retaining developing tadpoles in the vocal sacs is unique among anurans. During courtship, the male calls to attract a female. Amplexus is axillary. After the eggs are deposited, the male attends them for about 20 days. When the larvae are about to hatch and the egg mass is dissolving, the male gathers the hatchlings in his mouth. Male *Rhinoderma rufum* carry the larvae to water where they complete their development. In contrast, *Rhinoderma darwinii* males manipulate the larvae into the vocal sacs where the embryos undergo direct development and emerge as froglets about 50 days later. Both species are terrestrial residents of moist temperate forests of Chile and adjacent Argentina.

References Busse, 1970; Cei, 1980; Goicoechea et al., 1986.

Sooglossidae

Seychelles frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Myobatrachidae.

Content Two genera, *Nesomantis* and *Sooglossus*, with one and two species, respectively.

Distribution Granitic islands of the Seychelles (Fig. 17.23).

Characteristics Sooglossids range from tiny (9–18 mm adult SVL, *Sooglossus*) to moderate-sized (32–48 mm, *Nesomantis thomasseti*) terrestrial frogs. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is pseudoarciferal–firmisternal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology Sooglossids are inhabitants of moist forests and are nocturnal. *Sooglossus gardineri* and *Sooglossus sechellensis* live principally in the forest-floor litter,

FIGURE 17.22 Representative bufonoid anurans. Clockwise from upper left: Spencer's burrowing frog *Limnodynastes spenceri*, Limnodynastidae (photograph by P. Ryan); common eastern froglet *Crinia signifera*, Myobatrachidae (S. Wilson); Mjoberg toadlet *Uperoleia mjobergii*, Myobatrachidae (M. J. Tyler); paradox frog *Pseudis paradoxa*, Pseudidae (L. J. Vitt); dwarf paradox frog *Lysapsus limellus,* Pseudidae (J. P. Caldwell); and Darwin's mouthbreeder *Rhinoderma darwinii*, Rhinodermatidae (W. E. Duellman, courtesy of the Natural History Museum, The University of Kansas).

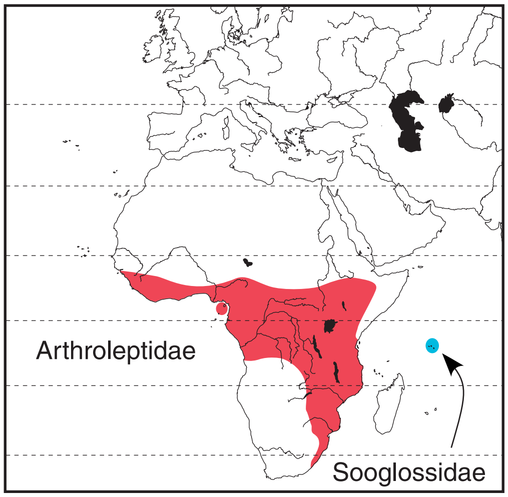


FIGURE 17.23 Geographic distributions of the extant Arthroleptidae and Sooglossidae.

although they occasionally hide in axils of tree ferns. *N. thomasseti* (Fig. 17.24) is also a forest-floor resident and commonly is found along streams and in rivulets. Males call individually, not in choruses, but both females and males lack tympana. Amplexus is inguinal and egg deposition is terrestrial. *S. gardineri* females deposit eggs beneath leaves and stay with them for 3 to 4 weeks until they hatch into tiny froglets. *S. sechellensis* also deposits eggs beneath forest-floor debris and attends them for 2 to 3 weeks; the eggs hatch into nonfeeding tadpoles that wriggle onto the female's back, where they remain until metamorphosis. The reproductive behavior of *N. thomasseti* is unknown, although large eggs in gravid females suggest direct development.

References Dodd, 1982; Mitchell and Altig, 1983; Nussbaum, 1980, 1985b; Nussbaum et al., 1982.

FIGURE 17.24 Representative ranoid anurans. Clockwise from upper left: Seychelles rock frog *Nesomantis thomasseti*, Sooglossidae (photograph by G. R. Zug); shovel-foot squeaker *Arthroleptis stenodactylus*, Arthroleptidae (L. W. Porras); undescribed *Colostethus*, Dendrobatidae (J. P. Caldwell); and white-bellied poison frog *Dendrobates ventrimaculatus*, Dendrobatidae (J. P. Caldwell).

“ranoids”

“Arthroleptidae”

Squeakers and cricket frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain, possibly “Ranidae.”

Content Two subfamilies, Arthroleptinae and Astylosterninae.

Distribution Sub-Saharan Africa (Fig. 17.23).

Characteristics Arthroleptids are mostly small frogs with pointed snouts and long limbs. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous except for a biconcave surface on the last presacral. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are blunt, pointed, or T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

References Branch, 1991; Dubois, 1981; Laurent, 1986; Passmore and Carruthers, 1995; Poynton and Broadley, 1985.

Arthroleptinae

Sister taxon Presumably Astylosterninae.

Content Three genera, *Arthroleptis*, *Cardioglossa,* and *Coracodichus*, with 50+ species.

Distribution Sub-Saharan Africa.

Characteristics Arthroleptines have horizontal pupils, the vomerine is edentate, and the terminal phalanges are T-shaped.

Biology Arthroleptines are predominantly small ranidlike frogs (12–42 mm adult SLV; most species <36 mm). They are terrestrial, occurring in a variety of habitats from grassland to open forest, usually away from standing water. They typically breed after heavy summer rains. Males with high-pitched, insectlike squeaks form large, diffuse choruses. Amplexus is axillary, and small clutches (10–30) of large yolky eggs are laid in leaf litter of the forest floor. About 4 weeks after deposition, tiny froglets hatch. Only *Cardioglossa* has indirect development.

References Lambiris, 1989; Perret, 1966; Poyton and Broadley, 1985; Stewart, 1967; Wager, 1986.

Astylosterninae

Sister taxon Presumably Arthroleptinae.

Distribution West and west-central Africa.

Content Five genera, *Astylosternus*, *Leptodactylodon*, *Nyctibates*, *Scotobleps,* and *Trichobatrachus*, with 25+ species.

Characteristics Astylosternines have vertical pupils (except *Leptodactylodon*), the vomerine bears teeth, and the terminal phalanges are pointed and usually somewhat hooked.

Biology Astylosternines range from the small *Leptodactylodon albiventris* (20–21 mm adult SVL) to the large *Trichobatrachus robustus* (80–130 mm SVL). All astylosternines are closely associated with running water, either living in the water or immediately adjacent to it. *T. robustus*, the hairy frog, is the most aquatic species. The “hair” is formed from dense patches of microvilli located on the sides in adult males. The microvilli are heavily vascularized and likely associated with cutaneous respiration. All astylosternines have indirect development.

References Noble, 1925; Perret, 1966.

Dendrobatidae

Poison frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain, although classified here as a ranoid with possible affinities to Arthroleptidae; molecular evidence supports a bufonoid placement (see Ruvinsky and Maxson, 1996).

Content Ten genera, *Allobates*, *Aromobates*, *Colostethus*, *Dendrobates*, *Epipedobates*, *Mannophryne*, *Minyobates, Nephelobates*, *Phobobates,* and *Phyllobates*, with 180+ species.

Distribution Southern Central America and northern South America through the Amazonian Basin to Atlantic forest (Fig. 17.25). *Colostethus* and *Dendrobates* are widely distributed and speciose, while other taxa are more restricted; for example, *Aromobates* occurs only in a cloud forest in Venezuela.

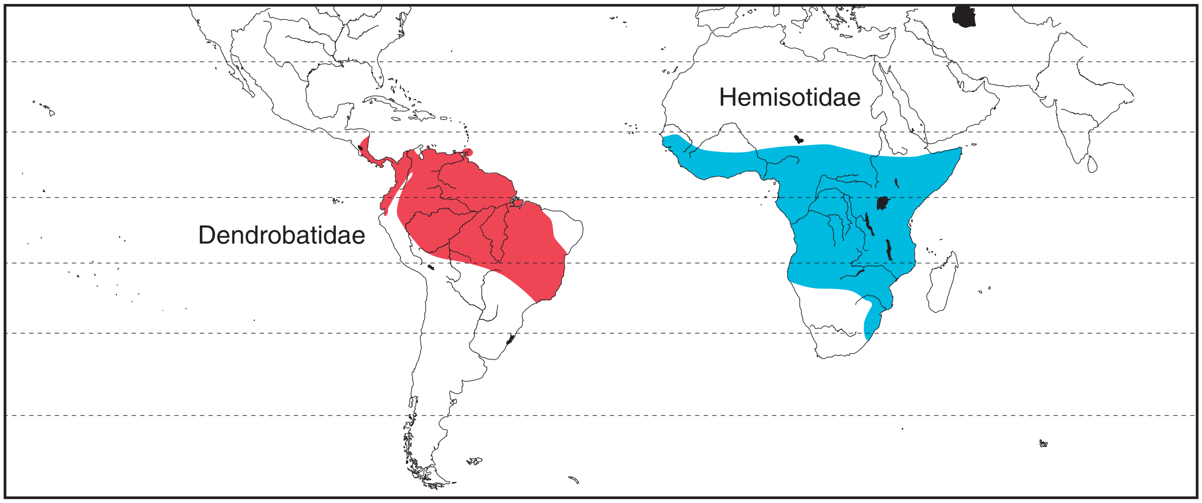


FIGURE 17.25 Geographic distributions of the extant Dendrobatidae and Hemisotidae.

Characteristics Dendrobatids are generally small to medium-sized frogs (12–19 mm adult SVL, *Minyobates*; 53–62 mm, female *Aromobates*), and all possess supradigital scutes. The dendrobatid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule, and the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses six to eight presacral holochordal vertebrae, and all are procoelous. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits, and the tips of the terminal phalanges are usually T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology Dendrobatids are diurnal frogs and may occur in riparian, terrestrial, or semiarboreal microhabitats in tropical forests. The monotypic *A. nocturnus*, thought to be the sister species of all other dendrobatids, is the only exception; it is nocturnal and usually found swimming or sitting in water. It has a unique volatile chemical defense, but its skin secretion lacks alkaloids. In other dendrobatids, toxic lipophilic alkaloids are produced in the granular glands and transferred to the predator by contact. In general, the brighter or more boldly colored dendrobatids are most toxic; several hundred alkaloids have been identified from their skin. *Colostethus* (Fig. 17.24) is generally nonpoisonous, and *Phyllobates* produces batrachotoxin, one of the most toxic alkaloids produced by any animal. At least in some taxa, alkaloid precursors may be derived from the frogs' diet of ants; the most poisonous taxa are ant specialists. Presumably all dendrobatids have parental care, and most often the male parent, but occasionally the female, attends the eggs. Males attract females by calling, although they do not form choruses. Amplexus is cephalic or absent, and eggs are laid among leaf litter on the forest floor, along streams, or in arboreal retreats. One parent attends the eggs until they hatch; the tadpoles then wriggle upward onto the back of the parent, who transports them to a nearby pool, tree hole, or bromeliad tank, where they complete development. One clade of *Dendrobates* has biparental care: the pair-bonded male and female return periodically to feed trophic eggs to their tadpoles. In another clade, only the female cares for the tadpoles by depositing eggs for them.

References Caldwell, 1996a,b; Caldwell and Oliveira, 1999; Ford, 1993; Grant et al., 1997; Myers and Daly, 1983; Myers et al., 1991.

Hemisotidae

Shovel-nosed frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content One genus, *Hemisus*, with nine species.

Distribution Tropical and subtropical sub-Saharan Africa (Fig. 17.25).

Characteristics Hemisotids are small to moderate-sized frogs (22–52 mm adult SVL, except *Hemisus guttatum*, which grows to 75 mm) with stout bodies and small, pointed heads. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae (first and second presacrals fused), and all are procoelous except for the biconcave surface of the last presacral. The transverse processes of the sacral vertebra are moderately expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are blunt to pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Biology *Hemisus* species are burrowers, burrowing head first. They use the pointed and hardened snout as a ramming-rod, moving the head up and down, throwing the soil to the rear with the forelimbs, and pushing forward with the hindlimbs. They are largely savanna inhabitants, although they also live in scrub and gallery forests. They appear to feed both beneath and on the surface, mainly on soft-bodied arthropods and worms. Reproduction begins with the earliest heavy rains of the wet season, or even before the rains arrive. The male calls from the ground; subsequently, a pair remains in inguinal amplexus while the female digs an incubation chamber near, but not in, an ephemeral pool. About 100 to 250 eggs in *Hemisus marmoratum* and about 2000 in *Hemisus guttatum* are fertilized in the chamber. The male burrows out of the chamber, and the female remains with the eggs. When the eggs hatch, the female carries or guides her tadpoles to the nearby pool, digging an escape tunnel or a surface channel. The tadpoles are free-living and metamorphose in approximately 3 to 4 weeks.

References Channing, 1995; Emerson, 1975; Kaminsky et al., 1999; Laurent, 1986; Rödel, 1996; Rödel et al., 1995; Wager, 1986.

Hyperoliidae

Reed and sedge frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain; Rhacophoridae is commonly proposed, but the data are inconclusive.

Content Four subfamilies, Hyperoliinae, Kassininae, Leptopelinae, and Tachycneminae.

Distribution Sub-Saharan Africa, Madagascar, and the Seychelles (Fig. 17.26).

Characteristics Most hyperoliids have a treefrog habitus with expanded toe pads. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous except for a biconcave surface on the last presacral (procoelous in *Acanthixalus* and *Callixalus*). The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum. Fibulare and tibiale are fused at their proximal and distal ends. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit; the tips of the terminal phalanges are blunt to pointed or T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

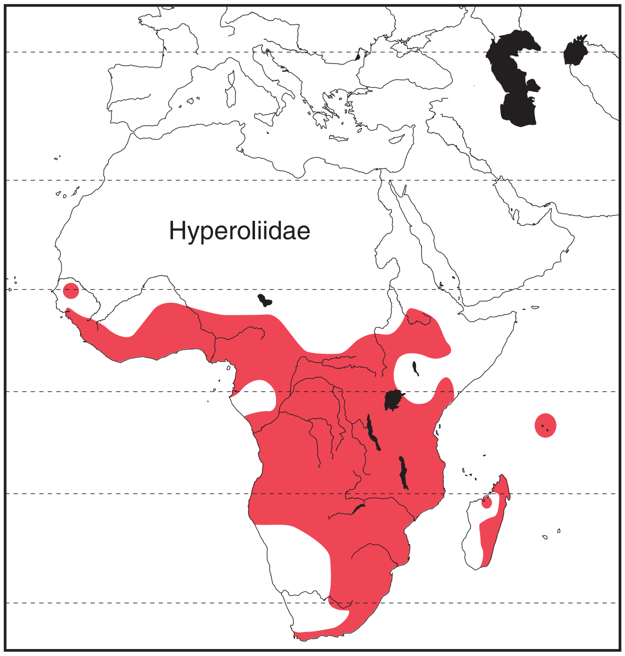


FIGURE 17.26 Geographic distribution of the extant Hyperoliidae.

References Channing, 1989; Drewes, 1984; Herrmann, 1993; Laurent, 1986; Liem, 1970; Passmore and Carruthers, 1995; Poyton and Broadley, 1987.

Hyperoliinae

Sister taxon Kassininae.

Content Eleven genera, *Acanthixalus*, *Afrixalus*, *Alexteroon*, *Arequinus*, *Callixalus*, *Chrysobatrachus*, *Cryptothylax*, *Heterixalus*, *Hyperolius*, *Kassinula,* and *Nesionixalus*, with 160+ species.

Distribution Sub-Saharan Africa and Madagascar.

Characteristics The vocal pouch and associated gular gland are present. The forearm gland is well developed, but the digital glands are absent. The aponeurosis of the palmar muscular is thin and fused to adjacent musculature.

Biology Hyperoliines have a treefrog habitus and range in size from small (17–22 mm adult SVL, e.g., *Afrixalus brachycnemis*, *Hyperolius pusillus*) to moderate (25–43 mm, e.g., *Hyperolius puncticulatus*). They occur in grasslands and marshes to full-canopied forest. Most are arboreal, whether living in grass and reeds or in shrubs and trees. Males call from a variety of sites, usually in choruses. Amplexus is axillary, and eggs are laid in or over water and invariably attached to the vegetation. Development is indirect (except in *Hyperolius obstetricans*); if the eggs are laid away from water, the tadpole must reach water upon hatching.

References Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994; Perret, 1966; Rödel, 1996; Schiotz, 1967, 1975; Stewart, 1967.

Kassininae

Sister taxon Hyperoliinae.

Content Five genera, *Kassina*, *Opisthothylax*, *Paracassina*, *Phlyctimantis,* and *Semnodactylus*, with 18+ species.

Distribution Sub-Saharan Africa.

Characteristics The vocal pouch and associated gular gland are present. The forearm gland and digital glands are well developed. The aponeurosis of the palmar musculature, if present, is thin and fused to adjacent musculature.

Biology The kassinines, or running frogs, are widespread but generally not in full-canopied forest. They are mainly savanna to open-woodland species, and although they have an elongate treefrog-like habitus, many are terrestrial or arboreal in low vegetation. These moderately small frogs (most 30–45 mm adult SVL) rarely hop or jump but instead walk or run. Males commonly call in choruses in or near water. Amplexus is axillary, and the eggs are deposited in water, commonly attached to vegetation, and usually scattered in small groups rather than deposited as single egg masses. Development is indirect.

References Perret, 1966; Rödel, 1996; Schiotz, 1967, 1975; Stewart, 1967; Wager, 1986.

Leptopelinae

Sister taxon The clade containing all other subfamilies of Hyperoliidae.

Content One genus, *Leptopelis*, with 50+ species.

Distribution Sub-Saharan Africa.

Characteristics The vocal pouch and associated gular gland are absent. The forearm gland is well developed, but digital glands are absent. The aponeurosis of the palmar musculature is well developed and mobile.

Biology *Leptopelis* consists mainly of arboreal forest species with the greatest diversity in equatorial Africa; however, in more arid areas, the species are terrestrial to subfossorial and climb into the trees only for breeding (e.g., *Leptopelis bocagii*, Zimbabwe). Most species are medium-sized and range from 26 to 42 mm adult SVL, but *Leptopelis palmatus* reaches 87 mm (45–87 mm SVL). Many species use a gaping defense display in which the mouth is opened fully, the eyes are half-closed, and the body may be arched. Breeding is associated with heavy rains, usually at the beginning of the wet season. Males call solitarily. Amplexus is axillary, and eggs are deposited in various situations from ephemeral pools or backwaters of streams to holes in the ground. Parental care has not been reported for any species, and development is indirect with a tadpole stage, except perhaps in *Leptopelis brevirostris,* in which the female has been reported to carry large eggs in her mouth.

References Lambiris, 1989; Perret, 1966; Schiotz, 1967, 1975; Wager, 1986.

Tachycneminae

Sister taxon The clade containing Hyperoliinae and the Kassininae.

Content Monotypic, *Tachycnemis seychellensis.*

Distribution Granitic islands of the Seychelles.

Characteristics The vocal pouch and associated gular gland are absent. The forearm gland and digital glands are absent. The aponeurosis of the palmar musculature is well developed and mobile.

Biology *T. seychellensis* (Fig. 17.27) is a moderate-sized treefrog (33–77 mm adult SVL) that lives in forests. Breeding appears to occur irregularly throughout the year. Males call in small choruses from low vegetation adjacent to ephemeral pools or forest streams. Eggs are usually deposited on vegetation overhanging the water, and the hatching tadpoles fall into the water. The duration of the tadpole phase is unknown.

References Nussbaum, 1984; Nussbaum and Wu, 1995.

Microhylidae

Narrowmouth frogs and toads

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain, possibly clade containing all other ranoids.

Content Ten subfamilies, Asterophryinae, Brevicipinae, Cophylinae, Dyscophinae, Genyophryninae, Melanobatrachinae, Microhylinae, Otophryninae, Phrynomerinae, and Scaphiophryinae.

Distribution Worldwide on all continents, except Antarctica (Fig. 17.28).

Characteristics Microhylids have a broad range of body forms from a pointed-head, fossorial habitus to a treefrog habitus. Body size is equally broad and ranges from the tiniest of frogs, *Syncope* and *Stumpffia* (9–13 mm adult SVL), to large *Glyphoglossus molossus* females (78–88 mm SVL). The microhylid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight, rarely seven, presacral holochordal vertebrae, and the vertebrae are all procoelous except for a biconcave surface on the last presacral (i.e., diplasiocoelous). The transverse processes of the sacral vertebra are cylindrical to broadly expanded, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum, although many microhylids show a reduction of the clavicle and procoracoid. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges, except in the phrynomerines; the tips of the terminal phalanges are blunt, pointed, or T-shaped. The larvae lack keratinized mouth parts (except *Otophryne*), and a large spiracular chamber is emptied by a caudomedial spiracle.

References Laurent, 1986; Parker, 1934.

Asterophryinae

Sister taxon Uncertain, possibly Genyophryninae.

Content Eight genera, *Asterophrys*, *Bargenys*, *Callulops*, *Hylophorbus*, *Mantophryne, Pherohapsis*, *Xenobatrachus,* and *Xenorhina*, with 40+ species.

Distribution New Guinea, its adjacent islands, and the Molucca Islands.

Characteristics The skull has paired ethmoids, a single large prevomer, and toothless maxillaries. The vertebral column is procoelous, and the pectoral girdle lacks clavicles and procoracoids.

Biology Asterophryines are terrestrial species that live in (e.g., fossorial *Bargenys*, *Xenobatrachus*) or on (e.g., *Asterophrys*, *Callulops*, *Xenorhina*) the forest floor, and some species occur in grasslands and disturbed habitats. Asterophryines range from small (20–24 mm adult SVL, *Hylophorbus rufescens*) to moderately large (60–80 mm SVL, *Callulops stictigaster*). Reproductive data are absent for most species, but where known, all species lay small clutches of large, well-yolked eggs in protected sites (forest floor or in trees), and a male is usually in attendance, hinting at direct development.

Comments All species formerly in New Guinean *Phrynomantis* are now *Callulops* (Duellman, 1993).

References Burton, 1986; Menzies, 1976; Zweifel, 1972.

Brevicipinae

Sister taxon Uncertain.

Content Five genera, *Balebreviceps*, *Breviceps*, *Callulina*, *Probreviceps,* and *Speleophryne*, with 20+ species.

Distribution Southern and eastern Africa.

Characteristics The skull has no ethmoids, a single, anteriorly narrowed prevomer, and toothless maxillaries. The vertebral column is diplasiocoelous, and the pectoral girdle has well-developed clavicles and procoracoids. In addition, the middle ear is absent, and the urostyle and sacral vertebra may be fused.

FIGURE 17.27 Representative hyperoliids. Clockwise from upper left: long reed frog, *Hyperolius nasutus*, Hyperoliinae (photograph by R. D. Bartlett); bubbling running frog *Kassina senegalensis*, Kassininae (R. D. Bartlett); forest treefrog *Leptopelis natalensis*, Leptopelinae (R. D. Bartlett); and Seychelles reed frog *Tachycnemis seychellensis*, Tachycneminae (G. R. Zug).

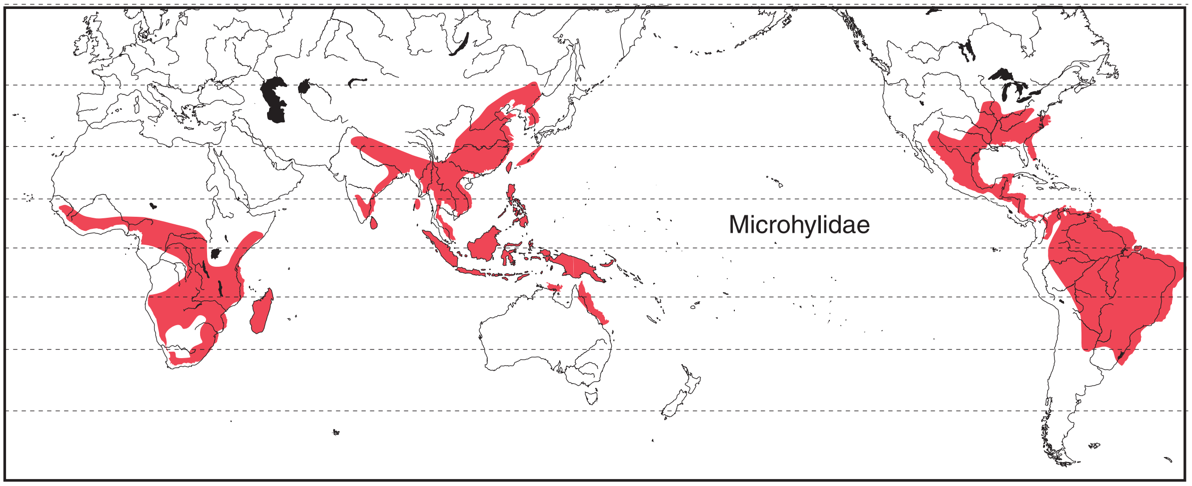


FIGURE 17.28 Geographic distribution of the extant Microhylidae.

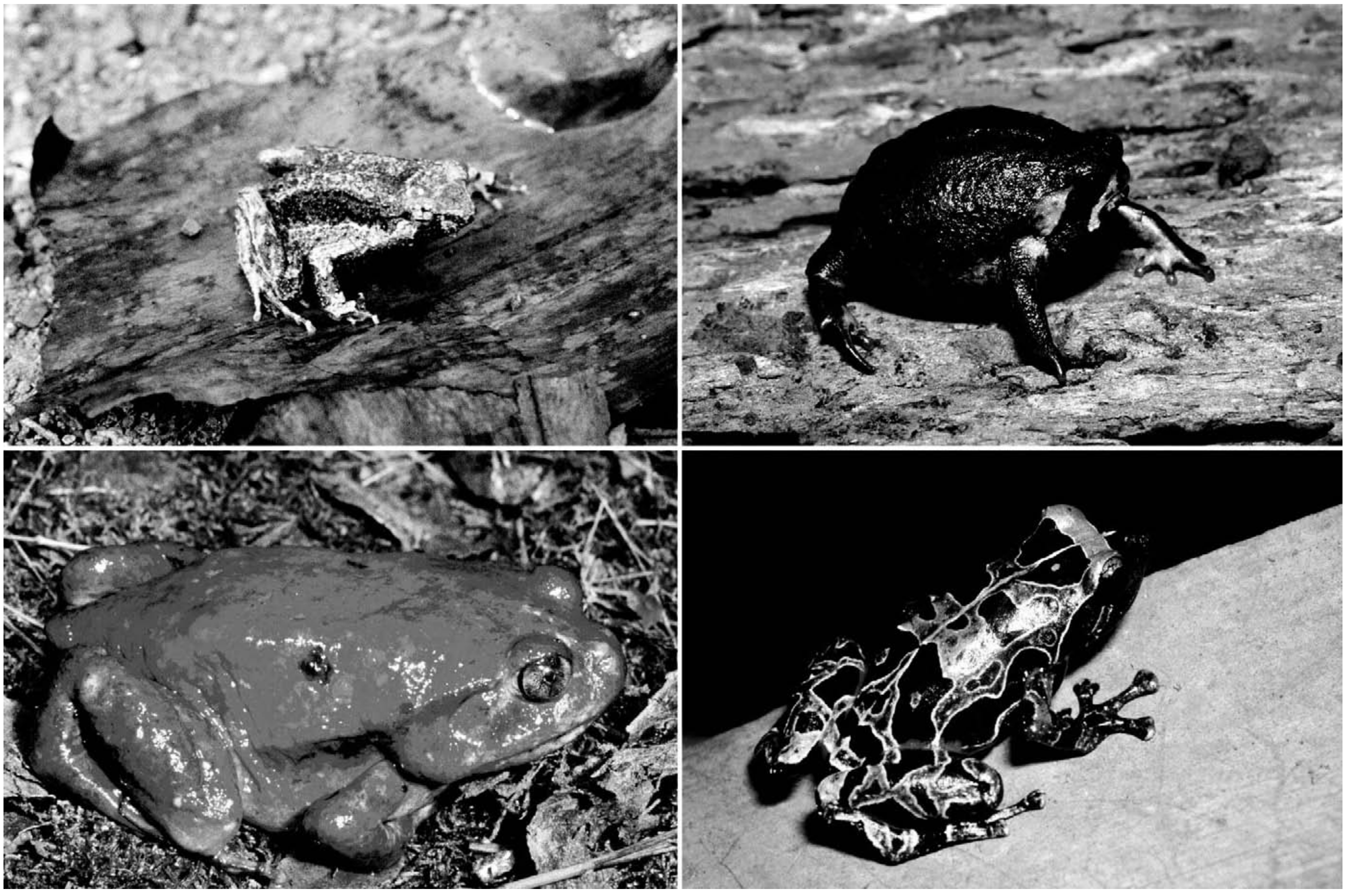


FIGURE 17.29 Representative microhylids. Clockwise from upper left: swamp toadlet *Asterophrys turpicola*, Asterophryinae (photograph by G. R. Zug); Transvaal forest rain frog *Breviceps sylvestris*, Brevicepinae (R. D. Bartlett); Millot's narrowmouth treefrog *Platypelis milloti*, Cophylinae (C. Raxworthy); and Antongil narrowmouth toad *Dyscophus antongilii*, Dyscophinae (M. Kearney).

Biology The rain frogs, *Breviceps*, and their relatives are nearly spherical in shape with the head barely distinguishable from the body; limbs are short and robust. Their globular appearance is further enhanced by a tendency to inflate the body when disturbed. These small to moderate-sized frogs (most 30–50 mm adult SVL) are backward burrowers and are found from forest to near-desert habitats. As is common in many of the robust microhylids, males are distinctly smaller than females; this size disparity and their short limbs prevent a typical amplexus. The problem is resolved by skin secretions that glue the male to the female's back for the duration of egg deposition. Small clutches of eggs are laid in subterranean nests and development is direct; the female remains with the eggs until they hatch, usually in 4 to 5 weeks.

References Channing, 1995; Lambiris, 1989; Passmore and Carruthers, 1995; Poynton and Broadley, 1985; Stewart, 1967; Wager, 1986.

Cophylinae

Sister taxon Uncertain.

Content Seven genera, *Anodonthyla, Cophyla*, *Madecassophryne*, *Platypelis*, *Plethodontohyla, Rhombophryne,* and *Stumpffia*, with 40+ species.

Distribution Madagascar.

Characteristics The skull has paired ethmoids, paired prevomers, and usually teeth on the maxillaries. The vertebral column is procoelous, and the pectoral girdle usually has well-developed clavicles and procoracoids.

Biology The cophylines consist of two clades with contrasting habits and reproductive behavior. *Anodonthyla*, *Cophyla*, and *Platypelis* are arboreal species; *Anodonthyla* occurs mainly on tree trunks or rocks, whereas the other two genera live on the branches and leaves of trees. All three taxa deposit small clutches of less than 100 eggs in tree holes or leaf axils (*Cophyla, Platypelis*) or in rock cavities (*Anodonthyla*). The eggs hatch into nonfeeding tadpoles that are attended by the male until metamorphosis. These three genera are mainly small to medium-sized frogs (16–40 mm SVL, but *Platypelis grandis* reaches 43–105 mm). The other genera include tiny (*Stumpffia pygmae* and *Stumpffia tridactyla*, 10–12 mm adult) to large (*Plethodontohyla inguinalis*, 55–100 mm) frogs with nearly exclusively terrestrial habits. These taxa typically lay eggs on the forest floor, either in cavities or in foam nests in the leaf litter. Their tadpoles are also nonfeeding and often have one parent in attendance.

References Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994; Köhler et al., 1997.

Dyscophinae

Sister taxon Uncertain.

Content Two genera, *Calluella* and *Dyscophus*, with six and three species, respectively.

Distribution Madagascar and western Southeast Asia.

Characteristics The skull has paired ethmoids, a single large prevomer, and teeth on the maxillaries. The vertebral column is diplasiocoelous. In the pectoral girdle, the clavicles and procoracoids range from well developed to vestigial.

Biology *Dyscophus* are moderate to large frogs (40–105 mm adult SVL) that inhabit the forest floors of Madagascar. They usually breed in ephemeral pools or slow-moving backwaters of streams and swamps. Eggs (1000+) are deposited on the water surface; they hatch within 36 hours, and the tadpoles grow moderately rapidly and metamorphose in 40 to 45 days. The Asian *Calluella* are moderate-sized forest frogs (30–60 mm adult SVL). They are rarely observed because of their strong fossorial habitats. All species are assumed to have indirect development like the widespread *Calluella guttulata*.

References Berry, 1975; Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994; Inger and Stuebing, 1997; Manthey and Grossman, 1997.

Genyophryninae

Sister taxon Uncertain, possibly Asterophryinae.

Content Seven genera, *Aphantophryne*, *Choerophryne*, *Cophixalus*, *Copiula*, *Genyophryne*, *Oreophryne,* and *Sphenophryne*, with 80+ species.

Distribution Southern Philippines, Sulawesi, and Lesser Sunda Islands eastward through New Guinea and northeastern Australia.

Characteristics The skull has paired ethmoids, a single large prevomer, and usually toothless maxillaries. The vertebral column is procoelous with seven or eight presacral vertebrae. In the pectoral girdle, the clavicles and procoracoids range from well developed to vestigial. The terminal phalanges are usually T-shaped.

Biology Most genophrynines are treefrog-like and have variously expanded digit tips. Many are arboreal, and others live among the boulders and cliffs of mountain streams. Some arboreal species hide in the forest-floor litter during the day and at night ascend into shrubs and lower tree branches to feed and reproduce. Other arboreal species rarely descend to the ground, sheltering during the day in epiphytes and holes and crevices in trees. Genophrynines are small, ranging from the tiny *Cophixalus variegatus* group (<14 mm adult SVL; Fig. 17.30) to other moderate-sized species of *Cophixalus* and *Sphenophryne* (50 mm SVL, but usually less than 35 mm). Reproductive data are absent for most species, but where known, females lay small clutches of large, well-yolked eggs in protected sites (forest floor or in trees), and males typically attend the eggs. Direct development has been observed in one species of *Oreophryne.*

References Burton and Zweifel, 1995; Menzies, 1976; Zweifel, 1985; Johnston and Richards, 1993.

Melanobatrachinae

Sister taxon Uncertain.

Content Three genera, *Hoplophryne*, *Melanobatrachus,* and *Parhoplophryne*, with four species.

Distribution Tanzania and southwestern India.

Characteristics The skull has a fused ethmoid and parasphenoid, the single prevomer is reduced anteriorly, and the maxillaries lack teeth. The vertebral column is procoelous, and the pectoral girdle has clavicles and procoracoids ranging from well developed to absent.

Biology The three African species are small (20–30 mm adult SVL) and toadlike. They are montane forest inhabitants and appear to be arboreal; they deposit eggs in holes in the stems of bamboo or axils of bananas. The tadpoles are free living, and there is no evidence of parental care. The single Indian species, *Melanobatrachus indicus*, is a small frog (24–28 mm SVL) that lives along permanent forest streams of the Western Ghats. Little is known of its biology.

FIGURE 17.30 Representative microhylids. Clockwise from upper left: pygmy narrowmouth treefrog *Cophixalus variegatus*, Genyophryninae (photograph by J. W. Lang); Amazon narrowmouth toad *Chiasmocleis* sp., Microhylinae (J. P. Caldwell); banded rubber frog *Phrynomantis bifasciatus,* Phrynomerinae (R. G. Tuck, Jr.); and spiny forest narrowmouth toad *Scaphiophryne marmorata,* Scaphiophryninae (R. D. Bartlett).

References Daltry and Martin, 1997; Laurent, 1986; Parker, 1934.

Microhylinae

Sister taxon Uncertain and likely paraphyletic.

Content Twenty-eight genera, *Adelastes*, *Arcovomer*, *Chaperina*, *Chiasmocleis* (Fig. 17.30), *Ctenophryne*, *Dasypops*, *Dermatonotus*, *Elachistocleis*, *Gastrophryne*, *Gastrophrynoides*, *Glyphoglossus*, *Hamptophryne*, *Hyophryne*, *Hypopachus*, *Kalophrynus*, *Kaloula*, *Metaphrynella*, *Microhyla*, *Micryletta*, *Myersiella*, *Nelsonophryne*, *Phrynella*, *Ramanella*, *Relictivomer*, *Stereocyclops, Synapturanus, Syncope,* and *Uperodon*, with 100+ species.

Distribution Americas and southern Asia southward through the East Indies to the Philippines.

Characteristics The skull usually has paired ethmoids, a single, generally small prevomer, and usually toothless maxillaries. The vertebral column is diplasiocoelous in most taxa, and occasionally procoelous. In the pectoral girdle, the clavicles and procoracoids range from well developed to vestigial.

Biology Microhylines are predominantly terrestrial, stout-bodied, microcephalic frogs. Most taxa are fossorial to semifossorial; they occupy a variety of habitats, from semiarid grasslands to scrub to rain forest. The South American *Syncope* is tiny (9–13 mm adult SVL) and has structural reduction, apparently because of the dwarfing. The widespread Asian *Kaloula* (±10 species) has an elongate body, long limbs, and expanded toe-tips; the species are active surface foragers, and even arboreal and scansorial in a few. Most microhylines have indirect development (American *Gastrophyrne* and *Hypopachus*, Asian *Microhyla*) whereas a few have direct development (American *Myersiella*). *Syncope antenori* has free-living but nonfeeding tadpoles; nutrition is derived solely from yolk.

References Donnelly et al., 1990; Dutta and Manamendra-Archchi, 1996; Inger and Stuebing, 1997; Manthey and Grossman, 1997; Wild, 1995; Zweifel, 1986; Krügel and Richter, 1995.

"Otophryninae"

Sister taxon A member of the New World microhylines (Wild, 1995); recognition of the Otophryninae makes Microhylinae paraphyletic.

Content One genus, *Otophryne*, with two species.

Distribution Northern South America.

Characteristics The skull has paired ethmoids, a pair of prevomers, and toothless maxillaries. The vertebral column is diplasiocoelous. In the pectoral girdle, the clavicles and procoracoids are well developed.

Biology *Otophryne robusta,* the pe-ret' toad, is a moderate-sized (44–60 mm adult SVL), forest-floor frog. This diurnally active frog is a leaf mimic with a dorsal pattern that shows the pinnation of dry leaves and ranges in color from yellow to shades of dusky red and brown. It walks, rather than hops, among the leaf litter. Breeding occurs adjacent to forest streams and the eggs are laid on land beneath wet leaves (perhaps in the water also, but that is not confirmed). The tadpoles have tiny needlelike, keratinized denticles and a long spiracular tube, apparently adaptations for their aquatic–fossorial habit of burrowing and feeding in the sand, either on streambanks or in the stream bottom. The length of the tadpole phase is thought to be less than 1 year.

References Parker, 1934; Wassersug and Pyburn, 1987; Wild, 1995.

Phrynomerinae

Sister taxon Uncertain.

Content One genus, *Phrynomantis*, with five species.

Distribution Sub-Saharan Africa.

Characteristics The skull has paired ethmoids, a single, anteriorly reduced prevomer, and toothless maxillaries. The vertebral column is diplasiocoelous. In the pectoral girdle, the clavicles and procoracoids are absent. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit.

Biology *Phrynomantis* (Fig. 17.30) looks like an elongated heavy-bodied *Dendrobates* with a similar skin texture and aposematic coloration. Skin secretions are toxic, at least in *Phrynomantis bifasciatus.* Like *Dendrobates*, all species are diurnal and terrestrial and have a diet composed of ants. *Phrynomantis* contains mostly moderate-sized frogs (30–45 mm adult SVL), although in some populations, *P. bifasciatus* reaches 80 mm. They walk or run, seldom hopping, and often climb in the lower branches of shrubs. Because they are mainly savanna inhabitants, they are seldom seen except in the wet season when they reproduce in ephemeral ponds. The eggs are laid in small masses (100–1400) at the surface of the water, attached to vegetation or floating. The eggs hatch quickly; the tadpoles are filter-feeders and remain suspended motionless, except for tiny vibrations of the tail, in the middle of the water column. Development is fairly rapid with metamorphosis occurring in 30–40 days.

Comments *Phrynomantis* is a presumed senior synonym, and hence replaces *Phrynomerus* (Duellman, 1993).

References Lambiris, 1989; Passmore and Carruthers, 1995; Poynton and Broadley, 1985; Rödel, 1996; Stewart, 1967.

"Scaphiophryninae"

Sister taxon Clade containing all other microhylids.

Content Two genera, *Paradoxophyla* and *Scaphiophryne*, with one and six species, respectively.

Distribution Madagascar.

Characteristics The skull has a single large ethmoid, a single large prevomer, and toothless maxillaries. The vertebral column is diplasiocoelous. In the pectoral girdle, the clavicles and procoracoids are well developed.

Biology Scaphiophryines are small to moderate-sized frogs (20–50 mm adult SVL). They are predominantly terrestrial, occurring either in moist forest or in grassland and scrublands. In the latter environments, they are burrowers and emerge for feeding and reproduction with the onset of the wet season. They usually breed explosively in ephemeral pools. Modest clutches of eggs (<1000) float on the surface of the water and hatch into free-living tadpoles. These forest dwellers feed nocturnally in the forest litter and have similar reproductive habits.

References Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994.

"Ranidae"

True frogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain; present taxa content likely makes Ranidae paraphyletic.

Content Seven subfamilies, Dicroglossinae, Petropedetinae, Ptychadeninae, Pyxicephalinae, Raninae, Ranixalinae, and Tomopterninae, but see Comments below.

Distribution Worldwide on all continents, except Antarctica, and largely limited in Australia and South America (Fig. 17.31).

Characteristics This diverse taxon ranges in size from the small petropedetines (15–30 mm adult SVL) to the world's largest frog, *Conraua goliath* (to 300 mm). The ranid skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous except for a biconcave surface on the last presacral. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal, rarely pseudoarciferal, with a distinct sternum. The fibulare and tibiale are fused at their proximal and distal ends. No intercalary cartilage occurs between the terminal and penultimate phalanges of the digits; the terminal phalanges are blunt, pointed, or T-shaped. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

Comments The taxonomy and classification of this account follow Duellman's checklist (1993), which in turn accepted the classification proposed in a series of articles by Dubois. Problems have been identified for Dubois's ranid classification (e.g., Inger, 1996; Emerson and Berrigan, 1993). One problem is apparent in the following subfamilial characterizations, that is, the incomplete and noncomparative characterizations of the subfamilies. Additionally, Dubois partitioned the genus *Rana* into many subgenera that subsequently were elevated to generic status without phylogenetic analysis. Dubois's genera are listed in this account, but the more conservative use of *Rana* presented in Frost (1985) is adopted elsewhere in this textbook.

References Blommers-Schlösser, 1993; Clarke, 1981; Dubois, 1981, 1992; Inger, 1996.

"Dicroglossinae"

Sister taxon Uncertain.

Content Thirteen genera, *Ceratobatrachus*, *Conraua*, *Discodeles*, *Elachyglossa*, *Euphlyctis*, *Hoplobatrachus*, *Ingerana*, *Limnonectes*, *Occidozyga*, *Palmatorappia*, *Phrynoglossus*, *Platymantis*, and *Taylorana*, with 140+ species.

Distribution Sub-Saharan to Central Africa, South Asia through the East Indies to the Philippines and New Guinea, and into the Southwest Pacific islands.

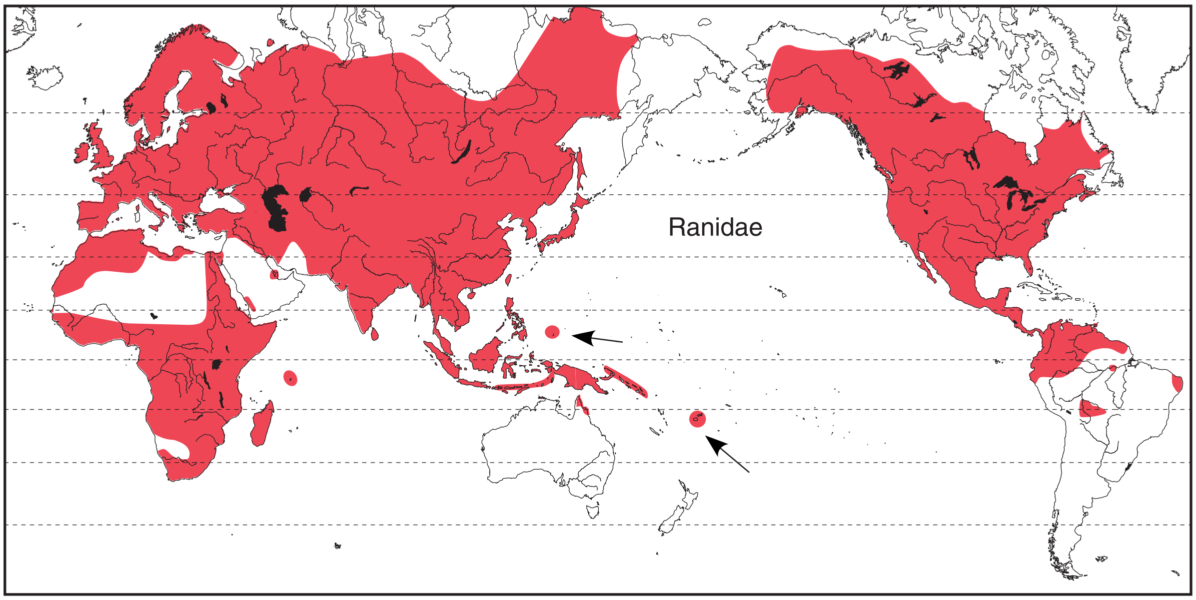


FIGURE 17.31 Geographic distribution of the extant Ranidae.

Characteristics The pectoral girdle is firmisternal and its sternum is moderate to strongly bifurcate posteriorly. In the skull, the nasals are generally in broad contact with one another and with the frontoparietals.

Biology Dicroglossines are a diverse group of frogs, ranging from small taxa (e.g., *Occidozyga baluensis*, 15–35 mm adult SVL) to the giant West African *Conraua goliath* (190–300 mm). Body form ranges from squat and toadlike (e.g., *Discodeles bufoniformis*) to treefrog-like (some *Platymantis*). Habitat association also ranges widely from terrestrial (e.g., *Hoplobatrachus tigerinus*) to aquatic (e.g., *Occidozyga laevis*) or arboreal (e.g., some *Platymantis*; (Fig. 17.32). Most dicroglossines have indirect development; the eggs are deposited in water and hatch into free-living tadpoles, but *Platymantis* and its relatives deposit terrestrial eggs that have direct development.

References Dutta and Manamendra-Arachchi, 1996; Emerson and Berrigan, 1993; Inger, 1996; Inger and Stuebing, 1997; Sabater-Pi, 1985.

Petropedetinae

Sister taxon Uncertain.

Content Thirteen genera, *Anhydrophryne*, *Arthroleptella*, *Arthroleptides*, *Cacosternum*, *Dimorphognathus*, *Ericabatrachus*, *Microbatrachella*, *Natalobatrachus*, *Nothophryne*, *Petropedetes*, *Phrynobatrachus*, *Phrynodon*, and *Poyntonia*, with 100+ species.

Distribution Sub-Saharan Africa.

Characteristics In the skull, the vomer is usually toothless or has only a small posterior patch of teeth. The tongue is notched. The terminal phalanges are usually T-shaped.

Biology Petropedetines are mostly small (<30 mm adult SVL, although *Petropedetes johnstoni* reaches 77 mm), terrestrial, and semiaquatic frogs with a *Rana*-like habitus and lightly warted skin. They generally live in moist habitats or in rocky montane streams, although

FIGURE 17.32 Representative ranids. Clockwise from upper left: Solomon's horned platymantine *Ceratobatrachus guentheri*, Dicroglossinae (photograph by P. Ryan); Seychelles ribbed frog *Ptychadena mascariensis*, Ptychadeninae (G. R. Zug); crawfish frog *Rana areolata*, Raninae (J. P. Caldwell); and Burmese spadefoot *Tomopterna breviceps*, Tomopterninae (G. R. Zug).

some live in savannas and emerge from subterranean retreats only with the arrival of the wet season. Some (e.g., *Cacosternum*, *Natalobatrachus*, *Phrynobatrachus*) deposit aquatic eggs that hatch into free-living tadpoles. Others have direct development. *Arthroleptella* lays small clutches of 20 to 40 eggs in damp cavities beneath moss or detritus; the eggs hatch into nonfeeding tadpoles that quickly metamorphose into tiny 3- to 4-mm froglets. *Anhydrophryne* and *Arthroleptides* lay small clutches of 10 to 30 terrestrial eggs that hatch directly into froglets.

References Lambiris, 1989; Largen, 1991; Laurent, 1986; Poynton and Broadley, 1985; Rödel, 1996, 1998; Wager, 1986.

Ptychadeninae

Sister taxon Uncertain.

Content Three genera, *Hildebrandtia*, *Lanzarana*, and *Ptychadena*, with 45+ species.

Distribution Egypt and sub-Saharan Africa, Madagascar, and the Seychelles.

Characteristics The skull lacks palatine bones and the otic process of the squamosal is reduced or absent. The last presacral and sacral vertebrae are fused, and the clavicle is reduced and usually fused to the coracoid.

Biology Most ptychadenines are slender, long-limbed frogs. Most species are moderate sized (40–60 mm adult SVL) and mainly inhabit savannas or grasslands. The ribbed or sharp-nosed frogs, *Ptychadena* (Fig. 17.32), are the most speciose (>40 species) and define the distribution of the Ptychadeninae. Owing to their semiarid habitats, they are most evident in the wet season and usually begin reproduction several weeks after the rains have begun. Males form noisy choruses in shallow, ephemeral pools, and females deposit modest-sized clutches of 200 to 500 eggs among the vegetation. The eggs hatch quickly and the tadpoles usually metamorphose within 4 to 5 weeks. *Ptychadena broadleyi* is unique because it deposits eggs on moist rocks, and the tadpoles live in the film of water covering the rock face.

References Lambiris, 1989; Perret, 1966; Rödel, 1996; Poynton and Broadley, 1985; Schiotz, 1963; Stewart, 1967; Wager, 1986.

Pyxicephalinae

Sister taxon Uncertain.

Content Two genera, *Aubria* and *Pyxicephalus*, each with two species.

Distribution Sub-Saharan Africa.

Characteristics The roofing bones of the skull are exostotic (i.e., the surface is sculptured owing to fusion of the bone and skin); the parasphenoid, pterygoid, and squamosal bones are uniquely shaped.

Biology Both pyxicephaline genera are moderately large and stocky frogs (*Aubria,* 50–100 mm, and *Pyxicephalus,* 60–195 mm adult SVL). These frogs mainly occur in dry habitats, usually savannas. The African bullfrog (*Pyxicephalus adspersus*) occurs throughout much of the distribution of pyxicephalines and accounts for much of our knowledge of the clade. It has several geographic morphs, and these morphs vary in size from moderately large to very large. In general, *P. adspersus* is active only during the summer months, emerging when the summer rains occur and feeding voraciously. Like the leptodactylid *Ceratophrys*, *P. adspersus* captures large prey, which it holds with two bony pseudoteeth in the front of the lower jaw. Reproduction occurs in ephemeral pools, and the 3000 to 4000 eggs are abandoned after deposition. Males have been reported to individually guard a pool filled with eggs and tadpoles, and in some instances, to construct channels between bodies of water, allowing tadpole schools to exit shallow pools. Although they occasionally eat tadpoles, no evidence exists indicating that they feed on their own tadpoles. *Aubria subsigillata* also deposits large egg clutches; when these hatch, the tadpoles form dense schools with the individual tadpoles appearing to touch one another.

References Branch, 1991; Channing et al., 1994; Kok et al., 1989; Lambiris, 1989; Perret, 1966; Rödel, 1996; Schiotz, 1963; Stewart, 1967.

"Raninae"

Sister taxon Uncertain.

Content Nine genera, *Altirana*, *Amolops*, *Batrachylodes*, *Chaparana*, *Micrixalus*, *Nanorana*, *Paa*, *Rana*, and *Staurois*, with 300+ species.

Distribution Similar to the family.

Characteristics The pectoral girdle is firmisternal and the sternum is slightly or not bifurcate posteriorly. In the skull, the nasals are reduced and do not touch.

Biology Ranines are a diverse group of frogs ranging from small Asian taxa (e.g., *Micrixalus tenasserimensis*, 20–35 mm adult SVL) to large species (American *Rana catesbeiana*, 85–180 mm; New Guinean *Rana arfaki,* 90–160 mm). Body form ranges from squat and toadlike (*Rana laticeps*) to slender and treefrog-like (e.g., *Rana* *chalconata*). Habitat choice also ranges widely from arid-terrestrial (e.g., *Rana bonaspei*) or moist-terrestrial (*Rana sylvatica*) to stream or river banks (*Rana palmipes*) and aquatic (*Rana grylio*) to arboreal (*R. chalconata*). Most ranines have indirect development; eggs are deposited in water and hatch into free-living tadpoles with a short (4–6 weeks) to extended (2–4 years, *R. catesbeiana*) tadpole stage.

References Berry, 1975; Inger, 1996; Inger and Stuebing, 1997; Wager, 1986.

Ranixalinae

Sister taxon Uncertain.

Content Three genera, *Indirana*, *Nannophrys*, and *Nyctibatrachus*, with 20+ species.

Distribution Sri Lanka and southern half of India.

Characteristics The tongue has large, anteromedial papillae on its dorsal surface. Digit tips are expanded and have T-shaped terminal phalanges. Adult males have large femoral glands. Tadpoles have generalized mouth parts, although *Indirana* tadpoles are nonaquatic and lack tail fins.

Biology Ranixalines are small to moderate-sized frogs (30–60 mm adult SVL), toadlike in appearance, with short heads and bodies and numerous tubercles and soft warts. The life histories of most species are largely unknown. All are associated with forested habitats, and the Sri Lankan species of *Nannophrys* live along mountain streams. The latter are reported to have typical aquatic larvae, although an earlier report noted that the tadpoles of *Nannophrys ceylonensis* hopped rather than swam. Although that observation remains unconfirmed, the larvae of *Indirana* (India) live beneath the bark of dead trees.

References Dubois, 1985; Dutta and Manamendra-Arachchi, 1996.

"Tomopterninae"

Sister taxon Uncertain.

Content Two genera, *Aglyptodactylus* and *Tomopterna,* with 3 and ±15 species, respectively.

Distribution South Asia, Madagascar, and sub-Saharan Africa.

Characteristics In the skull, the cultriform process of the parasphenoid is rounded, and the medial ramus of the pterygoid does not overlap the parasphenoid.

Biology *Tomopterna,* called pyxies, are pelobatid-like ranids with short, robust bodies (30–60 mm adult SVL) and an enlarged, spade-shaped tubercle on each hindfoot. These terrestrial frogs (Fig. 17.32) occur in dry habitats, such as open forests, scrub, and grasslands. They are semifossorial, emerging on moist evenings to forage on the surface. Most are explosive breeders; they appear in great numbers after heavy rains, depositing eggs in ephemeral pools before returning to their terrestrial homes. The tadpoles are free-living and develop quickly (4–5 weeks).

Comments Köhler et al. (1998) discovered two new species of *Aglyptodactylus*, and in their analysis of relationships, they found that *Aglyptodactylus* is phylogenetically most similar to Malagasian *Tomopterna*. They transferred *Aglyptodactylus* from the Rhacophoridae to the Raninae; they did not recognize a tomopternine group.

References Branch, 1991; Dutta and Manamendra-Arachchi, 1996; Glaw and Vences, 1994; Köhler et al., 1998; Lambiris, 1989; Poynton and Broadley, 1985.

Rhacophoridae

Afro-Asian treefrogs

Classification Amphibia; Lissamphibia; Anura; Neobatrachia.

Sister taxon Uncertain.

Content Three subfamilies, Buergeriinae, Mantellinae, and Rhacophorinae, with ±275 species.

Distribution Sub-Saharan Africa, Madagascar, and South Asia (Fig. 17.33).

Characteristics Rhacophorids are mainly treefrogs, ranging from small to large species. The skull has paired palatines and frontoparietals. The facial nerve exits through the anterior acoustic foramen in the auditory capsule; the trigeminal and facial nerve ganglia fuse to form a prootic ganglion. The vertebral column possesses eight presacral holochordal vertebrae, and all are procoelous except for a biconcave surface on the last presacral. The transverse processes of the sacral vertebra are cylindrical, and this vertebra has a bicondylar articulation with the urostyle. Postmetamorphs have no dorsal ribs on the presacral vertebrae. The pectoral girdle is firmisternal with a distinct sternum. Fibulare and tibiale are fused at their proximal and distal ends. An intercalary cartilage occurs between the terminal and penultimate phalanges of each digit, and the tips of the terminal phalanges are T-shaped and sometimes pointed. The larvae have keratinized mouth parts, and the left and right branchial chambers fuse behind the heart and are emptied by a spiracle on the left side at midbody.

References Channing, 1989; Herrmann, 1993; Liem, 1970; Richards and Moore, 1998.

Buergeriinae

Sister taxon Clade containing Mantellinae and Rhacophorinae.

Content One genus, *Buergeria*, with four species.

Distribution Taiwan through the Ryukyus to southern Japan.

Characteristics The anterior horn of the hyoid is present but consists only of the medial arch. The sphenethmoid is a single bone.

Biology Buergeriines (Fig. 17.34) are small to moderate-sized frogs (25–70 mm adult SVL); females are larger than males. Although they are treefrog-like, they are commonly found on the ground or in water, particularly in montane streams. They have an extended breeding season from early spring through summer. They do not form breeding aggregations or choruses; instead, the males establish and maintain territories along a stream, typically calling from the water's edge or in the water. Amplexus is axillary, and the eggs are deposited in the water. Development is indirect, and tadpoles metamorphose in about 8 weeks.

References Lue, 1991; Maeda and Matsui, 1989.

Mantellinae

Sister taxon Rhacophorinae, although the monophyly of Mantellinae has been questioned (Daly et al., 1996).

Content Three genera, *Laurentomantis*, *Mantella*, and *Mantidactylus*, with 70+ species.

Distribution Madagascar.

Characteristics The anterior horn of the hyoid is present and complete. The sphenethmoid is a single bone.

Biology Most mantellines are small to medium-sized (15–50 mm adult SVL; *Mantidactylus guttulatus* reaches 100–120 mm) terrestrial or arboreal frogs; most species live in semiarid to wet forested habitats. *Mantidactylus* is the most speciose (>55 species) and behaviorally diverse group; generally, they are cryptically colored in shades of green to brown. In contrast, *Mantella* (12+ species; Fig. 17.34) are commonly boldly, even gaudily, colored. Their bold and contrasting colors advertise their toxic skin secretions, containing lipophilic alkaloids. They share toxic skin secretions, advertising coloration, size, and habitus with some dendrobatids, but this similarity is because of convergence, not relationship. Reproductive behavior is diverse. Most, if not all, *Mantidactylus* species have male vocalization and axillary amplexus. In all three genera, eggs appear to be laid away from water. For those with aquatic larvae, the hatching tadpoles drop into the water from clutches deposited in overhanging vegetation (many *Mantidactylus*, e.g., *M. liber*) or are washed into streams or pools from terrestrial nests (e.g.,

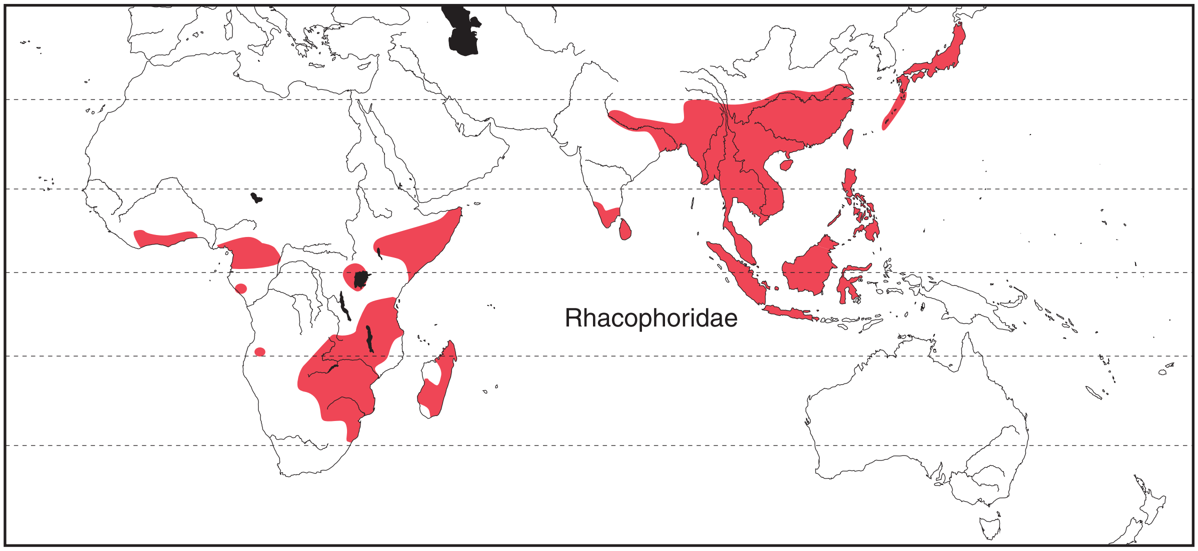


FIGURE 17.33 Geographic distribution of the extant Rhacophoridae.

Figure 17.34 Representative rhacophorids. Clockwise from upper left: Japanese Buerger's frog *Buergeria japonica*, Buergeriinae (photograph by L. Grismer); black goldenfrog *Mantella cowanii*, Mantellinae (R. D. Bartlett); fancy foot gliding frog *Rhacophorus prominanus*, Rhacophorinae (L. Grismer); and Nongkhor treefrog *Chirixalus nongkhorensis*, Rhacophorinae (C. Hansen) .

Mantidactylus betsileanus). Other species have terrestrial or arboreal nonfeeding larvae (e.g., *M. pseudoasper*), and direct development occurs in *M. eiselti,* although this species does not have parental care. In *Mantella*, courtship is brief with no real amplexus; the male either lays on the head and shoulder of the female or loosely grasps her on the trunk. Eggs are similarly deposited out of water.

References Blommers-Schlösser, 1993; Blommers-Schlösser and Blanc, 1991; Daly et al., 1996; Glaw and Vences, 1994.

Rhacophorinae

Sister taxon Mantellinae.

Content Eight genera, *Boophis*, *Chirixalus*, *Chiromantis*, *Nyctixalus*, *Philautus*, *Polypedates*, *Rhacophorus,* and *Theloderma*, with 200+ species.

Distribution Southern one-third of Africa (*Chiromantis*), Madagascar (*Boophis*), and southern Asia from India to the Philippines and Japan (other genera).

Characteristics The anterior horn of the hyoid is absent, and the sphenethmoid is paired.

Biology Rhacophorines are treefrogs. They range in size from small (e.g., *Chirixalus,* 30–45 mm adult SVL; Fig. 17.34) to large (e.g., *Polypedates dennysii*, 78–102 mm). The Asian *Philautus*, *Nyctixalus*, and *Theloderma* have tree hole egg deposition sites and nonfeeding tadpoles that have brief developmental periods. *Chiromantis*, *Polypedates*, *Rhacophorus*, and others deposit eggs in foam nests above water, mostly in shrubs and trees; upon hatching, the larvae drop into the water below and develop as free-living tadpoles. The foam nests often are created jointly by two or more amplectant pairs, and at least in *Chiromantis*, unpaired males may assist. The Malagasian taxa lay eggs directly in water and have a typical aquatic tadpole life cycle. A female *Rhacophorus microtympanum* or *reticulatus* (Sri Lanka) has been reported to carry eggs beneath its belly; this observation remains unconfirmed. The African *Chiromantis xerampelina* is an aridland species and has evolved special physiological and morphological adaptations to tolerate high temperatures and to reduce water loss (see Chapter 7).

References Berry, 1975; Channing, 1989; Dutta and Manamendra-Archchi, 1996; Glaw and Vences, 1994; Inger and Stuebing, 1997; Liu and Hu, 1961; Maeda and Matsui, 1989; Poynton and Broadley, 1987; Shoemaker et al., 1989.

This Page Intentionally Left Blank

Chapter

18

Turtles

OVERVIEW

Modern turtles are modestly speciose (285+ species), yet they occur worldwide in cool-temperate to tropical habitats. They are ecologically and morphologically diverse, and the clade includes giant marine and terrestrial species, as well as dwarf freshwater and terrestrial species. This diversity is reflected by a variety of shell shapes that range from nearly spherical to nautically streamlined and an equally broad array of physiological adaptations that allow some marine species to dive to depths of over a half-kilometer and some upland desert species to exist in habitats with less than 10 cm of rainfall each year. Turtles are noted for a slow, plodding locomotion that is more imaginary than real, but most do have a "slow" life history characterized by slow growth, late maturity, and long life. This life history now places them at great risk in a human-dominated world, and many species and populations are declining toward extinction.

Turtles (Testudines) are reptilian tanks, armored above and below, and capable of withdrawing the head and neck, limbs, and tails either partially or fully within the armor. No other tetrapod has a bony shell that encloses both the pectoral and pelvic girdles. The upper shell, the carapace, is formed from fusion of the eight trunk vertebrae and ribs to an overlying set of dermal bones; the lower shell, the plastron, arises from the fusion of parts of the sternum and pectoral girdle with external dermal bones. The shell is robust in some taxa, such as in tortoises and mud turtles, with only small openings for the head and appendages. In other turtles, such as leatherback seaturtles and softshell turtles, the shell is lightly built and has lost or reduced bony elements. The neck, whether long or short, is extremely flexible and consists of eight cervical vertebrae in all turtles. Extant turtles are divided into two clades based on the movement or retraction pattern of the neck. The Pleurodira or sideneck turtles retract the head and neck by laying it to the side; thus, the sides of the neck and head are exposed in the gap between the carapace and plastron (Fig. 18.1). The Cryptodira or hidden-neck turtles

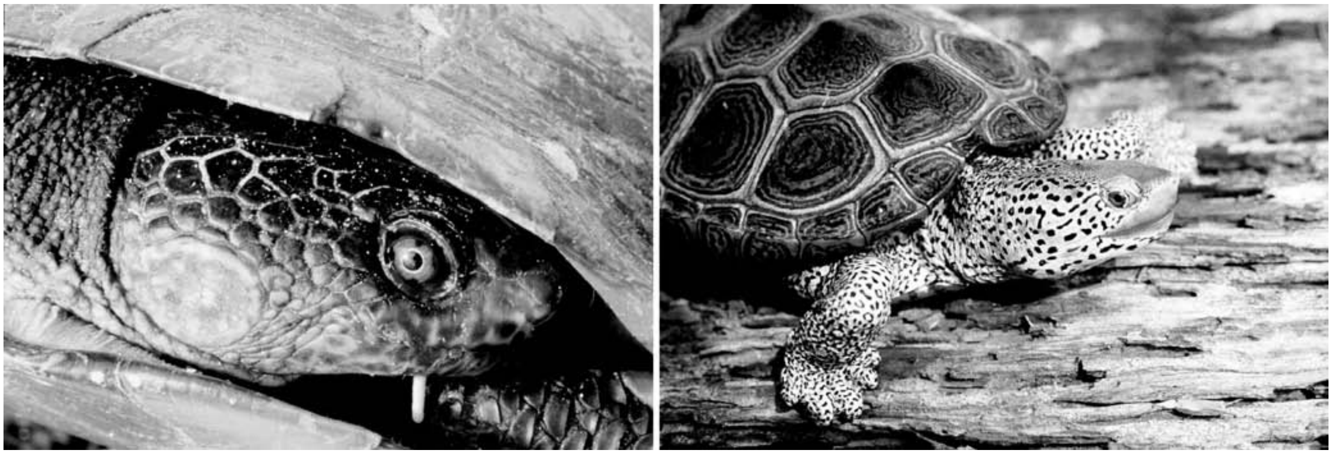


FIGURE 18.1 Sideneck turtles (Pleurodira), such as *Phrynops gibbus* (left), can withdraw their head and neck only within the outer margin of the shell, whereas hidden-necked turtles (Cryptodira), such as *Malaclemys terrapin* (right), withdraw the neck and head within the shell. Photographs by L. J. Vitt.

retract the neck posteriorly into a medial slot within the body cavity; the neck forms a vertical S-shape when viewed laterally, and only the tip of the nose is exposed between the shielding forearms. In spite of the different mechanics of neck retraction, the structure of the cervical vertebrae in the two groups is very similar.

All turtles are oviparous. The number of eggs deposited by females of different species ranges from one to more than a hundred. The number of eggs in a clutch is generally positively associated with female size; small turtles lay one or two eggs and larger turtles lay a dozen or more. Most turtles possess a stereotypic nest-digging behavior. Egg chambers are dug with the hindlimbs, which work alternately to scoop out a flask-shaped chamber as deep as the hindlimbs can reach. Fertilization is internal and, because the shell surrounds the body in both sexes, copulation can be hazardous to the male, who must balance his plastron on top of the female's carapace. Males of many species have a slightly concave plastron to facilitate mating.

Living and extinct turtles share a large suite of unique characteristics. No one questions the monophyly of turtles, although the origin of turtles is controversial (see Chapter 3). In addition to the uniquely evolved carapace and plastron, all testudines share a special cranial architecture (Gaffney and Meylan, 1988; Laurin and Reisz, 1995; also see Fig. 2.12) that includes the presence of a maxillary, a premaxillary, and a dentary without teeth and bearing a horny sheath; the absence of a postparietal, postfrontal, and ectopterygoid; a small or absent lacrimal; a large quadrate that abuts the squamosal to form the temporal surface of the skull; and a rodlike stapes without a foramen or processes. Some other features that distinguish turtles include the presence of a largely nonsensory but strongly secretory pineal organ; the absence of nasal conchae; the presence of a lower eyelid tendon; prominent epicondyles and an ectepicondylar foramen or groove on the humerus; and a subspherical and elevated femur head.

From the beginning of biological classification, turtles have been recognized as a unique and natural group. In his 1766 edition of the *Systema Naturae*, Linnaeus included all turtles in *Testudo* and recognized 15 species. The partitioning of turtle species into more genera began soon thereafter. In 1805, Brongniart subdivided turtles based on habitat into marine (*Chelonia*), freshwater (*Emys*), and land (*Testudo*) species. The first hierarchical arrangement appeared in 1806 when Duméril constructed a listing of sequentially indented pairs of diagnostic traits to differentiate the preceding three genera and a new one, *Chelus*. The recognition of new genera and species continues to the present time. Throughout the 19th and the 20th centuries, biologists have attempted to recognize natural groups, but the relative stability of turtle classification is recent, arriving in the mid-1970s. At that time, Gaffney (1975) used Hennigian phylogenetic analysis to determine phylogenetic relationships and to erect a classification of fossil and extant turtles from these relationships.

The phylogeny as outlined in Gaffney's classification (1975) and later refined remains largely unchanged in our current classification (Table 3.5) and cladogram (Fig. 18.2); however, a general acceptance of Gaffney's classification rather than a total agreement on all proposed relationships is implied. The discovery of new fossil turtles and the use of molecular data support the basal division of extant turtles into the pleurodires and cryptodires. This divergence of turtle clades is ancient, occurring more than 220 mybp, and these two clades lived contemporaneously with the most primitive turtle,

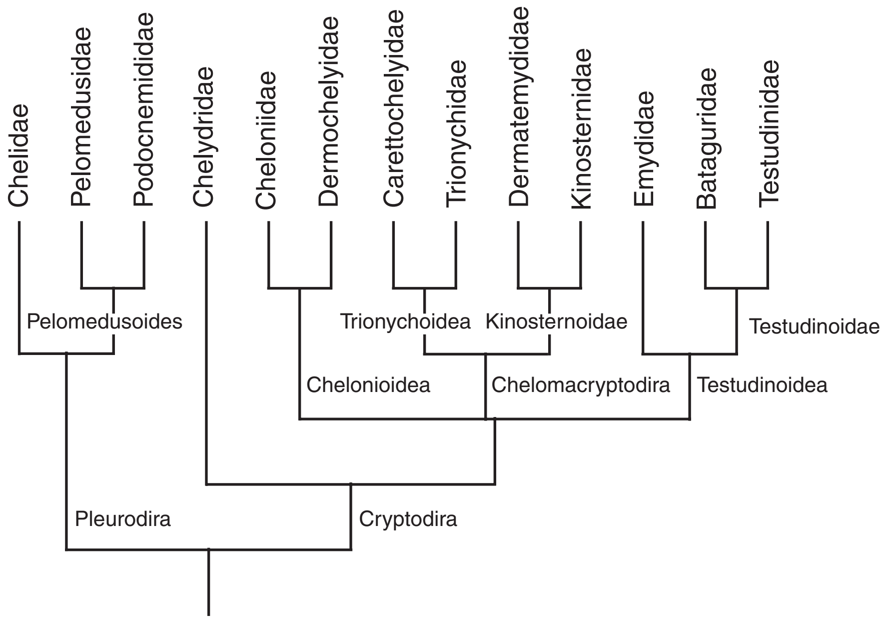


FIGURE 18.2 Cladogram depicting relationships among the families of extant turtles. The cladogram derives from Gaffney and Meylan (1988, Fig. 5.1 et seq.) and is modified based on the studies of Meylan (1996) and Shaffer et al. (1997). Cladogram redrawn from original for uniformity.

Proganochelys (see Chapter 3). The recognition of these two clades arose from their contrasting neck-retraction mechanics, but other characters support the monophyly of each. For example, pleurodiran turtles have the pelvic girdle fused to the plastron and a jaw closure mechanism with an articulation on the trochlear surface of the pterygoid; cryptodires have a flexible articulation of the pelvic girdle with the plastron and a jaw closure mechanism with an articulation on the trochlear surface of the otic capsule. Two clades of extant sidenecks, Pelomedusidae and Chelidae, have been recognized for much of the 20th century. As fossils were incorporated into phylogenetic analyses, it became evident that pelomedusids were polyphyletic. Resolution of this problem has occurred with the recognition of the Pelomedusoides as the sister group to the Chelidae, and the classification of the Pelomedusoides into two fossil clades and the extant Pelomedusidae and Podocnemididae clades (Meylan, 1996). Combined molecular and morphological data show the individual monophyly of the Australian chelids and the South American chelids (Shaffer et al., 1997; Seddon et al., 1997), and this relationship contrasts with the intermixing of these two clades as previously suggested (Gaffney, 1977). This issue is not totally resolved, but the proposed ancient separation of the American and Australian clades seems likely to gain additional support.

The Chelydridae appears to be an ancient clade and the sister group to all other extant families of cryptodiran turtles (Fig. 18.2). This proposed relationship has the strongest support from combined molecular and morphological data, although an alternative arrangement places the chelydrids as a sister group to all extant cryptodirans except a trionychid–carettochelyid clade (Shaffer et al., 1997). The combined data also support the sister-group relationship of snapping turtles to the big-headed turtle *Platysternon megacephalum* and the latter as a sole representative (monotypy) of a chelydrid subfamily. Some evidence, such as chromosomes, suggests a *Platysternon*–emydid relationship (Bickham and Carr, 1983).

Combined molecular and morphological data support the recognized groupings of Cheloniidae–Dermochelyidae, Trionychidae–Carettochelyidae, Kinosternidae Dermatemydidae, and Emydidae–Bataguridae–Testudinidae, each as a clade. The relationship of all extant seaturtles was recognized by Agassiz in his 1857 classification of turtles, but owing to the leatherback's extreme specializations, many subsequent biologists placed *Dermochelys* in a separate group (Atheca) equivalent to cryptodires and pleurodires. From fossil data, the long separation of the leatherback clade and hard-shelled seaturtles is recognized; nonetheless, they compose a monophyletic group. The five genera of extant cheloniids are commonly divided into two subgroups; however, the inclusion of fossil taxa suggests otherwise (Hirayama, 1994; Parham and Fastovsky, 1998). One set of molecular data proposes a different pattern of relationships among extant cheloniids but does not account for relationships among extant and fossil taxa (Dutton et al., 1996).

The trionychid-carettochelyid and the kinosternid–dermatemydid clades have been recognized as sister groups of a larger clade (Chelomacryptodira). Although morphological characters continue to support this relationship, molecular data alone or combined with morphological data suggest trionychids–carettochelyids as the sister group to all other cryptodires (Shaffer et al., 1997). Fossil evidence also supports the chelomacryptodiran clade and further indicates that trionychids and carettochelyids are sister taxa (Meylan and Gaffney, 1989). Dermatemydids, however, are the sister group to extant kinosternids and several fossil genera. Staurotypines and kinosternines are sister taxa based on all evidence except karyotype (Hutchinson, 1991).

The Emydidae-Bataguridae–Testudinidae clade (Testudinoidea) has a long history of recognition; however, the proposed relationships therein have been variable. Combined data indicate that the emydids are the sister group of the batagurids–testudinid clade (Testudinoidae). The monophyly of the emydids has strong support as do the clades Testudinoidae and Testudinidae; however, the monophyly of Bataguridae is uncertain. Both the emydids and the testudinids share sets of derived characters that confirm their monophyly. The batagurids do not, and it is possible that testudinids arose from within the presently conceived batagurid group (Shaffer et al., 1997).

General References Ananjeva et al., 1988; Cogger and Zweifel, 1998; David, 1994; Ernst and Barbour, 1989a; Ernst et al., 1994; Iverson, 1992; Legler and Georges, 1993.

Systematic References Bickham and Carr, 1983; Dutton et al., 1996; Gaffney, 1975, 1977, 1984; Gaffney and Meylan, 1988; Hirayama, 1994; Hutchinson, 1991; Laurin and Reisz, 1995; McDowell, 1964; Meylan, 1987, 1996; Meylan and Gaffney, 1989; Parham and Fastovsky, 1998; Seddon et al., 1997; Shaffer et al., 1997; Williams, 1950.

TAXONOMIC ACCOUNTS

Pleurodira

Chelidae

Australo-American sideneck turtles

Classification Reptilia; Parareptilia; Testudines; Pleurodira.

Sister taxa Pelomedusoides.

Content Eleven genera, *Acanthochelys*, *Chelodina* (Fig. 18.3), *Chelus*, *Elseya*, *Elusor*, *Emydura*, *Hydromedusa*, *Phrynops*, *Platemys*, *Pseudemydura*, and *Rheodytes*, with 50+ species.

Distribution Australia, New Guinea, and South American (Fig. 18.4).

Characteristics The adult Australo-American sidenecks range from 12 to 14 cm CL (straight carapace length) for *Pseudemydura umbrina* to about 48 cm for *Chelodina expansa*; most chelid species range from 20 to 35 cm CL (Fig. 18.3). As a group, they have flattened skulls and shells. The jaw closure mechanism articulates on a pterygoid trochlear surface that lacks a synovial capsule but contains a fluid-filled saclike duct from the buccal cavity. The skull lacks the epipterygoid but possesses an internal carotid canal in the prootic and strong parietal-squamosal and postorbital-squamosal contact. The facial nerve has a hyomandibular branch. The plastron lacks a mesoplastron and has well-developed plastral buttresses that articulate with the costals on each side of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws horizontally, and this mechanism is reflected in an anteriorly oriented articular surface of the first thoracic vertebra; other vertebral traits are the inclusion of the 10th thoracic vertebra in the sacral complex and procoelous caudal vertebrae. The pelvic girdle is firmly fused to the plastron, and the ilium lacks a thelial process. The karyotype is 2N = 50 or 54.

Biology Chelids (Fig. 18.3) are predominantly aquatic turtles, some highly so (e.g., *Elusor macrurus*, *Rheodytes leukops*), and they seldom leave the water except to deposit eggs. Species that live in seasonally drying marshes or ponds, such as *P. umbrina*, have extended estivation–hibernation periods, during which individuals remain buried in the mud. The Neotropical *Platemys platycephala* and *Phrynops zuliae* are semiaquatic; they commonly leave the water to forage on the forest floor. Overall, chelids are opportunistic omnivores and take food ranging from filamentous algae and periphyton to arthropods, mollusks, and small vertebrates. *Chelus fimbriatus* and the species of *Chelodina* are carnivores that regularly catch fish and other active prey by a gape-suck mechanism. Their long necks are retracted until a prey approaches, and then rapidly extended; as the head nears the prey, the mouth opens and the buccal cavity is rapidly enlarged to create a vacuum that sucks the prey into the enlarging cavity. Other taxa forage for small animal prey or carrion, or graze on aquatic vegetation. Seasonality of chelid reproduction varies considerably, and

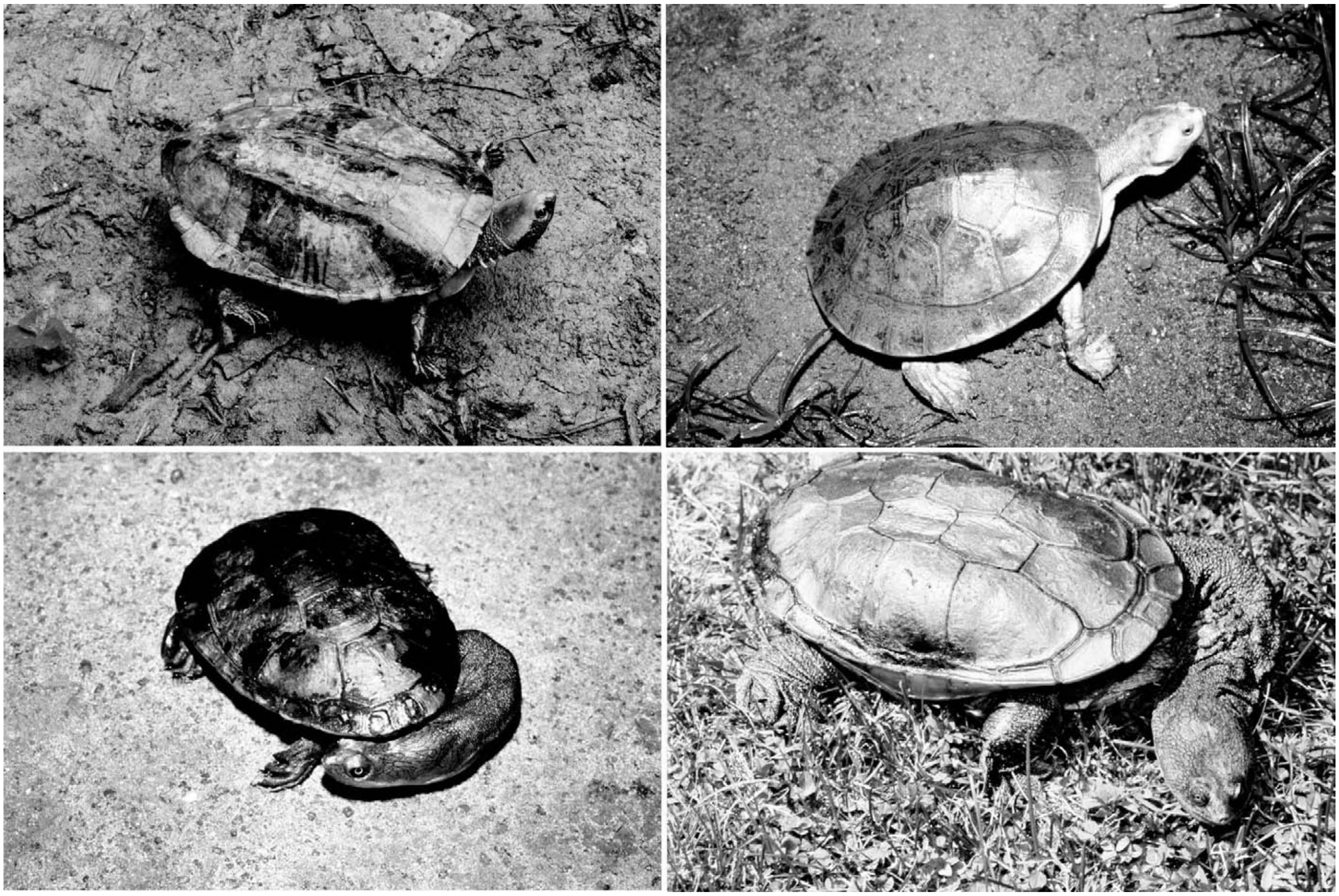


FIGURE 18.3 Representative chelid sideneck turtles. Clockwise from upper left: twist-neck turtle *Platemys platycephala*, Chelidae (photograph by L. J. Vitt); Australian big-headed turtle *Emydura australis*, Chelidae (C. K. Dodd, Jr.); narrow-breasted snakeneck turtle *Chelodina oblonga*, Chelidae (R. W. Barbour); and northern Australian snakeneck turtle *Chelodina rugosa*, Chelidae (C. K. Dodd, Jr.).

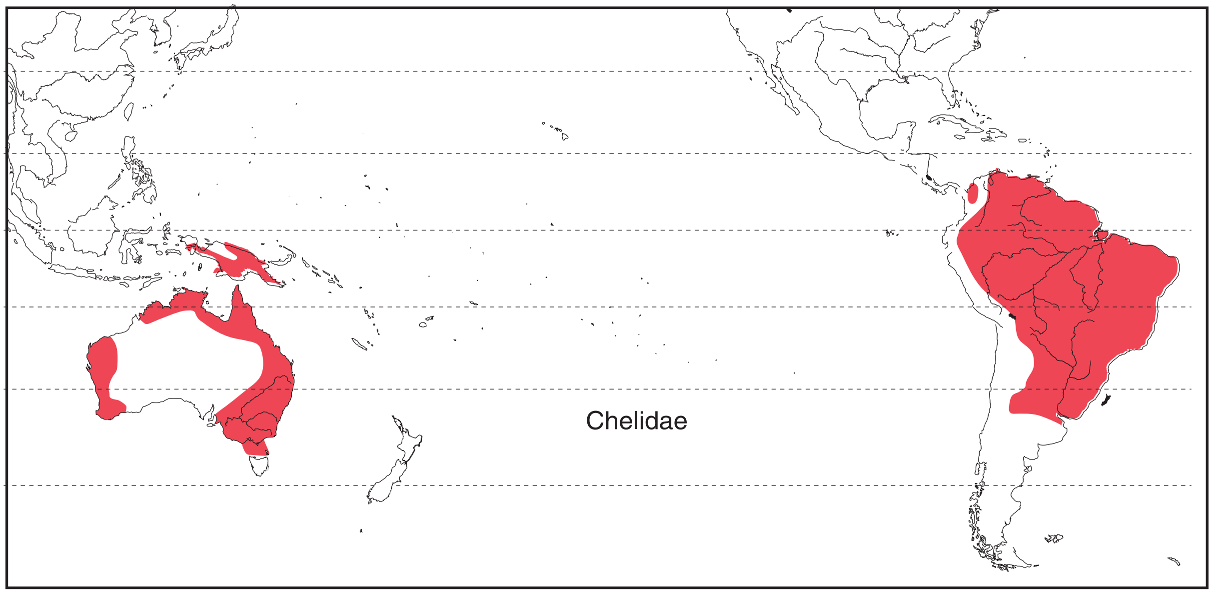


FIGURE 18.4 Geographic distribution of the extant Chelidae.

numerous patterns exist. They range from a "typical" spring or late dry season egg-laying period, with hatching 8 to 10 weeks later, to egg deposition before the summer drought and eggs hatching about 180 days later (*P. umbrina*). In some Australian chelids, egg deposition occurs in late fall and the eggs hatch about a year later (*Chelodina expansa*); eggs are deposited in submerged nests and hatch 9 to 10 months later at the beginning of the wet season in *Chelodina rugosa*.

Comment A recent molecular study (Georges et al., 1998) proposed three subfamilies (Chelodininae, Chelidinae [sic], Hydromedusinae). None of these groups was characterized morphologically, and the chelodinines are paraphyletic.

Reference Cann, 1998; Gaffney et al., 1991; Georges et al., 1993, 1998; Kennett et al., 1993a,b; Kuchling, 1999; Legler and Georges, 1993; Pritchard and Trebbau, 1984; Shaffer et al., 1997.

Pelomedusoides

Pelomedusidae

African mud terrapins

Classification Reptilia; Parareptilia; Testudines; Pleurodira.

Sister taxa Clade containing Podocnemididae and extinct Bothremydidae.

Content Two genera, *Pelomedusa* and *Pelusios*, with 1 and 15+ species, respectively.

Distribution Sub-Saharan Africa, Madagascar, and granitic Seychelles (Fig. 18.5).

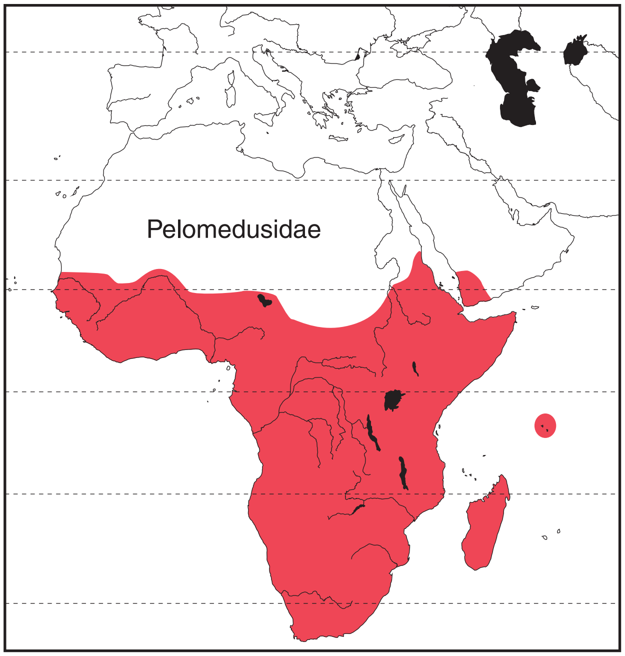


FIGURE 18.5 Geographic distribution of the extant Pelomedusidae.

Characteristics The African mud terrapins are small (12 cm adult CL, *Pelusios nanus*) to moderately large (46 cm CL, *Pelusios sinuatus*); most species are 20 to 30 cm CL. Most species have oblong, moderately high-domed carapaces, large plastra that are hinged in *Pelusios* and not hinged in *Pelomedusa*, and moderate-sized heads. The jaw closure mechanism articulates on a pterygoid trochlear surface that lacks a synovial capsule but contains a fluid-filled saclike duct from the buccal cavity. The skull lacks the epipterygoid and parietal-squamosal contact but possesses an internal carotid canal in the prootic and strong postorbital-squamosal contact. The facial nerve has a hyomandibular branch. The plastron has a mesoplastron and well-developed plastral buttresses that articulate with the costals on each side of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws horizontally, and this mechanism is reflected in an anteriorly oriented articular surface of the first thoracic vertebra; other vertebral traits are the inclusion of the 10th thoracic vertebra in the sacral complex and procoelous caudal vertebrae. The pelvic girdle is firmly fused to the plastron, and the ilium lacks a thelial process. The karyotype is 2N = 34 or 36.

Biology The mud terrapins (Fig. 18.6) are semiaquatic-aquatic, bottom-walking turtles of slow-moving waters, principally of lakes, swamps, marshes, and even ephemeral waterways. Their biology is little studied. They appear to be predominantly carnivorous, eating a variety of arthropods, worms, and other small animals, which they find by slow, methodical foraging on the bottom of their aquatic habitats. Species in seasonally dry waterways estivate or hibernate in the bottom or on shore immediately adjacent to the drying habitat. Pelomedusids generally produce small to modest clutches of 6 to 18 eggs, depending upon female size. Egg deposition occurs in the more equitable season of the year, with known incubation periods ranging from 8 to 10 weeks.

References Ernst and Barbour, 1989a; Gaffney et al., 1991; Meylan, 1996; Shaffer et al., 1997.

Podocnemididae

Madagascan big-headed turtle and American sideneck river turtles

Classification Reptilia; Parareptilia; Testudines; Pleurodira.

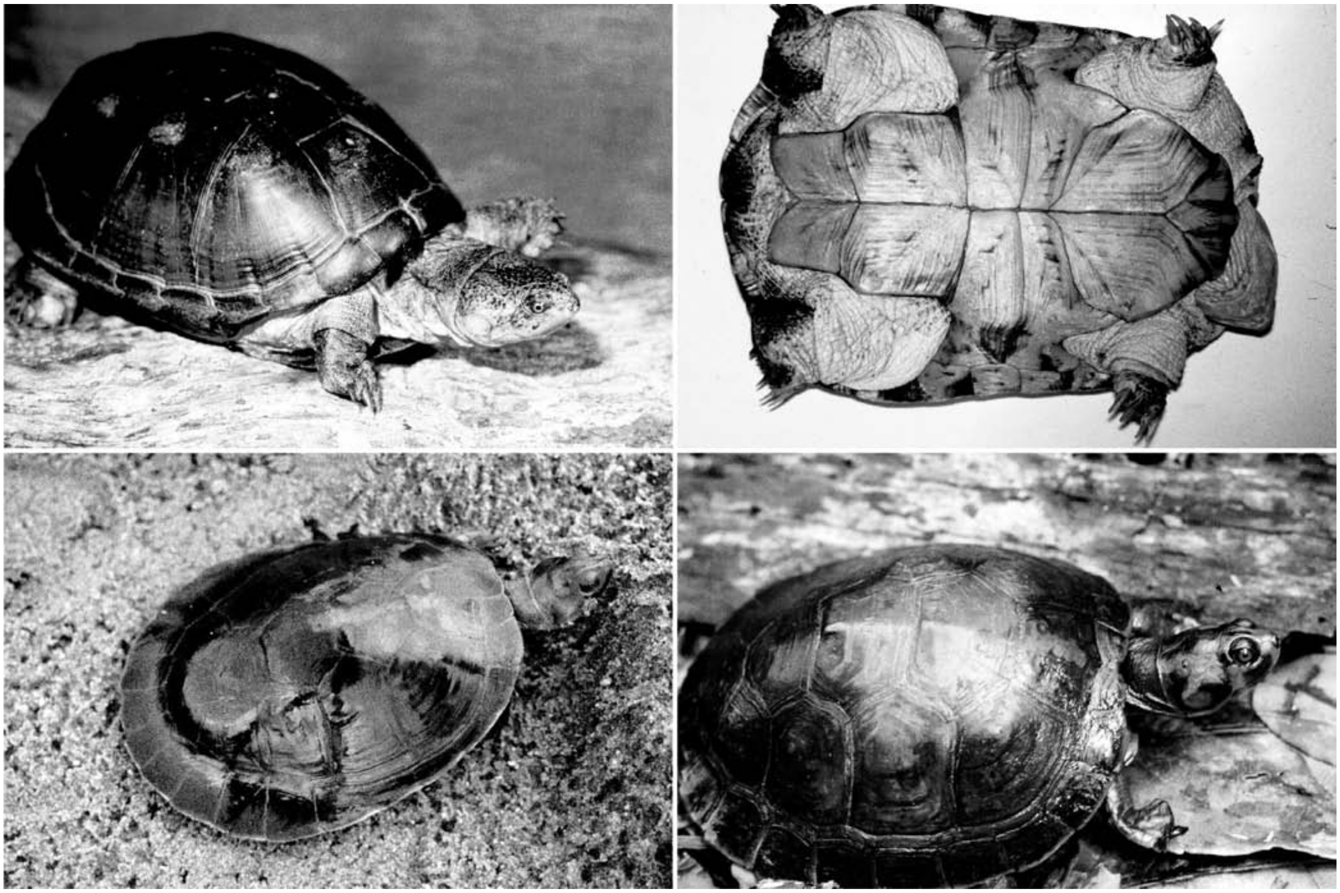


FIGURE 18.6 Representative pelomedusoid sideneck turtles. Clockwise from upper left: Adanson's mud terrapin *Pelusios adansonii*, Pelomedusidae (photograph by R. W. Barbour); helmet turtle *Pelomedusa subrufra*, Pelomedusidae (G. R. Zug); yellow-spotted river turtle *Podocnemis unifilis*, Podocnemididae (J. M. Howland); and red-headed river turtle *Podocnemis erythrocephala*, Podocnemididae (T. C. S. Avila-Pires).

Sister taxa Bothremydidae, a fossil clade.

Content Three genera, *Erymnochelys*, *Peltocephalus*, and *Podocnemis*, with one, one, and six species, respectively.

Distribution Madagascar and the northern half of South America, east of the Andes (Fig. 18.7).

Characteristics Podocnemidids are moderately large turtles, ranging in adult CL from 20 to 25 cm (male *Podocnemis erythrocephala*) to 80 cm (female *Podocnemis expansa*). The jaw closure mechanism articulates on a pterygoid trochlear surface that lacks a synovial capsule but contains a fluid-filled saclike duct from the buccal cavity. The skull lacks the epipterygoid and parietal-squamosal contact but possesses an internal carotid canal in the prootic, and strong postorbital-squamosal contact. The facial nerve has a hyomandibular branch. The plastron has a mesoplastron and well-developed plastral buttresses that articulate with the costals on each side of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws horizontally, and this mechanism is reflected in an anteriorly oriented articular surface of the first thoracic vertebra; other vertebral traits are the inclusion of the 10th thoracic vertebra in the sacral complex and procoelous caudal vertebrae. The pelvic girdle is firmly fused to the plastron, and the ilium lacks a thelial process. The karyotype is $2N = 28$.

Biology Podocnemidids (Fig. 18.6) are mainly river turtles that have broad, domed, streamlined shells for active swimming in moderate currents. Generally they feed on a variety of plant material, including aquatic vegetation and plant products that fall into the water; however, they are not strict herbivores and opportunistically catch and eat small, slow-moving animal prey and carrion. They nest predominantly on sandy riverbanks or sandbars. *P. expansa* nests en masse and each female lays

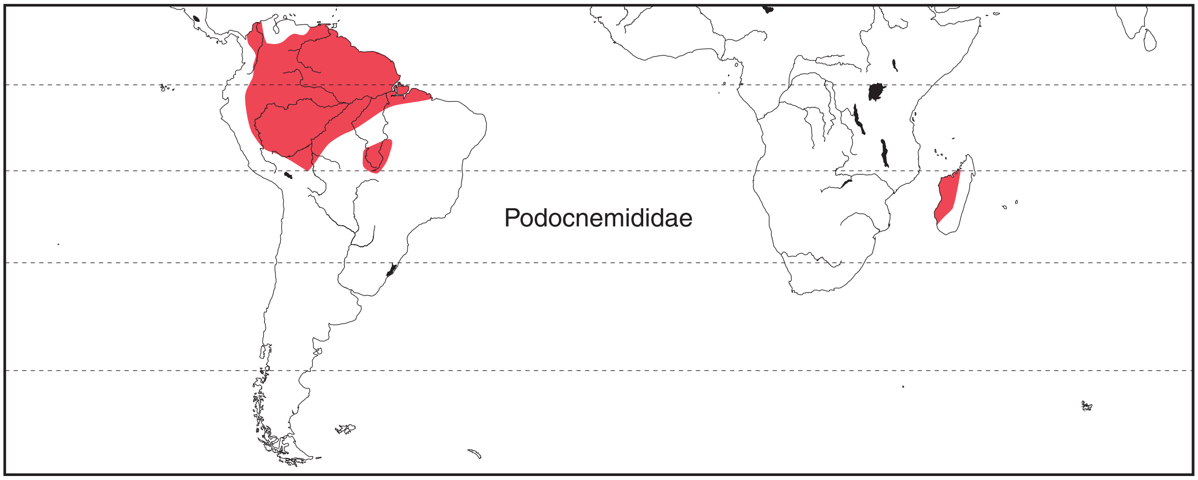


FIGURE 18.7 Geographic distribution of the extant Podocnemididae.

60 to 120 eggs. Smaller species accordingly deposit smaller clutches, and most are solitary nesters. Incubation is variable. Eggs of *P. expansa* require 42 to 47 days to hatch, whereas those of *Podocnemis vogli* require 127 to 149 days.

References Gaffney et al., 1991; Kuchling, 1999; Meylan, 1996; Pritchard and Trebbau, 1984; Shaffer et al., 1997.

Cryptodira

Chelydridae

Snapping and big-headed turtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Procoelocryptodira, which includes all other extant families of cryptodires.

Content Two subfamilies, Chelydrinae and Platysterninae (Fig. 18.8).

Distribution Eastern North America and portions of Central America, and mountainous Southeast Asia (Fig. 18.9).

Characteristics Chelydrids range in adult CL from the giant *Macrochelys temminckii* at 80 cm (maximum) to the much smaller *Platysternon megacephalum* at 18 cm. They are large-headed and have broad, flattened carapaces with reduced plastra; they possess the longest tails of all turtles. The jaw closure mechanism of chelydrids articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal–squamosal and postorbital–squamosal are in strong contact. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses articulate loosely or firmly with the costals of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal with large costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex, and amphicoelous and opisthocoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is 2N = 52 and 54.

References Gaffney et al., 1991; Shaffer et al., 1997.

Chelydrinae

Sister taxa Platysterninae.

Content Two genera, *Chelydra* and *Macrochelys*, with three and one species, respectively.

Distribution Southern two-thirds of North America, east of the Rockies, portions of Mesoamerica, and southernmost Central America into Ecuador (Fig. 18.9).

Characteristics The plastron is greatly reduced and cruciform, and the plastral bridge is rigid; the skull roof is strongly emarginated.

Biology *Chelydra* and *Macrochelys* (Fig. 18.8) are aquatic turtles. Individuals of the latter taxon rarely leave the water except to nest, whereas individuals of the former commonly make terrestrial forays in addition to nesting on land. Feeding, mating, and hibernation occur in water, so these terrestrial movements seem to be

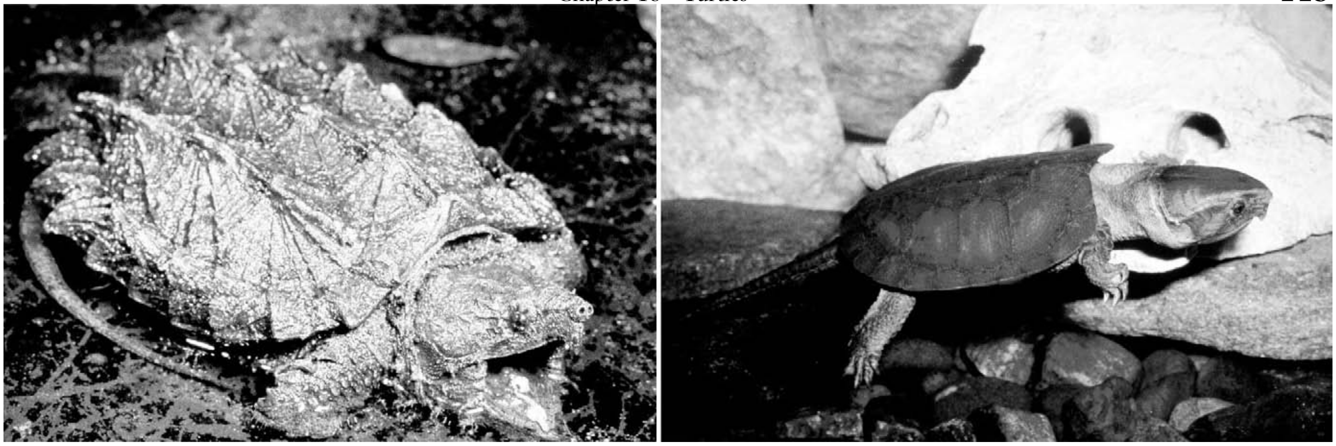


FIGURE 18.8 Representative turtles. From left: alligator snapping turtle *Macrochelys temminckii*, Chelydrinae (photograph by R. W. Barbour); and big-headed turtle *Platysternon megacephalum*, Platysterninae (R. W. Van Devender).

related to dispersal. Chelydrines are opportunistic omnivores; *Macrochelys temminckii* has a wormlike lingual appendage with which to lure fish, but it also eats mollusks, other invertebrates, and plant matter. *Chelydra* catches prey from ambush and also actively searches for prey, which includes all forms of aquatic vertebrates, invertebrates, and plant material. *M. temminckii* usually lives in lakes and deep, slow-moving streams, although it often travels long distances and forages in smaller streams. *Chelydra* is mainly a shallow-water inhabitant and occurs in freshwater habitats. Egg laying is mainly in spring and early summer for both taxa, and clutch size is related to female body size; *M. temminckii* has the largest clutches (20–50 eggs). Clutches of *M. temminckii* are not as large as might be expected based on its body size, differing little from the clutch size seen in *Chelydra*.

References Congdon et al., 1994; Ernst et al., 1994; Roman et al., 1999; Sites and Crandall, 1997.

Platysterninae

Sister taxa Chelydrinae

Content Monotypic, *Platysternon megacephalum*.

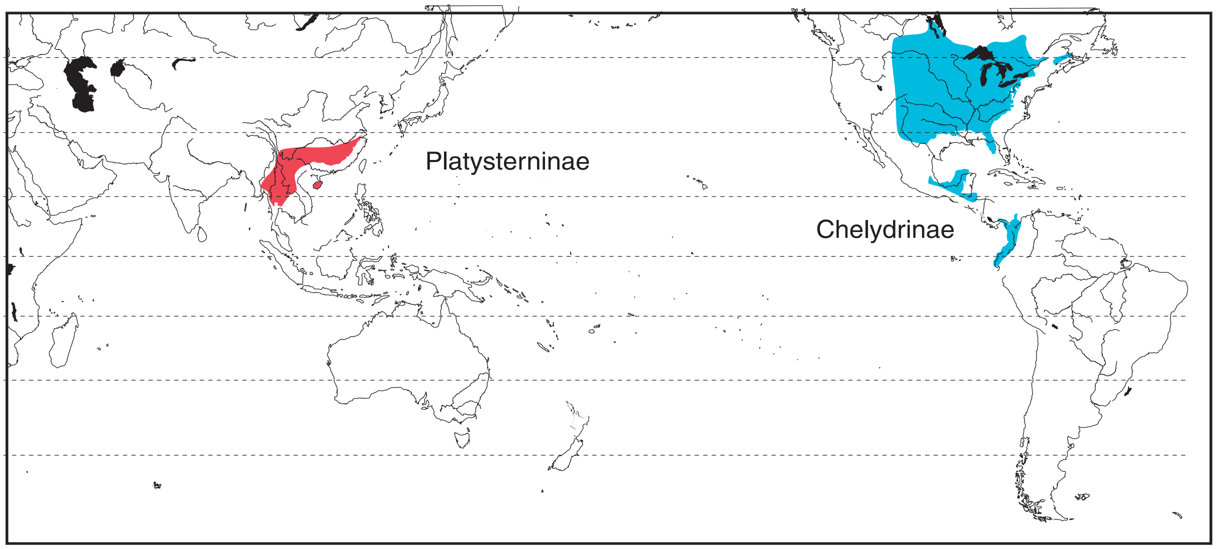


FIGURE 18.9 Geographic distribution of the extant Chelydridae.

Distribution Southern China southward into Thailand (Fig. 18.9).

Characteristics The plastron is moderate sized and the plastral bridge is flexible; the skull roof is complete.

Biology *Platysternon megacephalum* (Fig. 18.8) has been rarely studied in the wild, and its biology is known principally from captive animals. This species occurs in small, rocky streams in mountainous areas, mostly above 700 m in elevation. Presumably it forages at night and spends the day hiding beneath rocks and logs in streams. In captivity, its eats a variety of animal matter, and likely it also eats fish, frogs, and assorted invertebrates in the wild. Clutch size consists of one to three eggs.

References Cox et al., 1998; Ernst and Barbour, 1989a.

Chelonioidea

Cheloniidae

Hard-shelled seaturtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Dermochelyidae.

Content Five genera, *Caretta*, *Chelonia* (Fig. 18.10), *Eretmochelys*, *Lepidochelys*, and *Natator*, with six species.

Distribution Worldwide in tropical and temperate seas (Fig. 18.11).

Characteristics Cheloniid seaturtles are large, ranging in adult CL from about 60 cm (*Lepidochelys*) to 1.0–1.4 m (*Chelonia*). They have flattened, streamlined shells covered with epidermal scutes and forelimbs modified into large flippers. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and there is strong parietal–squamosal and postorbital–squamosal contact. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses do not join into the costals of the carapace; the carapace has 11 or more pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is $2N = 56$.

Biology Cheloniids are marine turtles, emerging on land only to nest and rarely to bask (Hawaiian and Galapagos *Chelonia mydas*). They swim via forelimb propulsion; the flippers move in a figure-eight stroke, just as in avian aerial flight but with forward thrust produced by both the up and the down stroke; strongly webbed hindfeet serve mainly as rudders. As adults, all cheloniids except *Lepidochelys olivacea* are nearshore or continental slope residents. Cheloniids appear to have a pelagic stage from immediately after hatching for about 4 to 12 years. Although this aspect of juvenile biology is unknown for *Natator depressus*, presumably newly hatched juveniles are not pelagic. Cheloniids tend to be dietary specialists as adults; for example, *C. mydas* (Fig. 18.10) eats mainly marine grasses or algae, *Caretta caretta* eats decapod

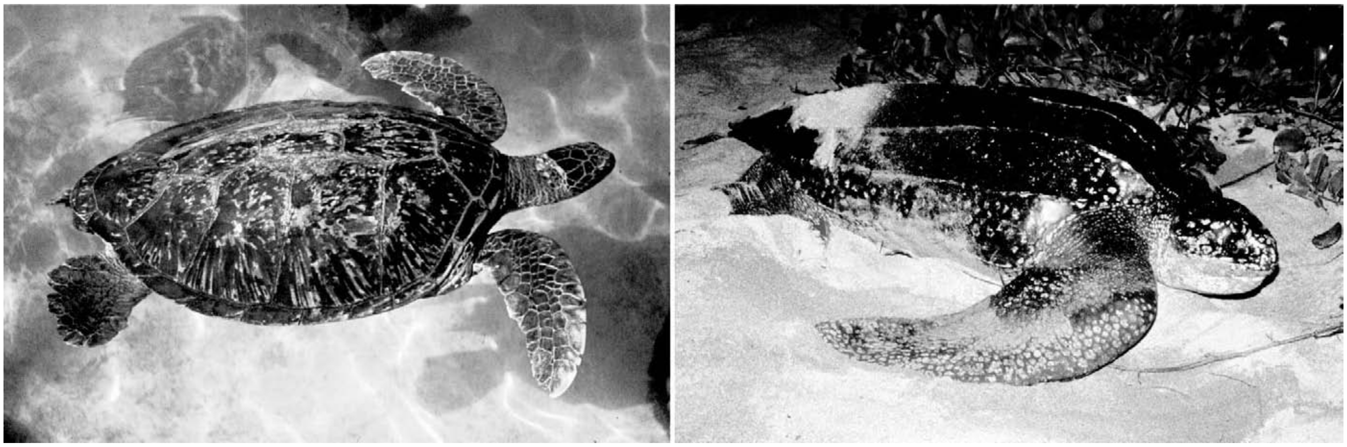


FIGURE 18.10 Representative chelonioid turtles. From left: green seaturtle *Chelonia mydas*, Cheloniidae (photograph by G. R. Zug); and leatherback seaturtle *Dermochelys coriacea*, Dermochelyidae (C. K. Dodd, Jr.).

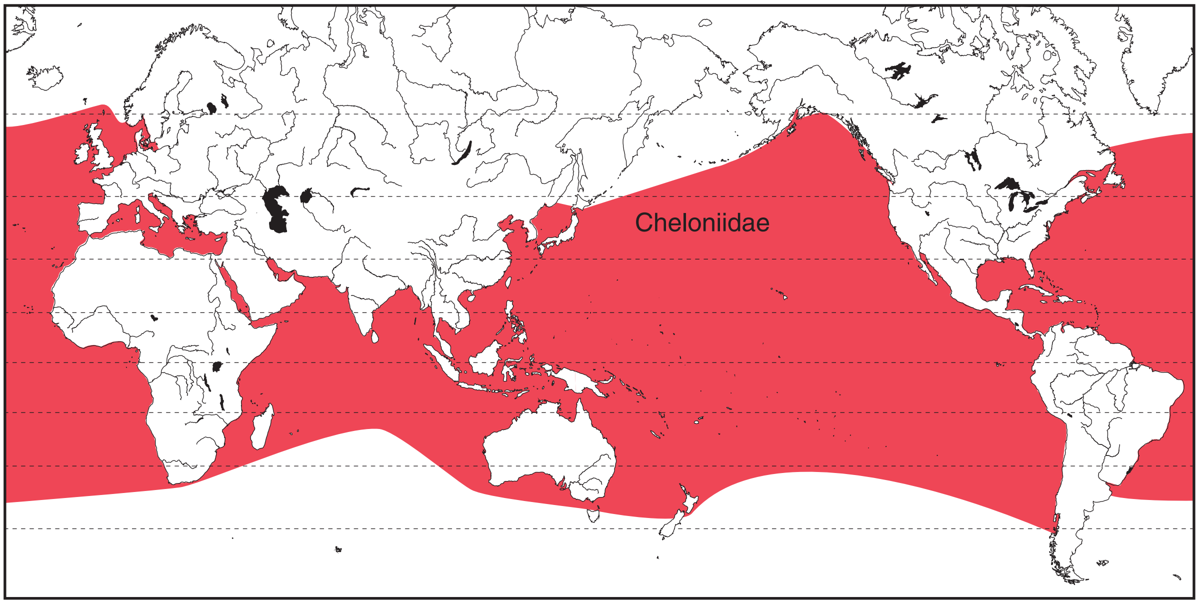


FIGURE 18.11 Geographic distribution of the extant Cheloniidae.

crustaceans and mollusks, and *Eretmochelys imbricata* eats sponges and soft corals. Most seaturtles (*Lepidochelys* excepted) require 25 or more years to reach reproductive maturity and have a multiyear reproductive cycle. During a reproductive season, a female typically deposits two to five clutches of eggs at approximately 2-week intervals. Clutch size is variable within a species, depending to some extent on female's body size and nourishment; typically clutch size is more than a 100 eggs. *E. imbricata* has the highest average clutch size, 130, and *N. depressus* the lowest, 52 eggs.

References Bjorndal, 1996; Gaffney et al., 1991; Limpus and Miller, 1993; Márquez, 1990; Miller, 1996; Shaffer et al., 1997.

Dermochelyidae

Leatherback seaturtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Cheloniidae.

Content Monotypic, *Dermochelys coriacea*.

Distribution Worldwide in tropical to cold temperate seas (Fig. 18.12).

Characteristics Adult leatherbacks average from 1.34 to 1.67 m CL among different populations. They have broad, streamlined, ridged shells that lack epidermal scutes (Fig. 18.10). Their forelimbs are modified into large flippers, and their hindlimbs are typical for turtles but strongly webbed. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and there is strong contact between the parietal and squamosal and the postorbital and squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses do not link into the costals of the carapace; the carapace has numerous atypical peripherals along the lateral margins and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is $2N = 56$.

Biology Leatherbacks are highly specialized, pelagic seaturtles (Fig. 18.10). They are unique among the living reptiles because they are inertial endotherms (see Chapter 7). They maintain body temperatures above ambient temperatures and do so even in the cooler waters of the north and south temperate zones. Body heat is generated by muscle activity, not by cellular metabolism as in avian reptiles. Heat loss is reduced by the large surface to body ratio and by the high insulation properties of an oil-laden skin. To further conserve body heat, the forelimbs have a circulatory counterflow system

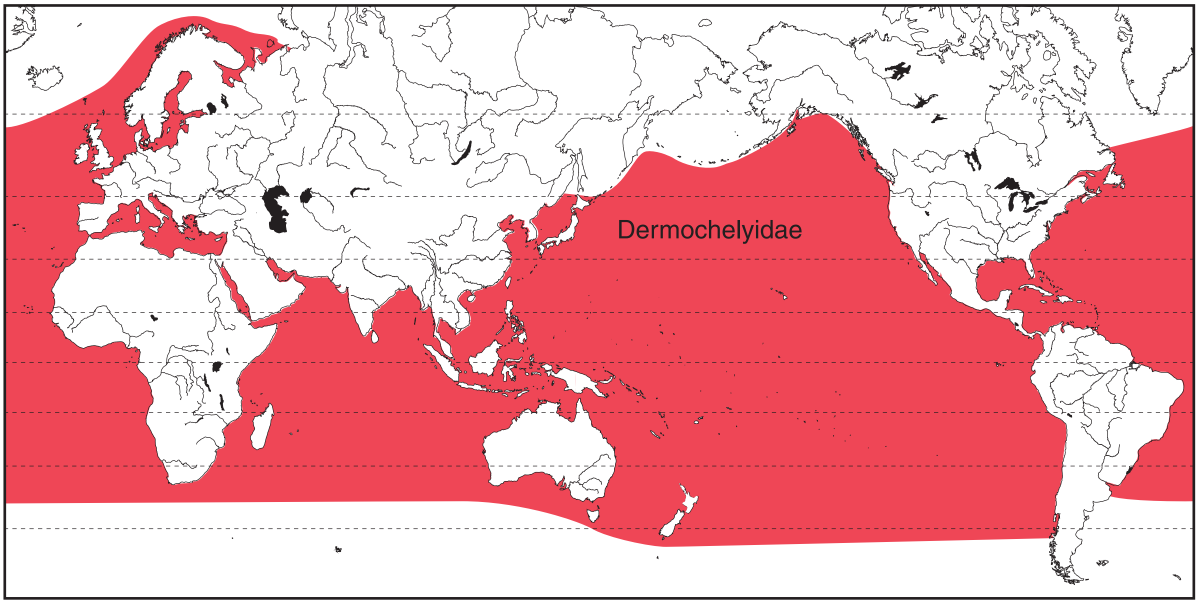


FIGURE 18.12 Geographic distribution of the extant Dermochelyidae.

that transfers heat from the arteries to the veins and back to the body core. It is unknown at what stage juveniles shift from ectothermy to inertial endothermy, although the shift is probably size related owing to the physics of heat exchange associated with surface to volume ratio. Amazingly, leatherbacks support their endothermy on a diet of jellyfish, salps, and other gelatinous invertebrates, prey more liquid than solid but obviously highly nutritious. Leatherbacks are highly migratory, potentially crossing and recrossing the length and breadth of entire ocean basins. Their movements seem tied to the pursuit of jellyfish blooms and other aggregations of their prey. Like their sister group, the cheloniids, dermochelyids have a multiyear reproductive cycle. Females return to their nesting beaches, mainly on biennial to triennial reproductive cycles, and lay multiple clutches within one nesting season. Clutch size averages about 80 eggs (range, 46–160), and most clutches contain a moderate percentage of yolkless eggs, the function of which remains a mystery.

References Bjorndal, 1996; Gaffney et al., 1991; Limpus, 1993; Márquez, 1990; Miller, 1996; Shaffer et al., 1997; Zug and Parham, 1996.

Chelomacryptodira, Trionychoidea

Carettochelyidae

Pig-nosed turtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Trionychidae.

Content Monotypic, *Carettochelys insculpta*.

Distribution Southern New Guinea and northwestern Australia (Fig. 18.13).

Characteristics Adults have heavy, moderately domed shells and range from 30 to 55 cm CL. The shell lacks epidermal scutes; instead, it is covered with a smooth epidermal skin. The forelimbs are modified

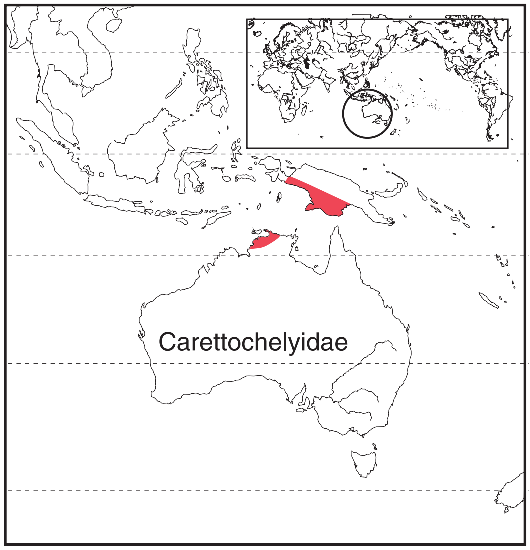


FIGURE 18.13 Geographic distribution of the extant Carettochelyidae.

flippers with two well-developed claws. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses form firm articulations with the costals of the carapace. The carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium has a thelial process. The karyotype is $2N = 68$.

Biology *Carettochelys insculpta* (Fig. 18.14) is a highly aquatic turtle. It lives mainly in large rivers and estuaries associated with rivers. Like seaturtles, the flipper-shaped forelimbs are the major locomotor appendages and propel the animal using a figure-eight stroke. This type of stroke mimics underwater flying in seaturtles and penguins, and apparently is used predominantly for slow and moderate-speed locomotion; when pursued, it reverts to the typical quadrapedal swimming gait of other aquatic turtles. The broadly webbed hindlimbs are typical of aquatic testudines. Pig-nosed turtles emerge from the water only to lay eggs. Nesting occurs in the latter part of the dry season, mainly from August to October when the river sandbanks and sandbars are exposed. Clutch size is about 7 to 19 eggs, which hatch after an 8- to 10-week incubation. *C. insculpta* is an opportunistic omnivore; fruit, seeds, and leaves of riparian vegetation and submergent plants are commonly eaten, as are a variety of invertebrates and vertebrates.

References Cann, 1998; Gaffney et al., 1991; Georges and Wombey, 1993; Shaffer et al., 1997; Webb et al., 1986.

Trionychidae

Softshell turtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Carettochelyidae.

Content Two subfamilies, Cyclanorbinae and Trionychinae.

Distribution North America, Africa, and South and East Asia to New Guinea (Fig. 18.15).

Characteristics Softshells are flattened, pancake-shaped turtles that have reduced bony carapaces and plastrons. The carapace and plastron are naked, lacking epidermal scutes, but are covered with a thick, leathery skin. The jaw closure mechanism articulates on the trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and plastral buttresses do not form. The flattened carapace lacks peripheral bones (except in *Lissemys*), and the nuchal lacks costiform processes. The neck withdraws vertically; this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra. Other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium has a thelial process. The karyotype is $2N = 66$.

References Meylan, 1987; Shaffer et al., 1997.

Cyclanorbinae

Sister taxa Trionychinae.

Content Three genera, *Cyclanorbis*, *Cycloderma*, and *Lissemys*, with six species.

Distribution Sub-Saharan and northeastern central Africa, and South Asia (Fig. 18.15).

Characteristics The latticelike plastral skeleton has bilaterally fused hyoplastral and hypoplastral bones, and externally the plastron has well-developed femoral flaps.

Biology Flap-shelled softshells are small to moderate-sized turtles. The smallest taxon is *Lissemys* (maximum adult CL, 37 cm) and the largest is *Cyclanorbis elegans* (to 60 cm). The biology of the African taxa, *Cyclanorbis* and *Cycloderma*, is little studied; the south Asian *Lissemys* is somewhat better known. All cyclanorbines are probably bottom-dwellers like trionychines. They actively forage and also lie partially hidden in the bottom silt or sand, waiting for passing prey. They are presumably opportunistic omnivores, eating invertebrates, small vertebrates, and occasional plant matter. Clutch size is small to modest; *Lissemys punctata* deposits 2 to 14 eggs. Good evidence indicates that clutch size varies geographically and that females produce multiple clutches each year. Incubation ranges from 30 to 40 days to more than 300 days.

References Das, 1995; Ernst and Barbour, 1994; Rashid and Swingland, 1998.

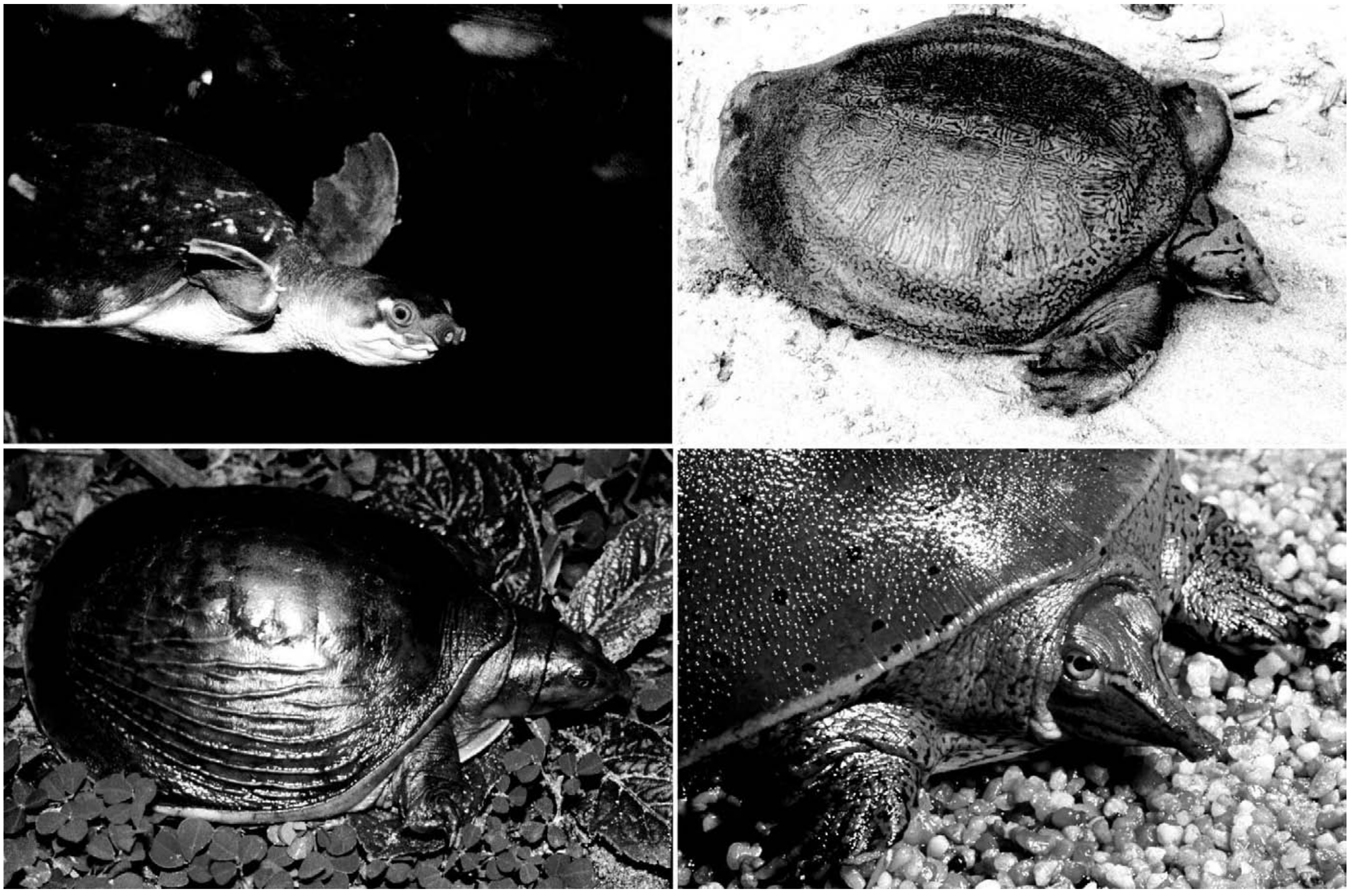


FIGURE 18.14 Representative trionychoid turtles. Clockwise from upper left: pig-nosed turtle *Carettochelys insculpta*, Carettochelyidae (photograph by R. W. Barbour); Indian softshell turtle *Aspideretes gangeticus*, Trionychinae (E. O. Moll); spiny softshell turtle *Apalone spinifera*, Trionychinae (R. W. Barbour); and Burmese flapshell turtle *Lissemys scutata*, Cyclanorbinae (G. R. Zug).

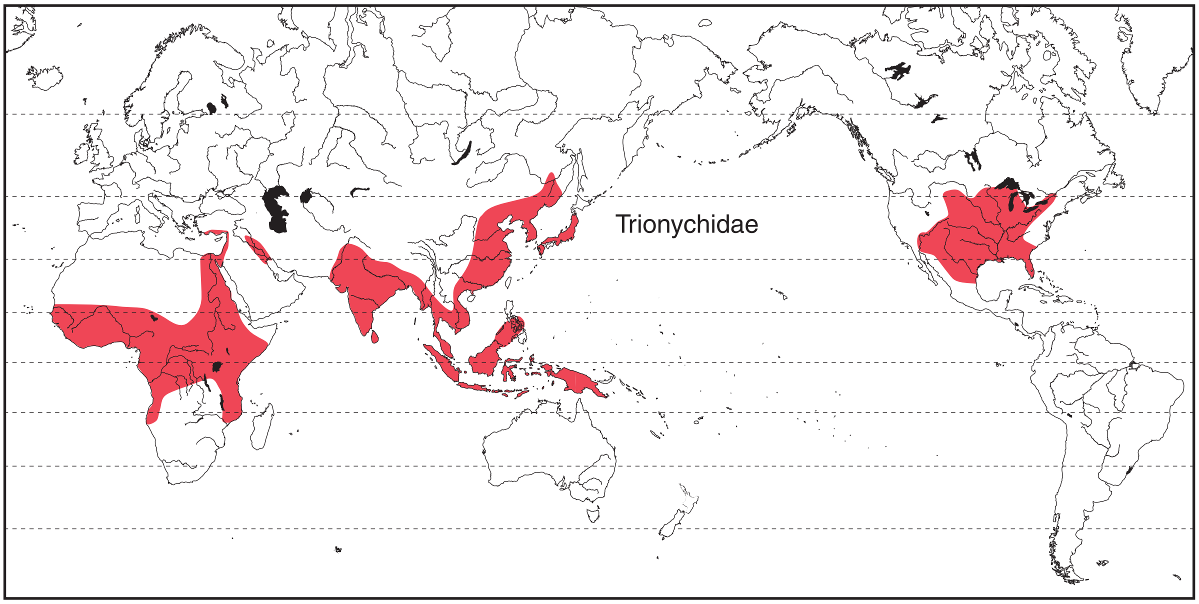


FIGURE 18.15 Geographic distribution of the extant Trionychidae.

Trionychinae

Sister taxa Cyclanorbinae.

Content Eleven genera, *Amyda*, *Apalone*, *Aspideretes*, *Chitra*, *Dogania*, *Nilssonia*, *Palea*, *Pelochelys*, *Pelodiscus*, *Rafetus*, and *Trionyx*, with 20+ species.

Distribution Eastern North America, South Asia to Japan and southward to New Guinea, and north-central sub-Saharan Africa into Southwest Asia (Fig. 18.15).

Characteristics The latticelike plastral skeleton has separate hyoplastral and hypoplastral bones on each side, and externally the plastron lacks femoral flaps.

Biology Trionychine softshells are moderate to large turtles (Fig. 18.14). *Pelodiscus sinensis*, the Chinese softshell, is the smallest species (20–25 cm adult CL); *Pelochelys* and *Chitra* are much larger with shell lengths to more than a meter as adults, and the other genera range in adult CL from 40 to 60 cm. All are highly aquatic turtles, spending much of their time partially buried on the bottom waiting for prey. Their long necks and protruding, snorkellike snouts permit them to extend their noses to the water surface to breathe; they also depend to some extent upon cutaneous respiration. They actively forage for prey, and their flattened hydrodynamically efficient habitus makes them excellent and fast swimmers. Softshells live primarily in rivers and lakes. *Dogania subplana* appears to be the only softshell that occurs in small, mountain streams. All trionychines are predominantly carnivorous, although they likely feed on plant matter, particularly when animal prey is not readily available. Temperate and subtemperate species are predominately spring breeders, and tropical species lay eggs in the early dry season. Clutch size is small to moderate; for example, the three species of *Apalone* deposit 4 to 30 eggs, whereas the smaller *P. sinensis* lays 9 to 15 eggs per clutch. *Trionyx triunguis* reaches 95 cm CL and can deposit over 100 eggs, but more typically it produces half that number. Incubation generally requires 8 to 10 weeks, although in *Aspideretes gangeticus*, it is 36 to 42 weeks or as brief as 28 days in *P. sinensis.*

References Das, 1995; Ernst and Barbour, 1989a; Ernst et al., 1994; Kuchling, 1999; Plummer, 1977a,b; Rashid and Swingland, 1998; Vasudevan, 1997.

Chelomacryptodira, Kinosternoidea

Dermatemydidae

Mesoamerican river turtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Kinosternidae.

Content Monotypic, *Dermatemys mawii.*

Distribution Caribbean–Gulf drainage of Mesoamerica (Fig. 18.16).

Characteristics *Dermatemys mawii* has an oblong, slightly domed carapace, a large plastron, and a moderately small head. Its jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses articulate with costals of the carapace; the carapace has 10 pairs of sutured peripherals around its margin and a nuchal with distinct costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium has a thelial process. The karyotype is 2N = 56.

Biology *D. mawii* is a moderately large and highly aquatic turtle (Fig. 18.17). Adults range in CL from 33 to 65 cm. They live predominantly in slow-moving areas of large rivers and lakes. Adults and juveniles are totally herbivorous; they eat a variety of aquatic plants and

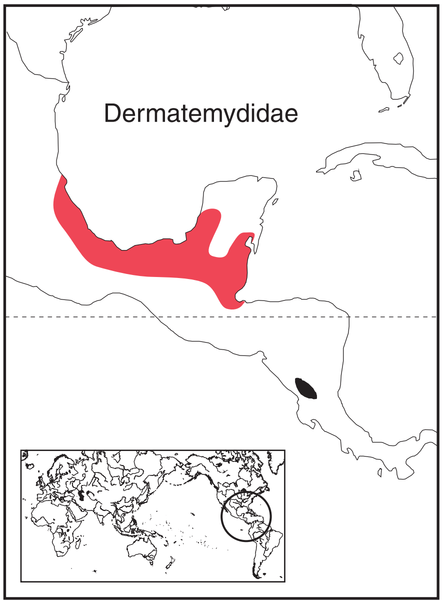


FIGURE 18.16 Geographic distribution of the extant Dermatemydidae.

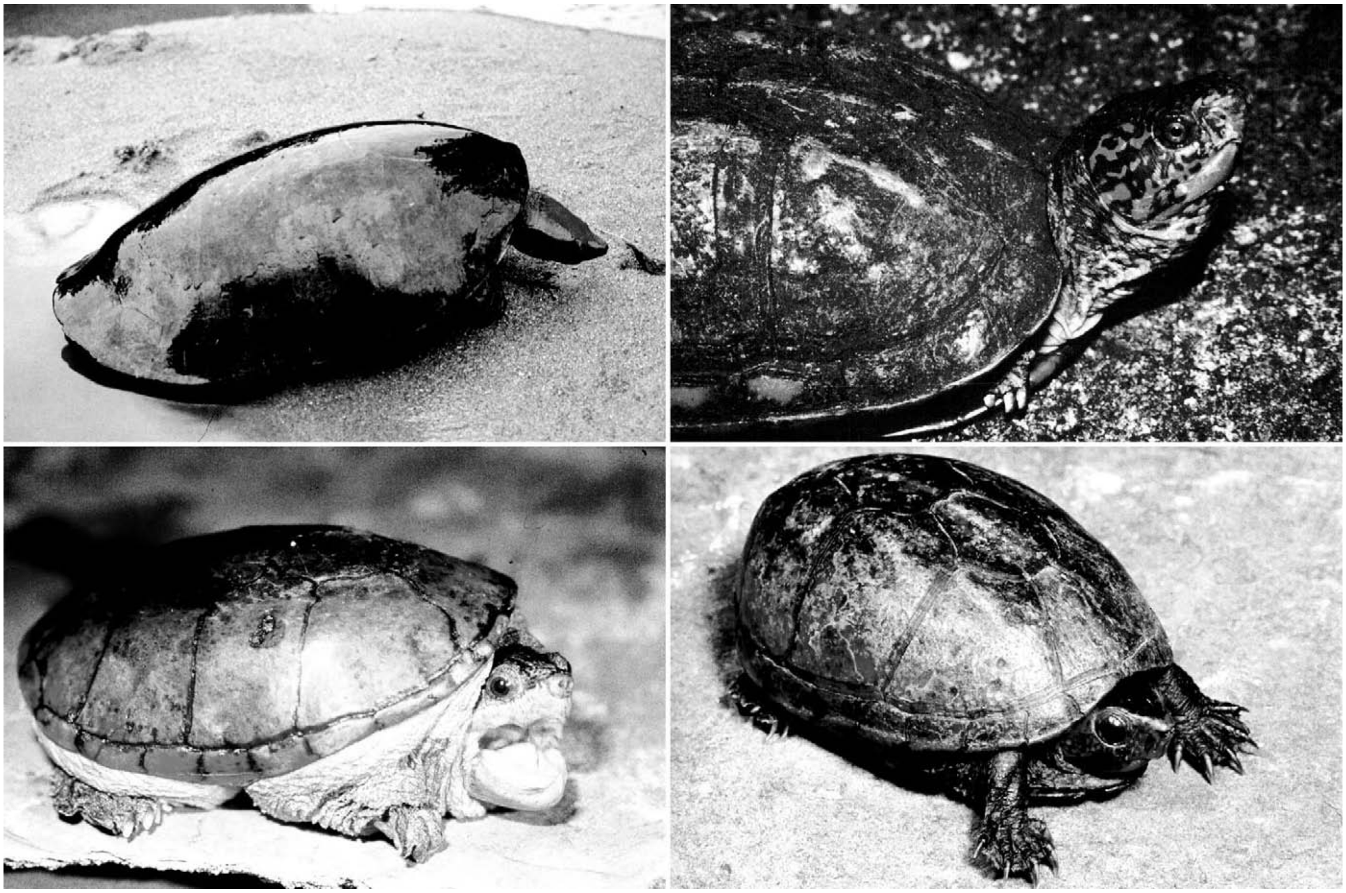


FIGURE 18.17 Representative kinosternoid turtles. Clockwise from upper left: Mesoamerica river turtle *Dermatemys mawii*, Dermatemydidae (photograph by D. Moll); Tabasco mudturtle *Kinosternon acutum*, Kinosterninae (G. R. Zug); striped mudturtle *Kinosternon baurii*, Kinosterninae (R. W. Barbour); and narrow-bridged muskturtle *Claudius angustatus*, Staurotypinae (R. W. Barbour).

streamside vegetation, fruits, and seeds that fall into the water, particularly figs. Presumably, they are nocturnal, spending the day resting near the bottom or basking at the surface of the water; foraging occurs at night. The turtles court and mate from May to September; egg deposition (2–20 eggs in a clutch) occurs mainly from October to December, and a single individual will deposit eggs as many as four times. Females nest along streams. In Belize, the nesting occurs during the period with greatest rainfall and rising river levels; some early nests are submerged, but developmental arrest allows the embryos to survive. Incubation in these populations is 8 to 10 months; hatching occurs in June and July with the beginning of the rainy season.

Comment This unique turtle is easily captured and prized as a local food item. Human exploitation has decimated and extirpated most populations throughout this taxon's small range, and it is now as endangered as many of the Asian turtles.

References Gaffney et al., 1991; Ernst et al., 1994; Moll, 1989; Polisar, 1996; Shaffer et al., 1997.

Kinosternidae

Mudturtles and muskturtles

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Dermatemydidae.

Content Two subfamilies, Kinosterninae and Staurotypinae.

Distribution Eastern North America to the Amazon drainage of South America (Fig. 18.18).

Characteristics Kinosternids have oblong, moderately domed carapaces and moderate to large heads. The plastron is commonly hinged and has 11 or fewer epidermal scutes. The jaw closure mechanism articulates

FIGURE 18.18 Geographic distribution of the extant Kinosternidae.

on the trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses do not form interdigitating articulations with costals of the carapace; the carapace has 10 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium has a thelial process. The karyotype is 2N = 54 or 56.

References Gaffney et al., 1991; Iverson, 1991a, 1998; Shaffer et al., 1997.

Kinosterninae

Sister taxa Staurotypinae.

Content Two genera, *Kinosternon* and *Sternotherus*, with 16+ and 4 species, respectively.

Distribution Eastern North America to the Amazon drainage of South America (Fig. 18.18).

Characteristics The well-developed plastron lacks an entoplastral bone and is usually hinged.

Biology Mud and muskturtles are small to moderate-sized turtles (Fig. 18.17), ranging in adult CL from 8 to 12 cm (e.g., *Sternotherus depressus*) and from 15 to 27 cm (*Kinosternon scorpioides*); most species have a maximum adult shell length of less than 18 cm. They are generally aquatic species and live in various waterways, including ephemeral pools, marshes and swamps, and large rivers and lakes. All are bottom-walkers and poor swimmers. They forage and mate in water; however, some species hibernate on land and others, particularly tropical species, appear to forage on land during wet weather. Their generally small size correlates with small clutch sizes, most commonly 1 to 4 eggs, although clutches of up to 16 eggs are deposited in the larger taxa. Incubation is moderately long, usually 100 to 150 days. Kinosternines are omnivorous to carnivorous; their diets are dominated by aquatic invertebrates, small vertebrates, and carrion. Some taxa (e.g., *Sternotherus minor*) are molluscivores, and these turtles have proportionately larger heads because of large jaw muscles and broad jaw surfaces for crushing snails and bivalves. This molluscivore megacephaly occurs in other turtle clades.

References Ernst et al., 1994; Frazer et al., 1991; Gibbons, 1970; Iverson, 1991b; Iverson et al., 1993; Moll, 1990; van Loben Sels et al., 1997.

Staurotypinae

Sister taxa Kinosterninae.

Content Two genera, *Claudius* and *Staurotypus* (Fig. 18.17), with one and two species, respectively.

Distribution The Caribbean and Gulf of Mexico and Pacific drainage of Mesoamerica (Fig. 18.18).

Characteristics The plastron has an entoplastral bone, and the plastron is either moderately reduced with a hinge (*Staurotypus*) or strongly reduced (cruciform) without a hinge (*Claudius*).

Biology Staurotypines include the small species *Claudius angustatus* (9–15 cm adult CL) and the largest kinosternid species, *Staurotypus triporcatus* (30–38 cm CL). The biology of the three species is poorly known. *C. angustatus* occurs principally in seasonally flooded marshes or pastures and appears to be active only during the rainy season (June–February). Nesting occurs at the end of the wet season (November–February), and from one to five eggs are deposited beneath vegetation; the stereotypic nest digging does not occur. The natural incubation period is unknown, and captive incubation is long, about 100 to 200 days. The two *Staurotypus* inhabit slow- to fast-flowing waters of marshes to large rivers, and rarely occur in ephemeral waters.

Reproduction in captive individuals suggests only a slightly larger clutch (3–10 eggs) for *Staurotypus*. All staurotypines are carnivorous, feeding on a variety of aquatic invertebrates and small vertebrates; *S. triporcatus* feeds heavily on snails year around and occasionally other turtles become a major prey.

References Ernst and Barbour, 1989a; Flores-Villela and Zug, 1995; Moll, 1990; Vogt and Guzman, 1988.

Testudinoidea

Emydidae

Cooters, sliders, American boxturtles, and allies

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Clade containing Bataguridae and Testudinidae.

Content Ten genera, *Chrysemys*, *Clemmys*, *Deirochelys* (Fig. 18.19), *Emydoidea*, *Emys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, and *Trachemys*, with 40+ species.

Distribution Europe to Ural Mountains and North America southward to northeastern Brazil (Fig. 18.20).

Characteristics Emydids include small species such as *Clemmys muhlenbergii* (8–11 cm adult CL) to moderate-sized species, such as *Pseudemys concinna* (35–40 cm CL). These turtles have oval to oblong and moderately domed carapaces; the plastron is large and occasionally hinged. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses usually articulate with the costals of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is $2N = 50$.

Biology Emydids are predominantly semiaquatic to aquatic turtles (Fig. 18.19); they live in most permanent water habitats from marshes to large rivers and lakes. *Terrapene* is mainly a terrestrial group, whereas *Malaclemys terrapin* is largely estuarine and adapted to brackish water. With the exceptions of *Pseudemys* and female *Trachemys* and *Graptemys*, adult CL of emydids is less than 20 cm. Sexual dimorphism is common and often strikingly so in *Pseudemys* and *Graptemys*. In *Graptemys*, adult males are commonly one-half the size of adult females; for example, female *Graptemys barbouri* are 17 to 26 cm CL and males only 9 to 13 cm. Most taxa are omnivores, and juveniles eat mainly animal prey; in contrast, the large *Pseudemys* are strongly herbivorous. These predominantly temperate turtles deposit eggs in spring; hatching occurs later in the summer, commonly with a 60- to 80-day incubation period. Hatchlings of some species, for example, *Chrysemys picta*, regularly overwinter in the nest in the northern part

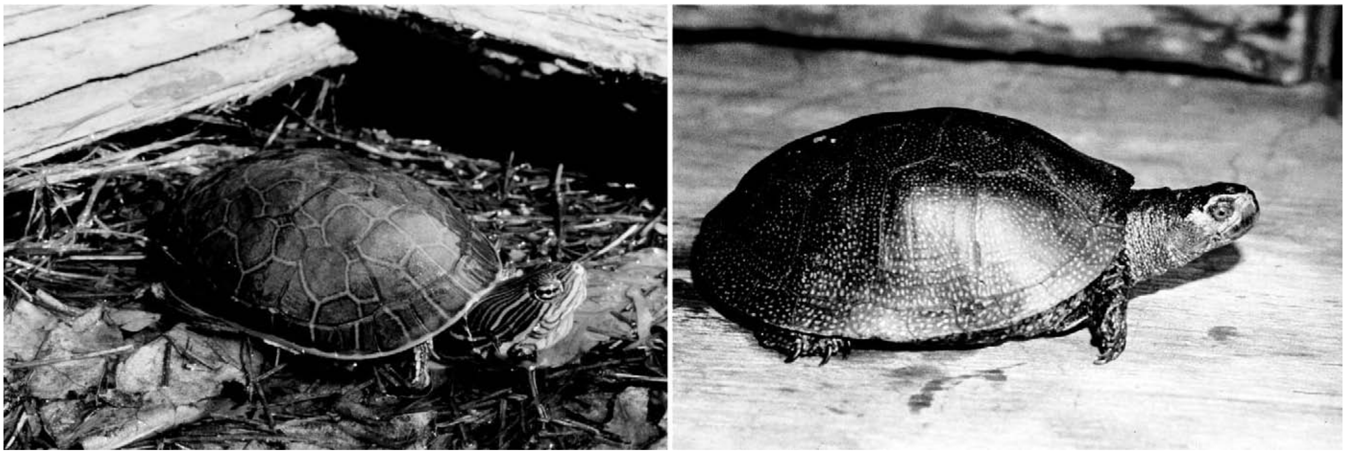


FIGURE 18.19 Representative emydid turtles. (Left) Chicken turtle *Deirochelys reticularia*, Emydidae (photograph by L. J. Vitt). (Right) European pond turtle *Emys orbicularis*, Emydidae (R. W. Barbour).

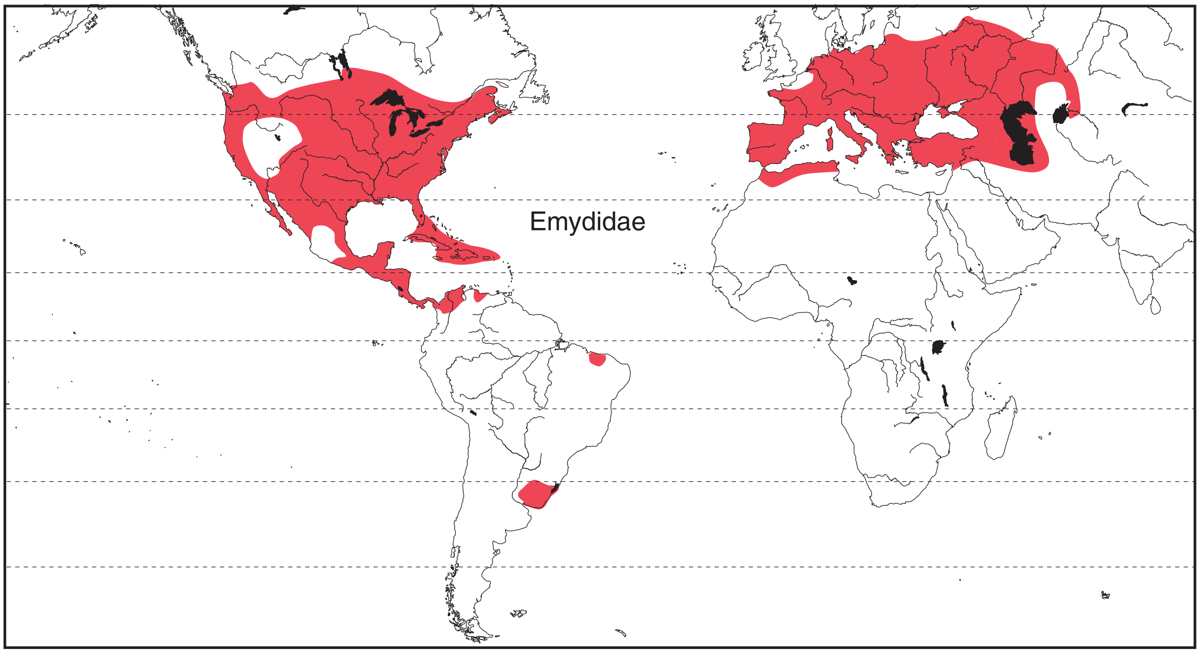


FIGURE 18.20 Geographic distribution of the extant Emydidae.

of their distribution. Clutch size is small to modest; 2 to 10 eggs compose the average clutch for most emydids, although *Pseudemys* and *Trachemys* typically have larger clutches.

References Ernst et al., 1994; Gaffney et al., 1991; Gibbons, 1990; Shaffer et al., 1997.

Testudinoidea, Testudinoidea

Bataguridae

Asian river turtles, leaf and roofed turtles, Asian box-turtles, and allies

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Testudinidae.

Content Twenty-three genera, *Annamemys, Batagur, Callagur, Chinemys, Cuora, Cyclemys, Geoclemys, Geoemyda, Hardella, Heosemys, Hieremys, Kachuga, Malayemys, Mauremys, Melanochelys, Morenia, Notochelys, Ocadia, Orlitia, Pyxidea, Rhinoclemmys, Sacalia, and Siebenrockiella, with 65+ species.*

Distribution Southern Europe to Japan and East Indies, and Central and northern South America (Fig. 18.21).

Characteristics Batagurids are small to large turtles with oval to oblong and moderately domed or flattened carapaces; the plastron is large and occasionally hinged. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses usually articulate firmly with the costals of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is 2N = 52.

Biology Batagurids are a diverse group of turtles (Fig. 18.22). They range in adult CL from the small *Geoemyda spengleri* and *Heosemys silvatica* (to 13 cm) to the large *Orlitia borneensis* (to 80 cm), and from totally terrestrial (*G. spengleri*, *H. silvatica*) to highly aquatic species that emerge on land only to lay eggs (*O. borneensis*, *Batagur baska*). Some species live in mountain streams (*Cyclemys dentata*, *Cuora trifasciata*) or estuaries (*B. baska*, *Callagur borneoensis*). Taxa are specialized carnivores (aquatic snails eaten by male *Malayemys subtrijuga*) to strict herbivores (*Kachuga*

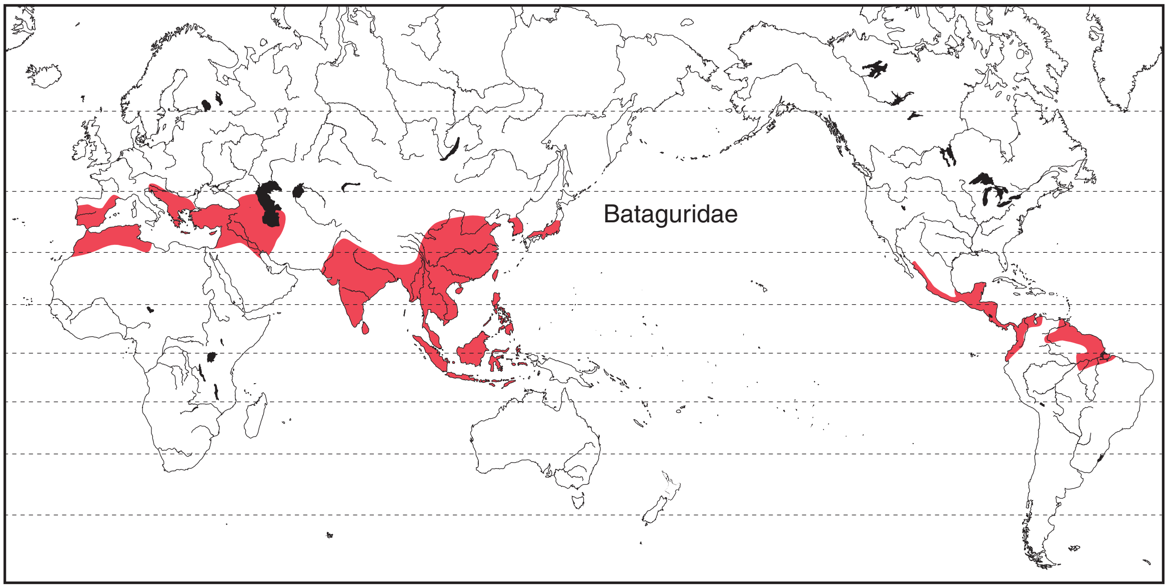


FIGURE 18.21 Geographic distribution of the extant Bataguridae.

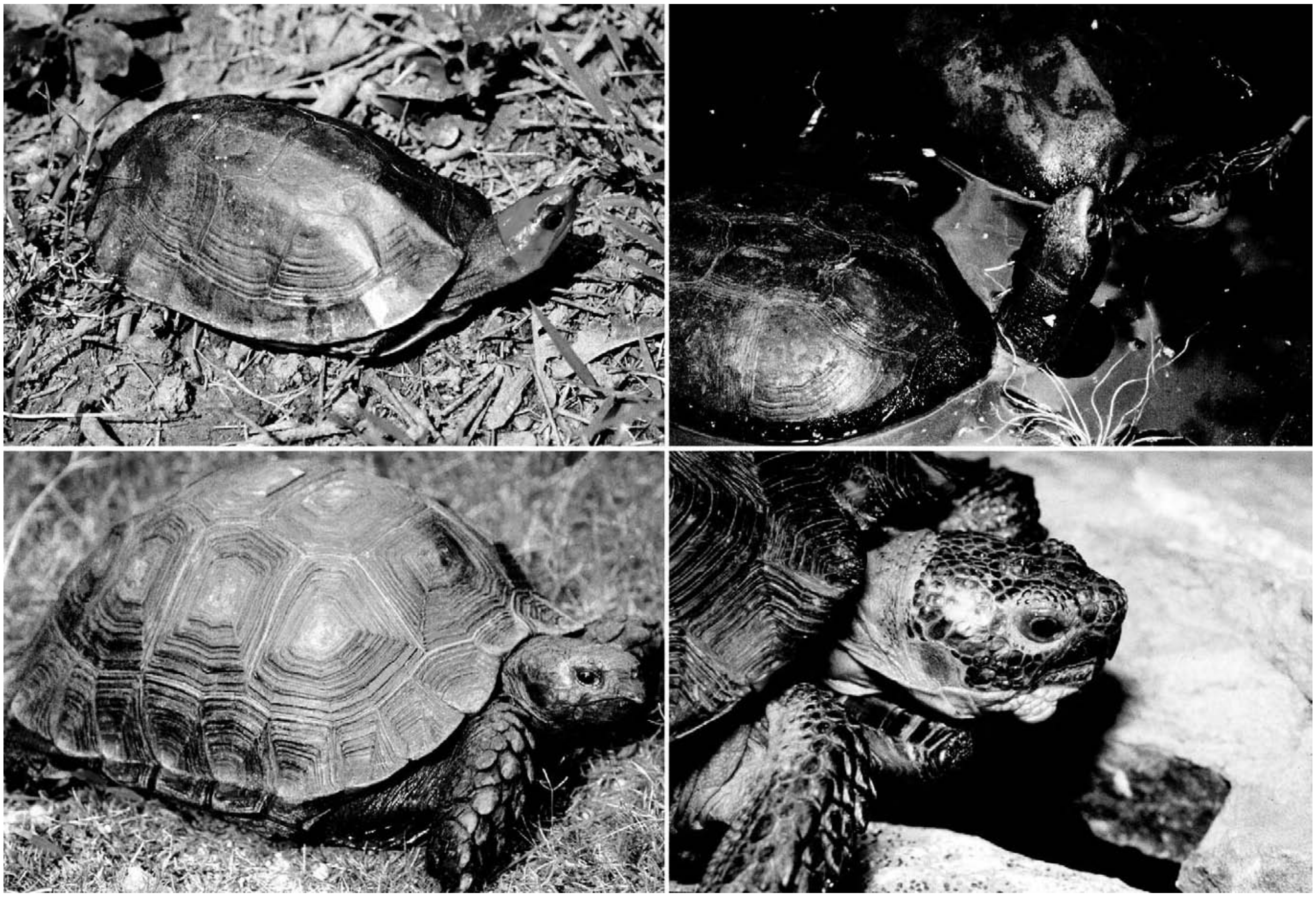


FIGURE 18.22 Representative batagurid turtles and tortoises. Clockwise from upper left: yellow-headed box turtle *Cuora aurocapita*, Bataguridae (photograph by C. H. Ernst); giant Asian pond turtle *Heosemys grandis*, Bataguridae (G. R. Zug); Berlandier's tortoise *Gopherus berlandieri*, Testudinidae (R. W. Van Devender); and Asian brown tortoise *Manouria emys*, Testudinidae (R. W. Barbour).

smithi). Within a single clade, habits and habitat preferences can be strikingly different. For example, the Neotropical *Rhinoclemmys* has totally terrestrial species (e.g., *annulata*), semiaquatic species (*aerolata*), and highly aquatic species (*nasuta*); the terrestrial and aquatic species are either herbivorous or omnivorous. Shell morphology is similarly diverse and includes high-domed to flattened species. Reproductive behavior is only beginning to be documented. Most species produce fewer than 10 eggs per clutch, although many appear to have multiple clutches within a single reproductive season. The largest clutches occur in *Geoclemys hamiltoni* (18–30 eggs; females 30–40 cm CL) and *Kachuga dhongoka* (30–35 eggs; females to 48 cm CL); yet the large *B. baska* (50–60 cm CL) averages 20 eggs per clutch, and the similar sized *Ca. borneoensis* (50–60 cm CL) has clutches of 15 to 25 eggs. Incubation period is unknown for most species, but where known, it is commonly from 3 to 5 months.

Comment Batagurids are the most speciose group of extant turtles. Because many species have small distributions and occur in the most densely human-populated part of the world, they are subjected to the highest levels of human predation. Conservation and culture are in conflict. The former is largely ignored, and the likely consequence is that many Asian turtles will become extinct during the next decade.

References Cox et al., 1998; Das, 1995; Ernst and Barbour, 1989a; Gaffney et al., 1991; Rashid and Swingland, 1998; Shaffer et al., 1997.

Testudinidae

Tortoises

Classification Reptilia; Parareptilia; Testudines; Cryptodira.

Sister taxa Bataguridae.

Content Eleven genera, *Chersina*, *Geochelone*, *Gopherus*, *Homopus*, *Indotestudo*, *Kinixys*, *Malacochersus*, *Manouria*, *Psammobates*, *Pyxis*, and *Testudo*, with 45+ species.

Distribution Southern North America to southern South America, circum-Mediterranean Euro-Africa to Indo-Malaysia, sub-Saharan Africa, Madagascar, and some oceanic islands (Fig. 18.23).

Characteristics With a single exception (*Malacochersus tornieri*), all tortoises have well-developed, high-domed shells, and without exception, all share unique columnar or elephantine hindlimbs. The jaw closure mechanism articulates on a trochlear surface of the otic capsule and is enclosed in a synovial capsule. An epipterygoid is present in the skull; the internal carotid canal lies in the pterygoid, and the parietal but not the postorbital touches the squamosal. The facial nerve lacks a hyomandibular branch. The plastron lacks a mesoplastron, and the plastral buttresses articulate firmly with the costals of the carapace; the carapace has 11 pairs of sutured peripherals around its margin and a nuchal without costiform processes. The neck withdraws vertically, and this

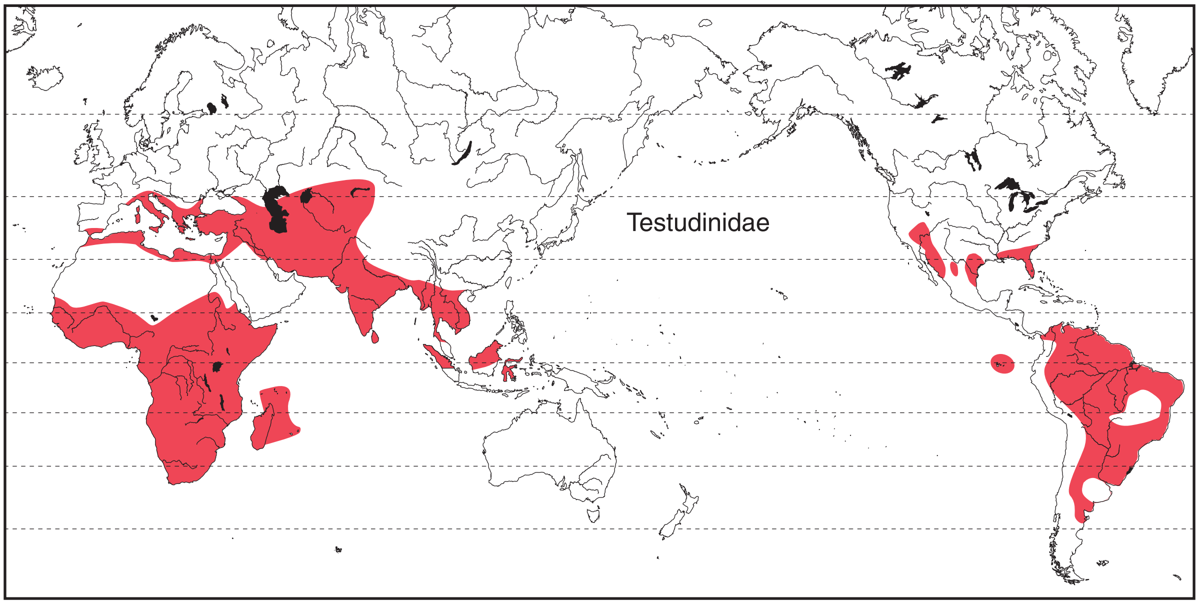


FIGURE 18.23 Geographic distribution of the extant Testudinidae.

mechanism is reflected in an anteroventrally oriented articular surface of the first thoracic vertebra; other vertebral traits are the exclusion of the 10th thoracic vertebra from the sacral complex and procoelous caudal vertebrae. The pelvic girdle flexibly articulates with the plastron, and the ilium lacks a thelial process. The karyotype is 2N = 52.

Biology All tortoises are terrestrial (Fig. 18.22). They live in diverse habitats, including deserts, arid grasslands and scrub (*Gopherus agassizii*, *Testudo kleinmanni*), and wet evergreen forests (*Geochelone denticulata*, *Kinixys erosa*), and from sea level (*Geochelone gigantea*) to mountainsides (1000 m elevation; *Indotestudo forsteni*). Most species, however, occupy semiarid habitats. Adult CL ranges from 8.5 cm in the smallest tortoise, *Homopus signatus*, to 130 cm in the largest, *Geochelone elephantopus*. Most tortoises are herbivores and eat flowers, seeds, fruits, and foliage; a few species, such as *Geochelone carbonaria*, are opportunistic omnivores, eating what they can find on the forest floor. Most species lay small clutches, seldom exceeding 20 eggs (including the Galapagos and Aldabran giant tortoises), and many species have clutches of only 1 to 2 eggs. *Manouria* is the exception; *Manouria impressa* averages more than 30 eggs in a clutch. Incubation is characteristically long in tortoises; the average incubation periods are between 100 and 160 days for most species and supposedly as long as 18 months in *Geochelone pardalis*.

Comment The taxonomy and classification of this familial account follows Crumly's cladistic analyses (1982, 1984) and his interpretation of generic clades. We adopt a conservative approach to the retention of long-standing and widely used names as recommended by the *International Code of Zoological Nomenclature* (1961, 1985, 1999).

References Crumly, 1982, 1984; Ernst and Barbour, 1989a; Gaffney et al., 1991; Moll and Klemens, 1996; Shaffer et al., 1997; Swingland and Klemens, 1989.

Chapter

19

Crocodylians

OVERVIEW

Today's crocodilians represent only a small fraction of the species that have lived since their origin in the Late Triassic over 220 million years ago. Modern crocodilians consist of 23 species distributed throughout the world's tropics and subtropics, even extending slightly into the temperate zone. The extant species consist of three families that form the clade Crocodylia, which also includes some Tertiary and Late Cretaceous species. This restricted use of Crocodylia is recent and derives from cladistic analyses of diverse fossil crocodilians (see Chapter 3). The broader clade, Crocodyliformes, includes all fossil and extant taxa. It has usurped "crocodilians" as its vernacular name, and "crocodylians" is now being used for the more restricted clade, Crocodylia.

All crocodylians share a similar elongated body with a robust skull, a long snout and strongly toothed jaws, a short neck, a robust cylindrical trunk extending without constriction into a thick laterally compressed tail, and short but strongly developed limbs. The neck, trunk, and tail are armored dorsally and sometimes ventrally by bony plates (osteoderms) that are covered with thick keratinous skin. This body form is an ancient one, and hence the frequent labeling of crocodylians as living fossils, which they are not. The ancient body form persists owing to the functional success of an aquatic predator that ambushes prey in shallow water or at waterside. All modern crocodylians are semiaquatic and spend much of their life in water, although they regularly bask on the shoreline and construct terrestrial nests for the incubation of their eggs.

All crocodylians are oviparous, and fertilization is internal. Moderate-sized clutches average from 12 to 48 eggs (Thorbjarnarson, 1993). There is a general trend for clutch size to increase with body size among the various taxa; for example, the small caiman *Paleosuchus trigonatus* (1.3 m adult SVL) has an average of 15 eggs in a clutch, and *Crocodylus porosus* (2.7 m SVL) 48 eggs per clutch. Similarly, clutch size increases with female body size within a species. Eggs usually are deposited in mounds of vegetation and other detritus near the shoreline or on floating vegetation mats in shallow water. The mounds are created by the female, using all parts of the body to bulldoze the available debris into a mound. If surface debris is inadequate, females resort to digging a nest cavity in the ground. Parental care as nest attendance is common. The guarding parent is usually the female, although a male may also attend the nest, as in *Crocodylus novaeguineae*. Parental care can extend beyond nest attendance. The female may open the nest, help to break the eggshells and free hatchlings, and transport the hatchlings to the water. This level of parental care and crèche or juvenile guarding has not been reported for all species; in fact, the reproductive behavior of wild crocodylians is not fully documented for over a third of the extant species.

Crocodylians are uniquely characterized by a shared set of skeletal features. These features include an earflap on the skull table; a foramen magnum formed by the basioccipital and exoccipitals; dorsal skull sculpturing of pits and ridges; bony eustachian tubes; the trunk covered with a dorsal shield of unfused osteoderms; and a unique rod-shaped pubic process on the ischium. All members of Crocodylia possess a scapula with nearly horizontal anterior and posterior edges (Benton and Clark, 1988).

In the 10th edition of the *Systema Naturae*, Linnaeus classified a single crocodylian as the lizard *Lacerta Crocodilus*, diagnosed as a four-legged animal with a compressed tail. Eighteenth century naturalists recognized the existence of other crocodylians at that time, even though Linnaeus described only one species. Other species were soon formally described. In a later edition, Linnaeus adopted Gmelin's Crocodili (= Crocodylia) for the group and thereby recognized crocodylians as a natural group. Since then, their monophyly has not been questioned, although assorted higher-level group names have been applied to them.

Recent phylogenetic studies of crocodylians have yielded two competing hypotheses to explain the relationships of the extant genera and families (Fig. 19.1). The difference between the two cladograms rests on the proposed relationship of *Tomistoma*. Is *Tomistoma* a false or true gharial? That is, is *Tomistoma* more closely related to *Crocodylus* and *Osteolaemus* or to *Gavialis*? Morphology supports the former relationship (e.g., Tarsitano et al., 1989; Norell, 1989; Brochu, 1997a), although molecular data support the latter (e.g., Densmore, 1983; Hass et al., 1992); combined, morphological and molecular data support the *Tomistoma–Gavialis* pair (Poe, 1997). Among extant crocodylians, all data sets indicate a sister-group relationship between *Crocodylus* and *Osteolaemus*, and a sister-group relationship between *Alligator* and the caimans. In the latter group, the relationships among species are variable, but the most frequent phylogeny is (*Alligator* (*Paleosuchus* (*Caiman*, *Melanosuchus*))) (Brochu, 1997a). The latter pairing also indicates that *Caiman* is paraphyletic.

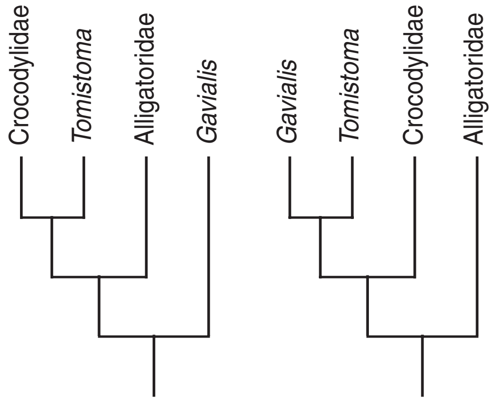


FIGURE 19.1 Cladograms depicting the two most likely relationship patterns among extant crocodylians. The cladograms derive from Brochu (1997a, Fig. 1). Cladograms redrawn from originals for uniformity.

Higher-level classification issues remain unresolved. Molecular data cannot address relationships among the numerous extinct crocodylians. Because the morphology of extinct crocodylians strongly supports an alligatorid-crocodylid relationship, we use the classification resulting from the cladogram described above (Fig. 19.1, left). Two additional aspects of the cladogram are noteworthy. Time-of-origin estimates from molecular data indicate that the divergence of *Gavialis* from extant crocodylians occurred in the Middle Miocene, but gavialid fossils occur as early as the Late Cretaceous. To accommodate and to portray accurately the relationships of the numerous fossil taxa, several new higher-level group names have been proposed (Table 3.4; those group names appear in subsequent subsection headings).

General References Cogger and Zweifel, 1998; Ross, 1989; Thorbjarnarson, 1992, 1996; Webb and Manolis, 1993; Webb et al., 1987.

Systematic References Benton and Clark, 1988; Brochu, 1997a, 1999; Clark, 1994; Densmore, 1983; Densmore and White, 1991; Hass et al., 1992; Norell, 1989; Poe, 1997; Tarsitano et al., 1989.

TAXONOMIC ACCOUNTS

Gavialoidea

Gavialidae

Gharials

Classification Reptilia; Diapsida; Sauria; Archosauria; Crocodylia.

Sister taxon Clade containing Alligatoroidea and Crocodyloidea.

Content One genus, *Gavialis*, with one species.

Distribution South Asia and formerly in the upper portions of the Indus, Ganges, Brahmaputra, Bhima, Manahandi, and Ayeydrwady rivers, but now extinct in many areas (Fig. 19.2).

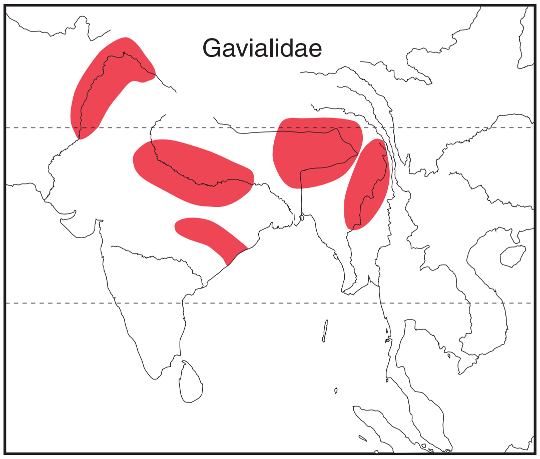


FIGURE 19.2 Geographic distribution of the extant Gavialidae.

Characteristics The single species, *Gavialis gangeticus*, attains a total length of 6.5 m. Among living crocodylians, gharials have the longest and narrowest jaws. All teeth in the anterior half of the upper and lower jaws lie outside the closed mouth, a character unique to gharials. The lower jaws are joined anteriorly by a long symphyseal articulation, and the anterior processes of the surangular have distinctly different lengths. In the skull, the ectopterygoid abuts the maxillary at its tooth row margin; the anterior process of the palatine is long and extends beyond the suborbital fenestra; and each parietal contains a sinus that opens into the cranial pneumatic system. The vertebral column contains a large, blocklike proatlas, a crested neural spine on the axis, and a slightly or unnotched axial hypapophysis. Lingual salt glands are absent or poorly developed and their exit pores are small; the surface of the tongue is not keratinized.

Biology: Gharials are the most aquatic of living crocodilians and seldom move far from water (Fig. 19.3). They prefer deep fast-flowing rivers, where the adults congregate in deep holes at river bends and at the confluence of smaller streams. The juveniles select smaller side streams or river backwaters. As in other crocodylians, gharials regularly bask, particularly in winter when the water of their upstream habitats is cooler. The narrow, elongate, tooth-filled jaws are highly effective for catching fish, their primary food. Gharials catch fish with a quick sideward snap of the jaws. With the fish impaled on the teeth, the head is lifted out of the water and backward, and then with a sideward head jerk, the fish drops headfirst deep into the mouth. Frogs are also a common prey, and birds and mammals are eaten less frequently.

Male gharials usually reach maturity in about 15–18 years and at about 4 m TL; females mature sooner at about 7–8 years and at a smaller size (2.6-3 m TL). As males mature, they develop an irregular growth, the boss, on the tip of the snout. This boss grows progressively larger with age. Although its function is uncertain, it overlaps the nostrils and can cause a hissing and buzzing sound with each breath. Because this sound becomes part of the male's territorial defense behavior and may be important in courting, males with larger bosses have a social advantage. Today, most adult gharials are 4 m or less; an old record verified a maximum 6.45 m total length.

Nesting occurs in the late dry season (March–April), several months after mating. The females lay clutches consisting of 35 to 60 large eggs in nests typically dug on steep-sloped stream banks. The female guards her nest during an incubation period of 60+ days. When the eggs begin to hatch, the female assists the hatchlings as they emerge from the eggs. The hatchlings remain in a crèche with the female in attendance until the monsoon rains arrive. Flooding disrupts the nesting area and disperses the young.

References Brochu, 1997a; Lang, 1989; Magnusson et al., 1989; Shine, 1988; Thorbjarnarson, 1990; Webb and Manolis, 1993; Whitaker and Basu, 1983.

Alligatoroidea

Alligatoridae

Alligators and caimans

Classification Reptilia; Diapsida; Sauria; Archosauria; Crocodylia.

Sister taxon Crocodylidae.

Content Two subfamilies, Alligatorinae and Caimaninae, with nine species.

Distribution Eastern North America, Central and South America, and eastern China (Fig. 19.4).

Characteristics: Alligators and caimans commonly have broad, moderately long jaws. All teeth of the lower jaw lie inside the closed mouth. The lower jaws are joined anteriorly by a narrow symphyseal articulation, and the anterior processes of the surangular are subequal. In the skull, the ectopterygoid is broadly separated from the maxillary tooth row; the anterior process of the palatine is long and extends beyond the suborbital fenestra; and each parietal is solid. The vertebral column contains a moderate-sized and flattened proatlas, a crested neural spine on the axis, and a deeply notched axial hypapophysis. Lingual salt glands are absent, and the surface of the tongue is keratinized.

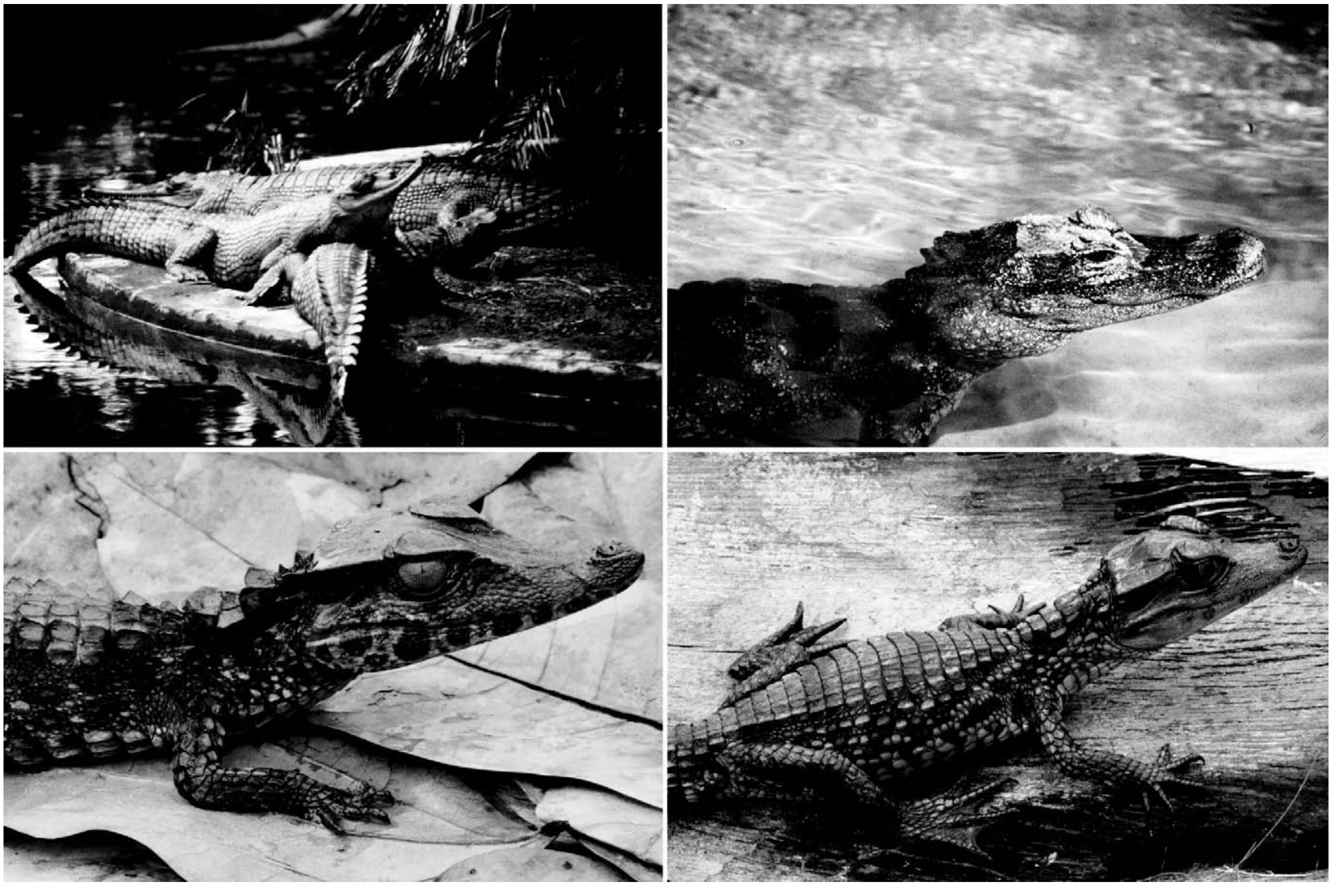


FIGURE 19.3 Representative crocodylians. Clockwise from upper left: gharial *Gavialis gangeticus*, Gavialidae (photograph by C. A. Ross); Chinese alligator *Alligator sinensis*, Alligatorinae (C. K. Dodd, Jr.); spectacled caiman *Caiman crocodilus*, Caimaninae (J. P. Caldwell); and Cuvier's dwarf caiman *Paleosuchus palpebrosus*, Caimaninae (J. P. Caldwell).

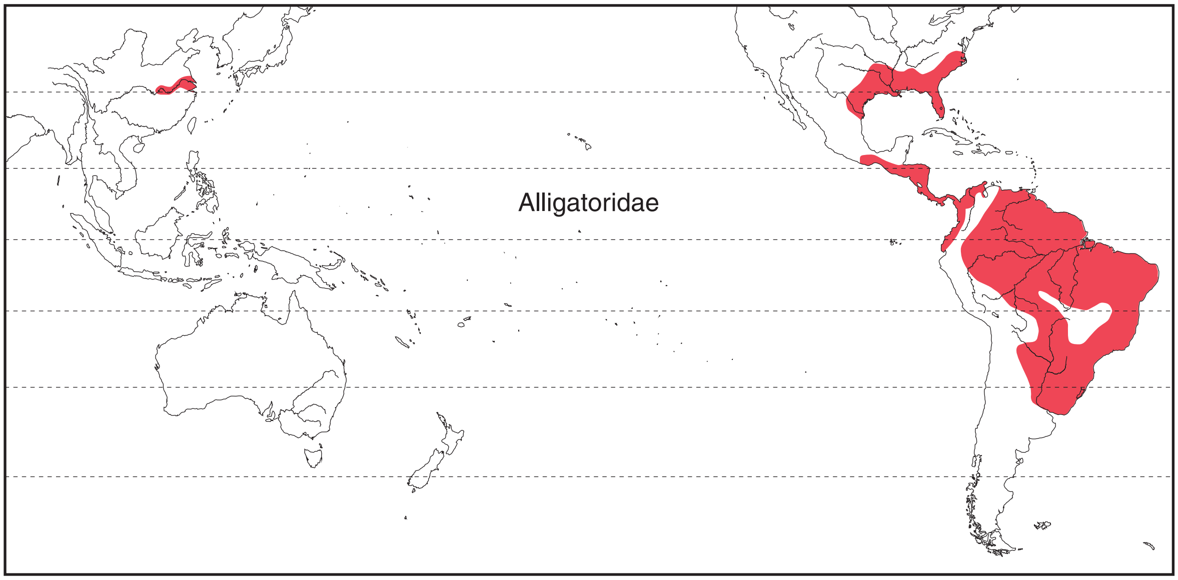


FIGURE 19.4 Geographic distribution of the extant Alligatoridae.

References Brochu, 1999; Lang, 1989; Magnusson et al., 1989; Thorbjarnarson, 1992.

Alligatorinae

Sister taxon Caimaninae.

Content One genus, *Alligator*, with two species.

Distribution Extant alligators are exclusively Holarctic. *Alligator mississippiensis* occurs in southeastern North America, and *Alligator sinensis* is in the lower reaches of the Yangtze River of eastern China.

Characteristics Alligators are moderate-sized crocodylians, attaining lengths to 2.1 m TL (*A. sinensis*; Fig. 19.3) and four meters (*A. mississippiensis*). They possess a narrow, parallel-sided dorsal horn on the hyoid plate, paired nasal foramina (Fig. 2.12), and a pointed anterior tip of the angular extending dorsally to or beyond the posterior intermandibular foramen.

Biology *A. mississippiensis* lives in a wide range of habitats, including freshwater sloughs immediately behind coastal sand dunes, marshes and swamps, and large lakes and rivers. While seriously overharvested in the 1950s and 1960s, government protection, coupled with the alligator's high reproductive potential and relatively short generation time, has allowed populations in its core distribution area to rebound. American alligators have again assumed their role as top predator of aquatic vertebrates in some regions. The situation for *A. sinensis* has improved but remains fragile. There is now an effective breeding program and it has produced sufficient animals for reintroduction; unfortunately there are no available protected areas for such releases. Populations in a single, large reserve have increased in the areas of preferred habits; elsewhere populations are small or extinct.

American alligators are opportunistic carnivores and eat a wide variety of animals. Vertebrates from fish to mammals (including other gators) are regularly eaten. In contrast, the Chinese alligator feeds heavily on mollusks, about 40–50% of its diet, and they also eat a variety of small vertebrates.

Of all crocodylians, alligators are the only taxon capable of living in areas where seasonal temperatures are below freezing. *A. mississippiensis* does not hibernate in cold weather, whereas *A. sinensis* does. Large juvenile and adult *A. mississippiensis* select steep-sided shorelines where they can float with the tip of snout above water and the body and tail in deeper, warmer water. If the shoreline water freezes, an alligator will maintain an ice-free hole around its snout in order to breathe (Fig. 19.5). If possible, American alligators will stay in burrows during cold days and emerge to bask during

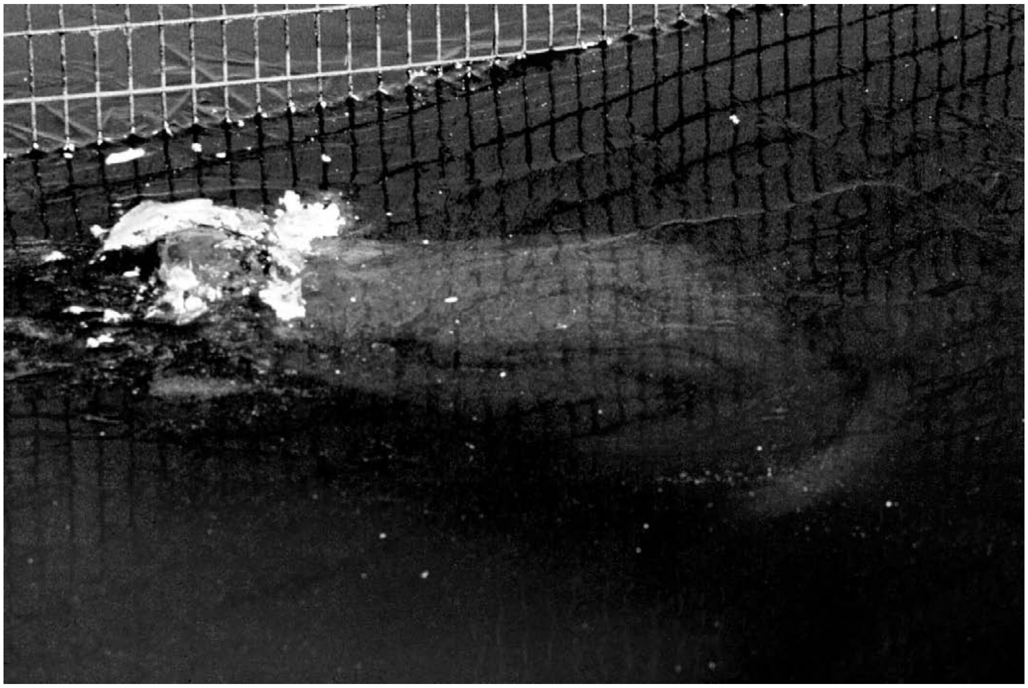


FIGURE 19.5 American alligator, *Alligator mississippiensis*, with its snout broken through ice covering the water. Photograph courtesy of Savannah River Ecology Laboratory.

warm, sunny ones. *A. sinensis* digs extensive burrow systems and resides in them year around; the burrow systems are complex, containing numerous tunnels and watered and dry chambers. These chambers are used for hibernation from about October through February; indeed, hibernation seems necessary to stimulate reproduction in Chinese alligators.

In the southern half of their distribution, *A. mississippiensis* reaches sexual maturity at about 2.0 m TL in 7 to 10 years. Because of their small relative size, young, sexually mature males are usually unable to compete with larger males for territories and females, so most males do not breed for the first time until they are 2.4–2.8 m TL and about 15 to 20 years old. Courtship begins 8 to 10 weeks before the eggs are deposited in mid-June, and females frequently mate with more than one male. Nesting begins with mound construction; the female heaps dirt and vegetation into a large mound, usually near the shoreline, although occasionally on a floating vegetation mat in shallow water. She digs a cavity in the mound and deposits an average 35 to 40 eggs, which will hatch in 65 to 70 days. Parental care includes guarding the nest and the crèche. *A. sinensis* has a similar reproductive pattern, but because it is a smaller species, it matures somewhat earlier. They mate May to June and begin nesting in July; they produce smaller clutches (average of 24 eggs).

References Joanen and McNease, 1980; Lang, 1989; McIlhenny, 1935; Webb and Manolis, 1993; Webb and Vernon, 1992.

Caimaninae

Sister taxon Alligatorinae.

Content Three genera, *Caiman*, *Melanosuchus,* and *Paleosuchus,* with seven species.

Distribution Central and southern Mexico to Ecuador and east of the Andes into Uruguay, Paraguay, and northern Argentina (Fig. 19.4).

Characteristics Caimans are small to large crocodilians, reaching up to 1.7 m TL in *Paleosuchus* and 2 to 5 m in *Caiman*. They possess a broad flaring dorsal horn on the hyoid plate, a large nasal foramen, and a blunt anterior tip of the angular not extending to the posterior intermandibular foramen.

Biology Caimans occur in a diversity of freshwater habitats throughout the lowlands of Central and South America. *Caiman crocodilus* and *Caiman fuscus* are the most widespread species and appear to be the most tolerant ecologically. They occupy the broadest range of habitats, preferring slow-moving backwaters of rivers and ponds and lakes. *C. crocodilus* is still fairly abundant in the llanos of Venezuela and elsewhere, but it is heavily harvested. Harvesting, habitat modifications, and the lower reproductive potential of caimans continue to threaten their survival in many regions.

All species of caimans build nest mounds in which they deposit their eggs. Clutch size is related to body size, and smaller individuals and the smaller species lay fewer eggs. Clutch size is 10 to 15 eggs in *Paleosuchus trigonatus*, 15 to 40 in *C. crocodilus*, and 30 to 60 in *Melanosuchus niger*. Evidence suggests that all caimans display parental care that includes guarding the nest and the crèche. Most crocodylians select open-canopy microhabitats that may often be adjacent to or marginally in forest, but *P. trigonatus* is a regular inhabitant of closed-canopied, small streams in the rain forests of the Amazon and Orinoco basins although it also occurs in open areas. Because the shallow streams offer little protection, adults often seek shelter in deep cavities under stream banks or in logs and debris away from the stream. The closed canopy does not permit sunlight to heat the nesting mounds, so females often place their nests adjacent to and partially on termite mounds to obtain additional heat generated by the termite nest chamber.

References Amato and Gatesy, 1994; Brazaitis et al., 1998; Lang, 1989; Magnusson et al., 1989; Ouboter and Nanhoe, 1987; Webb and Manolis, 1993.

Crocodyloidea

Crocodylidae

Crocodiles and false gharials

Classification Reptilia; Diapsida; Sauria; Archosauria; Crocodylia.

Sister taxon Alligatoridae.

Content Two subfamilies, Crocodylinae and Tomistominae (Fig.19.6).

Distribution Pantropical in continental estuaries and freshwater streams (Fig. 19.7).

Characterization Most crocodiles have moderately long and often broad jaws. A unique feature is that only the fourth mandibular tooth lies externally on each side of the mouth when it is closed. Occasionally, the first mandibular tooth perforates the upper jaw and its tip is visible as well when the mouth is closed. The lower jaws are usually joined anteriorly by a narrow symphyseal articulation, and the anterior processes of the surangular have distinctly different lengths. In the skull, the ectopterygoid abuts the maxillary at its tooth row margin; the anterior process of the palatine is short and does not

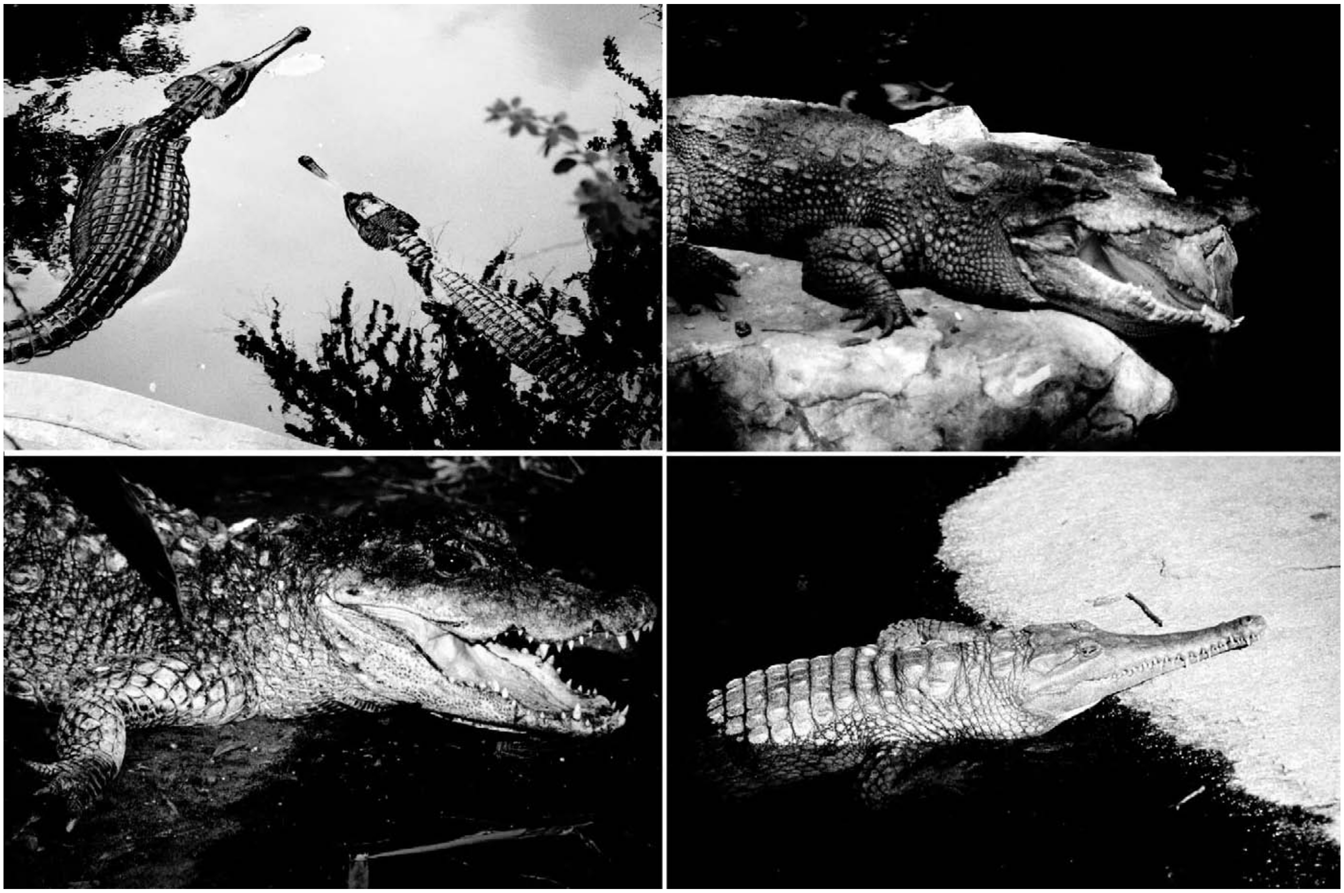


FIGURE 19.6 Representative crocodiles. Clockwise from upper left: false gharial *Tomistoma schlegelii*, Tomistominae (photograph by G. Webb); Siamese crocodile *Crocodylus siamensis*, Crocodylinae (G. R. Zug); Johnstone's crocodile *Crocodylus johnsoni*, Crocodylinae (G. R. Zug); and dwarf crocodile *Osteolaemus tetraspis*, Crocodylinae (A. Britton).

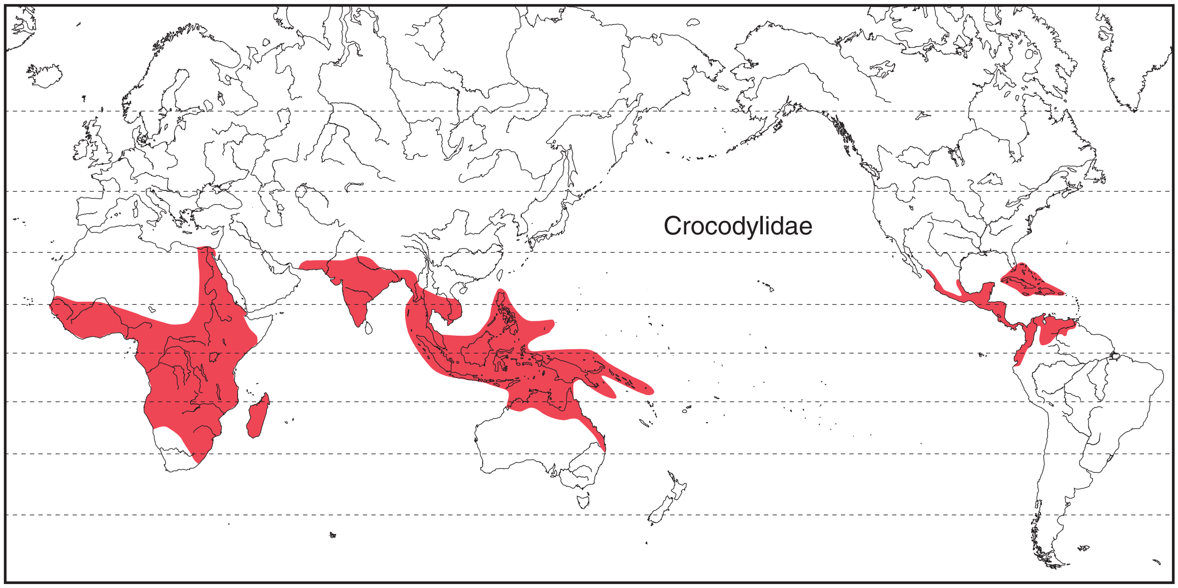


FIGURE 19.7 Geographic distribution of the extant Crocodylidae.

extend beyond the suborbital fenestra; and each parietal is solid. The vertebral column contains a moderate-sized and flattened proatlas, an uncrested neural spine on the axis, and a deeply notched axial hypapophysis. Lingual salt glands are well developed and their exit pores are large; the surface of the tongue is not keratinized.

References Brochu, 1999; Lang, 1989; Magnusson et al., 1989; Webb and Manolis, 1993; Webb et al., 1987.

Crocodylinae

Sister taxon Tomistominae.

Content Two genera, *Crocodylus* and *Osteolaemus*, with 13 and 1 species, respectively.

Distribution The genus *Crocodylus* is pantropic

Characteristics Crocodiles range in total length from the small (2.5 m TL) dwarf crocodile *Osteolaemus tetraspis* to the largest extant crocodylian *Crocodylus porosus* (to 7 m TL). Crocodiles differ from the false gharials by having broader snouts, lower jaws with short splenial symphyses, postorbitals touching the quadrates and quadratojugals, and suborbital fenestrae without a distinct posterior notch.

Biology Species of *Crocodylus* occur mainly in aquatic habitats with open canopies, including freshwater marshes, the margins of large rivers and lakes, tidal marshes, and mangrove forests. *Crocodylus cataphractus* and *Osteolaemus tetraspis* are exceptions, living in small to moderate-sized rain forest streams, often beneath a closed canopy. *O. tetraspis* is exclusively nocturnal, differing from other crocodiles. Most other crocodiles hunt at night, but they are also active diurnal predators as well. About one-third of the species, including *Crocodylus acutus*, *Crocodylus intermedius*, *Crocodylus niloticus*, and *C. porosus,* reach lengths greater than 4 m TL; the others are mostly 2 to 3 m, and *O. tetraspis* is seldom larger than 1.5 m.

All crocodiles appear to be mound builders and nesters if given the opportunity; if adequate vegetation and surface detritus are not available the female digs a nest in the sand or soil of the shoreline. Where data are available, all crocodiles display parental care that includes nest and crèche guarding. Clutch size is related to body size, and the small-bodied species (e.g., *O. tetraspis*, *C. cataphractus*) seldom lay more than 25 eggs, whereas the large species (e.g., *C. niloticus*, *C. porosus*) regularly lay more than 50 eggs.

References Cott, 1961; Graham and Beard, 1973; Lang, 1989; Ouboter and Nanhoe, 1987; Thorbjarnarson, 1996; Webb and Manolis, 1989.

Tomistominae

Sister taxon Crocodylinae.

Content One genus, *Tomistoma*, with one species.

Distribution Freshwater streams of the Malay Peninsula, Sumatra, and Borneo.

Characteristics The single species *Tomistoma schlegelii* (Fig. 19.6) attains 4 m TL. It differs from all living crocodiles by having a narrow, elongate snout, a lower jaw with a long splenial symphysis, a postorbital that does not touch the quadrate or quadratojugal, and a suborbital fenestra with a distinct posterior notch.

Biology The false gharial is commonly identified as a fish-eater like the true gharial; however, it appears to be mainly an ambusher of waterside prey. Mammals and birds figure heavily among its prey, and in some areas, crab-eating macaques are a common prey. Its natural history is poorly known because its populations have been extirpated or reduced throughout its range. In captivity, females mature in 6 to 10 years at 2.5–3 m TL. Females construct large detritus nesting mounds and, typically in June and July, lay 20 to 40 eggs. The *T. schlegelii* eggs are very large, each egg double or triple the mass of any other crocodylian egg. Eggs have a 10- to 12-week incubation. Presumably the hatchlings experience the same level of parental care as in other crocodylians but this is uncertain.

References Thorbjarnarson, 1996; Webb and Manolis, 1993.

Chapter

20

Tuataras and Lizards

OVERVIEW—SPHENODONTIDA

The tuataras are the least successful extant reptiles. They are relics because they are the sole survivors of a formerly more diverse group that now persists only on small islets off the main islands of New Zealand. Even before the arrival of humans, tuataras were less diverse than lizards in the same area. Why have the tuataras dwindled to so few species? Only speculative answers are possible, and all hypotheses are likely to include a competitive component. At least during the Tertiary, lizards were probably their main competitors, but the real answer is certainly more complex than just competition with lizards.

Sphenodontidans and squamates compose the Lepidosauria. Lepidosaurs share numerous derived characters, including a transverse cloacal opening (the vent); tongue notched distally and used to capture prey; full-body ecdysis; imperforate stapes; teeth attached superficially to the jaw bones; pelvic bones fused in adults; fracture planes or septa in the caudal vertebrae; and numerous other anatomical traits. The sphenodontidans and squamates apparently diverged in the early Late Triassic, and the sphenodontidans seemingly have always been a group with low diversity (see Chapter 3 for fossil history).

The sphenodontidans differ from the squamates by the presence of gastralia; a narrow quadrate with greatly reduced or lateral concha; lower temporal fenestra enclosed or partially so; jugal in the midtemporal arch touching the squamosal posteriorly; prominent coronoid process on the mandible; several anterior teeth of the palatine series enlarged; dentary and mandibular teeth generally enlarged, regionalized, and fused to dorsal margin of bone; and the premaxillary teeth replaced by chisel-shaped extensions of the premaxillary bones that have given rise to the tuatara's other vernacular name, half-beaks (see Fig. 3.16 for some of these skull features).

General References Cogger and Zweifel, 1998; Gill and Whitaker, 1996; Robb, 1986.

Systematic References Daughtery et al., 1990; Gauthier et al., 1988a.

TAXONOMIC ACCOUNT

Sphenodontidae

Tuataras

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Sphenodontida.

Sister taxon Clade containing extinct sapheosaurs and *Homeosaurus.*

Content One extant genus, *Sphenodon*, with two species.

Distribution New Zealand, but now restricted to small coastal islands; *Sphenodon punctatus* occurs on about 30 islands off the northeast coast of the North Island and western Cook Strait, and *Sphenodon guntheri* is restricted to a single island, the North Brother Island in the Cook Strait.

Characteristics Tuataras are lizardlike, stout-bodied (19–28 cm adult SVL) reptiles with large heads and thick tails. They have a chisel-beaked upper jaw overhanging the lower jaw, a series of erect spines on the nape and back, and rudimentary hemipenes. They lack a tympanum.

Biology Adult tuataras forage principally at night, commonly at temperatures that range from 12 to 16°C. They are not exclusively nocturnal animals and, in warm summer months, bask at their burrow entrances, retreating when they become too hot and reemerging after they cool. Their prey consists predominantly of insects and other arthropods, although they occasionally eat skinks, geckos, and seabirds. *S. punctatus* (Fig. 20.1) is most numerous on those islands shared with nesting seabirds, an indication of a lack of, or a reduction in, rat predators; additionally, bird nesting activities yield abundant arthropod prey and burrows for daily shelter and winter hibernation. Islands with moderate to high rat populations have tuatara populations composed nearly exclusively of adults because rats prey on the eggs and juveniles. Such populations persist only because tuataras are long lived—more than 30 years.

Courtship and mating occur in January, but egg laying is delayed until October–December; evidence indicates sperm storage occurs rather than delayed development. The female digs a small nest cavity and deposits 8 to 15 eggs. Development is slow and stops during the winter; hatching occurs 11 to 16 months after deposition. Optimal incubation temperatures in the laboratory are 18–22°C, the lowest known in living reptiles. The eggs absorb moisture during incubation, so the mass of the hatchlings is 1.2–1.3 times greater than the original egg mass.

References Castanet et al., 1988; Newman, 1987; Newman et al., 1994.

FIGURE 20.1 Full body (left) and head (right) of the Tuatara *Sphenodon punctatus* (photographs by P. Ryan).

OVERVIEW—SQUAMATA

The nearly 7200 species of lizards are the most diverse and speciose living clade of reptiles; of course this total includes the snakes, which are actually reduced-limbed or limbless lizards. Our vernacular recognizes lizards and snakes as two different groups, but our classificatory label, Squamata, denotes the monophyletic status of these reptiles and requires the use of the vernacular squamates. Squamates thus have a precise definition and diagnosis; lizards do not, and they require a shared perception between reader and writer. That perception is generally adequate, but it cannot be formalized with a name, such as Lacertilia, because that classification excludes snakes and creates a paraphyletic taxon. Because snakes are a monophyletic group arising from within a group of lizards, the taxon Serpentes and its definition delimit a monophyletic group. Herein, the term lizard represents our shared perception and excludes Serpentes.

This chapter is about lizards, but first, Squamata must be defined. Squamates possess more than 50 shared derived features attesting to their monophyly. Skeletal features include a single (fused) premaxillary and a single parietal; reduced nasals; no vomerine teeth; specialized ulnare–ulna and radiale–radius joints (wrist); a specialized ankle joint; and a hooked fifth metatarsal. Among the soft anatomical structures, squamates have well-developed paired copulatory organs (hemipenes); saccular ovaries; a vomeronasal (Jacobson's) organ separated from the nasal capsule; a lacrimal duct joined to the vomeronasal duct; femoral and preanal glands; and no caruncle, but instead have an egg tooth.

The lizards and their snake descendants are the only living squamates. Excluding the snakes, lizards are still the most speciose extant reptiles, with about 4450 species (Uetz, 1999). Lizards occur on all continents, except Antarctica, and on most tropical and subtropical oceanic islands. This widespread occurrence denotes their broad ecological, physiological, and behavioral adaptations to extremely hot to cold climates, extremely arid to freshwater and marine habitats, and lowland to high-elevation regions. Their highest species diversity appears to be in semiarid habitats; for example, 53 species of lizards occur at one site in the Great Victoria Desert, Australia (Pianka, 1994a), and in some areas, particularly islands, densities can be greater than 3000 per hectare (*Emoia cyanura*; Zug, 1991).

Charles C. Camp's *Classification of Lizards* (1923) represents the first explicit attempt at an evolutionary analysis of squamate relationships. His dendrogram provides a series of dichotomous branches, and the overall pattern is not strikingly different from the patterns seen in recent phylogenetic (explicitly cladistic) studies. For example, his analysis recognized the iguanians as the first branch of the dendrogram and geckos as the next branch; his results also suggest that varanoids and snakes are sister groups, although the sister-group concept was not adopted for reptilian classification until the 1960s. The first explicitly cladistic analysis of squamates appeared in 1988 (Estes et al., 1988). This analysis examined a wide representation of squamate genera and families and several hundred characters that were reduced to 148 useful ones. The resulting cladogram and other more recent ones are similar to Camp's; the classifications are also similar, although today's classifications recognize only monophyletic groups (Fig. 20.2).

The major branches of the Estes et al. cladogram and of most subsequent ones show the Iguania as the sister group of all other squamates, the Scleroglossa (e.g., Lee, 1998; Rieppel, 1994; Wu et al., 1996); the Scleroglossa then branches into the geckos and allies and the autarchoglossans. Other similarities include sister-group relationships between Teiidae and Gymnophthalmidae, between the latter pair and Lacertidae, between *Varanus* and *Lanthanotus*, and between the latter pair and *Heloderma*, but thereafter the sister-group pairings do not match. One cause of the dissimilarities is that the analyses compare different sets of taxa. This aspect alone can account for different branching patterns; additional differences arise from the size of the character data set and its diversity, which includes the level of interrelatedness of the characters (e.g., whether characters represent one functional unit or many). Because a consensus does not yet exist, our selection of a squamate cladogram is arbitrary (Fig. 20.2).

The Iguania branch contains as few as 2 groups or as many as 12. Historically, Iguania consisted of the Agamidae, Chamaeleonidae, and Iguanidae. The Agamidae and Chamaeleonidae, which compose the Acrodonta, are more closely related to one another than either is to the Iguanidae; that generality is still supported by the majority of the phylogenetic analyses. However, is the Agamidae or the Iguanidae monophyletic? One cladistic analysis (Frost and Etheridge, 1989) indicated that neither lineage was monophyletic and proposed a new classification that recognized numerous new families (Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Opluridae, Phrynosomatidae, Polychrotidae, Tropiduridae) for the original Iguanidae, and a single family for the agamids and chameleons (also see Hallermann, 1994). This classification has been adopted widely, although not unanimously (Schwenk, 1994b; Williams, 1988). Another study that used molecular

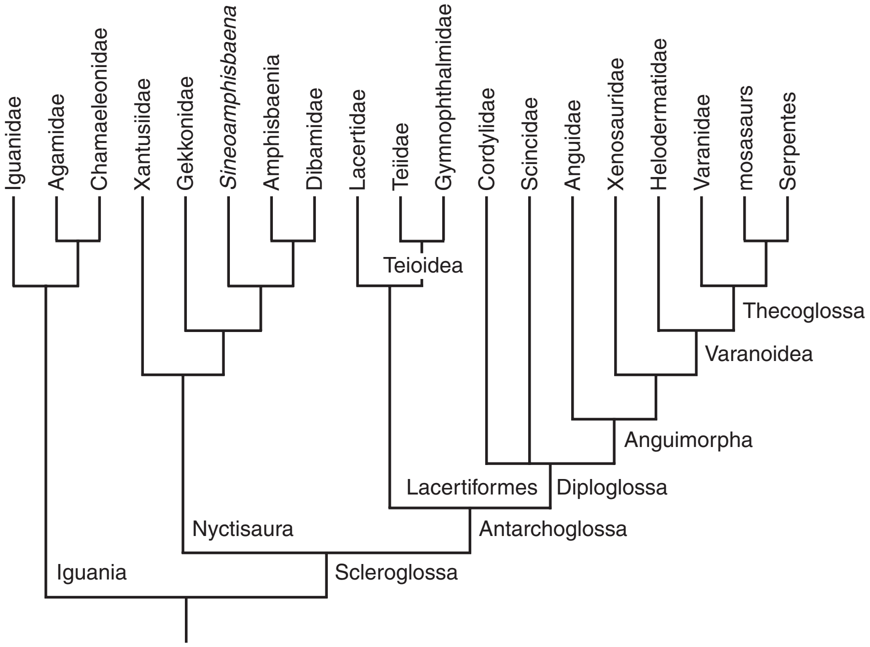


FIGURE 20.2 Cladogram depicting relationships among extant taxa of squamates with emphasis on the phylogeny of lizards. The cladogram derives mainly from Lee (1988, Fig. 5.1) for the basic branching patterns; the position of the Annulata group derives from Wu and collaborators (1996). Cladogram redrawn from original for uniformity.

data and also reanalyzed the Frost–Etheridge data supported the monophyly of the Iguanidae, Acrodonta, and Chamaeleonidae but was unable to confirm or reject the monophyly of the Agamidae (Macey et al., 1997).

The membership of and relationships within the Gekkota and its component families also differ among systematists. All agree that the membership of the geckos (gekkonoids) includes the eublepharids, gekkonids, pygopods, and diplodactylines, although the analyses yield different branching patterns and different assessments of monophyly of these groups. A multicharacter study recognized the monophyly of the Gekkonidae and the Pygopodidae including the diplodactylines (Kluge, 1987). Subsequently, other authors included the pygopods in the Gekkonidae, an arrangement that does not alter the monophyly of the latter. More recently, a molecular study confirmed the monophyly of the Gekkonidae, Diplodactylinae, Pygopodinae, and Gekkoninae, and the sister-group relationship of the diplodactylines and pygopodines (Donnellan et al., 1999). That study did not resolve the relationships of the gekkonines, the eublepharines, or each of these to the diplodactyline–pygopodine clade; indeed, it suggested that eublepharines are either a sister group of diplodactyline–pygopodines or of gekkonines rather than the sister group of all other geckos.

Although gekkonoid monophyly is well supported, its sister-group relationship is uncertain. A common interpretation is that gekkonoids are the same as Gekkota, which is the sister group of all other extant lizards (Autarchoglossa) except iguanians (Estes et al., 1988; Rieppel, 1994). Other relationships have been proposed. Proposed sister taxa are the Annulata (= amphisbaenians, dibamids) and snakes (Wu et al., 1996); all other lizards excluding the Iguania and Annulata (Hallermann, 1998); the anguimorphs (Gao and Norell, 1998); the scincomorphs (Russell, 1988); and the Xantusiidae (Schwenk, 1988). These different hypotheses emphasize that our resolution of phylogenetic relationships among lizards is not firmly resolved and that several alternative classifications are equally likely at this time.

Some relationships persist among all or most analyses. The teioids (Gymnophthalmidae and Teiidae) are consistently paired and, in turn, usually linked to the Lacertidae, forming the Lacertiformes or lacertoids, although a teioid–amphisbaenian pairing has been suggested (Schwenk, 1988). The genera *Lanthanotus* and *Varanus* are another consistent pair that forms the sister group to *Heloderma*. Thereafter, relationships within the scleroglossans or the autarchoglossans are less certain, as indicated by the numerous proposals of Gekkota relationships. But in spite of these differing hypotheses on interfamilial relationships among the squamates, neither snakes nor amphisbaenians currently are considered a basal sister group to all other squamates. Their origins (i.e., sister-group relationships) are to a subgroup of lizards. The two current competing hypotheses are that the Serpentes is a sister group to varanids/varanoids (e.g., Lee, 1998; Rieppel, 1994; Schwenk, 1988) or to a dibamid–amphisbaenid clade (e.g., Hallermann, 1998; Wu et al., 1996).

General References Ananjeva et al., 1988; Cogger and Zweifel, 1998.

Systematic References Camp, 1923; Donnellan et al., 1999; Estes et al., 1988; Frost and Etheridge, 1989; Gao and Norell, 1998; Gauthier et al., 1988a; Hallermann, 1994, 1998; Kluge, 1987, 1989; Lee, 1998; Macey et al., 1997; Rieppel, 1994; Russell, 1988; Schwenk, 1988, 1994b; Williams, 1988; Wu et al., 1996.

TAXONOMIC ACCOUNTS

Iguania

Agamidae

Angleheads, calotes, dragon lizards, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Chamaeleonidae.

Content Two subfamilies, Agaminae and "Leiolepidinae" (Fig.20.3).

Distribution Africa, Asia, and Australia (Fig. 20.4).

Characteristics Agamids are small to large lizards (45–350 cm adult SVL), covered dorsally and ventrally by overlapping scales or granular, juxtaposed scales. No osteoderms occur dorsally or ventrally on the trunk. All species are limbed, and the pectoral girdle has a T-shaped or cruciform interclavicle and curved rod-shaped clavicles. The tail is usually long to moderately long (from just less than to 1.4 times SVL) and lacks fracture planes in the caudal vertebrae (except in some *Uromastyx*). The tongue is covered dorsally with reticular papillae and lacks lingual scales; the foretongue is nonretractable. The skull possesses paired nasals, postorbitals and squamosals, and a frontal and a parietal; a parietal foramen usually perforates the frontoparietal suture. Attachment of the marginal dentition is acrodont, and the pterygoid lacks teeth.

Comments Opinion varies on the reality of Leiolepidinae as a clade. Primitive morphological characters appear to link *Leiolepis* and *Uromastyx*, so it possible that they are not sister groups (e.g., Joger, 1991; Macey et al., 1997).

References Estes et al., 1988; Frost and Etheridge, 1989; Hallermann, 1998; Joger, 1991; Schwenk, 1988; Witten, 1993.

Agaminae

Sister taxon "Leiolepidinae."

Content Fifty genera, *Acanthosaura*, *Acanthocercus*, *Agama*, *Amphibolurus*, *Aphaniotis*, *Bronchocoela*, *Bufoniceps*, *Caimanops*, *Calotes*, *Ceratophora*, *Chelosania*, *Clamydosaurus*, *Complicitis*, *Cophotis*, *Cryptagama*, *Ctenophorus*, *Dendragama*, *Diporiphora*, *Draco*, *Gemmatophora*, *Gonocephalus*, *Harpesaurus*, *Hydrosaurus*, *Hylagama*, *Hypsilurus*, *Japalura*, *Laudakia*, *Lophocalotes*, *Lophognathus*, *Lyriocephalus*, *Megalochilus*, *Mictopholis*, *Moloch*, *Oriocalotes*, *Otocryptis*, *Phoxophrys*, *Phrynocephalus*, *Physignathus*, *Plocederma*, *Pogona*, *Psammophilus*, *Pseudocalotes*, *Pseudocophotis*, *Ptyctolaemus*, *Salea*, *Sitana*, *Thaumatorhynchus*, *Trapelus*, *Tympanocryptis*, and *Xenagama*, with ±400 species.

Distribution Africa, Asia, and Australia (Fig. 20.4).

Characteristics Agamines possess large lacrimal foramina and epiotic foramina.

Biology Agamines are a diverse clade of predominantly terrestrial and semiarboreal lizards (Fig. 20.3); a few are highly arboreal, but none is fossorial. The diversity results in part from their extensive distribution in the Old World and independent adaptive radiations in Africa, Asia, and Australia. They range in size from the small *Cryptagama aurita* (40–45 mm adult SVL) to the large water dragon *Hydrosaurus amboinensis* (350 mm SVL, 1.1 m TL), and in body shape from stout-bodied, short-limbed taxa (e.g., *Moloch*, *Phrynocephalus*) to slender and long-limbed taxa (e.g., *Draco*, *Sitana*, *Diporiphora*). Agamines are usually diurnal, and most are heliotherms that regularly bask to maintain elevated body temperatures. They are predominantly carnivores, preying largely on arthropods by using a sit-and-wait foraging behavior. Most, perhaps all, agamines are oviparous, although reports suggest that some *Phrynocephalus* and *Cophotis ceylanica* are viviparous. Clutch size is generally correlated with body

FIGURE 20.3 Representative acrodontan lizards. Clockwise from upper left: two-lined chameleon *Chamaeleo bitaenatus*, Chamaeleonidae (photograph by R. G. Tuck, Jr.); variable calotes *Calotes versicolor*, Agaminae (G. R. Zug); military dragon *Ctenophorus isolepis*, Agaminae (J. M. Howland); and Dabb's mastigure *Uromastyx acanthinurus*, Leiolepidinae (L. L. Grismer).

size within species; small-bodied taxa deposit smaller clutches (e.g., 2 eggs, *Ctenophorus fordi*) and larger-bodied species deposit larger clutches (e.g., 30–35 eggs, *Pogona*). For most taxa, clutch size varies from 4 to 10 eggs. Eggs are deposited in nests dug by the females, and incubation is commonly 6 to 8 weeks.

References Böhme, 1981; Cox et al., 1998; Daniel, 1983; Fitch, 1970; Greer, 1989; Witten, 1993.

"Leiolepidinae"

Sister taxon Agaminae.

Content Two genera, *Leiolepis* and *Uromastyx*, with 7 and 14 species, respectively.

Distribution Northern Africa eastward to Southeast Asia.

Characteristics Leiolepidines have small lacrimal foramina and lack epiotic foramina.

Biology All leiolepidine species are terrestrial (Fig. 20.3) and use burrows for daily and seasonal retreats. They can climb and occasionally forage in low shrubs. All are predominantly herbivorous, eating foliage, flowers, fruits, and seeds. Both *Leiolepis* and *Uromastyx* are oviparous. Clutch size is moderate in both taxa, ranging from 2 to 8 eggs in *Leiolepis* (110–150 mm adult SVL) and 8 to 20 eggs in *Uromastyx hardwickii* (340–400 mm adult TL). All species usually lay their eggs within the female's burrow system, either in late spring–early summer or at the beginning of the dry season. Incubation is approxi-

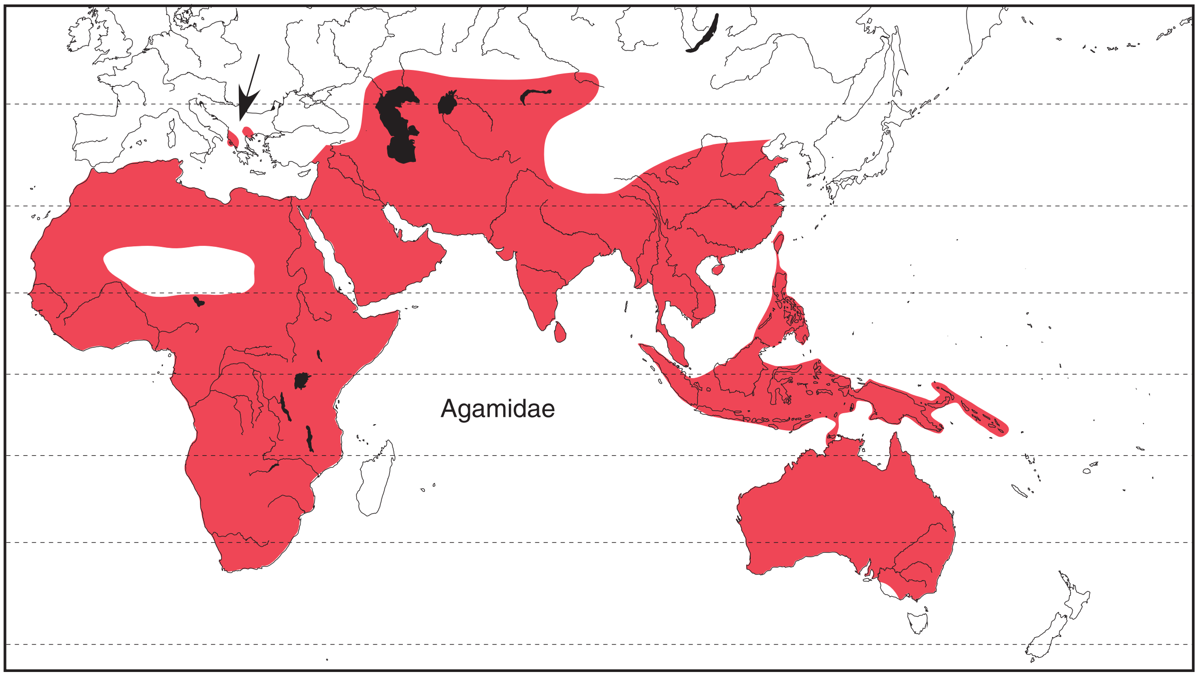


FIGURE 20.4 Geographic distribution of the extant Agamidae.

mately 8 to 10 weeks, and the hatchlings appear to stay within the parent's burrow system for several weeks to several months before leaving to establish their own burrows.

References Cox et al., 1998; Daniel, 1983; Peters, 1971.

Chamaeleonidae

Chameleons

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Agamidae.

Content Four genera, *Bradypodion*, *Brookesia*, *Chamaeleo,* and *Rhampholeon*, with 130+ species.

Distribution Africa, Madagascar, and India (Fig. 20.5).

Characteristics Chameleons are unique lizards that have strongly laterally compressed bodies, prehensile tails, head casques covering their necks (Fig. 20.3), zygodactylous feet (i.e., fusion of sets of two and three digits, forming opposable, two-digited mittenlike fore- and hindfeet, with a manus fusion of 1–2–3 and 4–5, and a pes one of 1–2 and 3–4–5), projectile tongues, and independently movable eyes with mufflerlike lids. Most species have a skin of small, juxtaposed scales. No osteoderms occur dorsally or ventrally on the trunk. All species are limbed; the specialized pectoral girdle lacks an interclavicle and clavicles. The tail is moderately short (about two-thirds SVL) to long and usually prehensile; the caudal vertebrae lack fracture planes. The tongue is covered dorsally with reticular papillae and lacks lingual scales; the foretongue is nonretractable into the hindtongue. The skull possesses paired nasals (occasionally fused), postorbitals, squamosals, and a single frontal and parietal; a parietal foramen, when present, perforates the frontal bone. Attachment of the marginal dentition is acrodont, and the pterygoid lacks teeth.

Biology Chameleons are largely although not exclusively arboreal. Many features of their morphology described above are associated with a specialized arboreal existence and prey capture. They are stalkers, walking along narrow branches with a slow, somewhat jerky gait that suggests a leaf shaken by the wind. After insect prey is located visually, locomotion is frozen, and the independently mobile eyes focus with the head adjusted to center the eyes binocularly on the prey (but see Chapter 11); the tongue shoots forward—nearly the length of the body—and entraps the prey and recoils into the mouth. In addition to camouflaging their gait and other body movements, chameleons adjust their

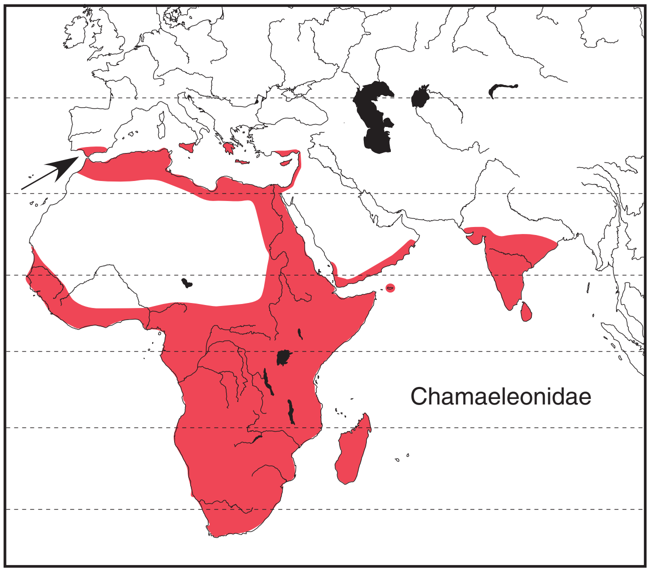


FIGURE 20.5 Geographic distribution of the extant Chamaeleonidae.

body colors to match their background to escape detection by visual-searching bird and mammal predators.

Chameleons vary greatly in adult size, from the tiny leaf chameleons (*Brookesia*, Madagascar; *Rhampholeon*, Africa) that are 25 to 55 mm SVL to the larger, more diverse *Chamaeleo* that are 70 to 630 mm SVL. They live in diverse forest habitats from scrub to evergreen rain forest; some live high in the canopy, others in the shrubs of the understory, and a few mainly on the ground in grassy or scrub habitats. Both egg-laying and live-bearing taxa are known. Clutch and litter size generally correlates with body size; the smaller taxa generally produce 2 to 8 eggs or neonates, and the larger species typically deposit more than 20 and as many as 50 eggs, but litter size is generally 20 embryos or less, even for large females. Incubation duration is variable and may reach 300 days for winter-nesting *Chamaeleo dilepis*. In *Brookesia stumpffi*, which apparently lays eggs containing advanced embryos, the incubation period varies from 28 to 30 days.

Comment Recent phylogenetic analysis does not support a classification of terrestrial versus arboreal chamaeleonid groups (Klaver and Böhme, 1986; Rieppel and Crumly, 1997).

References Bauer, 1997; Branch, 1988; Burrage, 1973; Estes et al., 1988; Fitch, 1970; Glaw and Vences, 1994; Hallermann, 1998; Hofman et al., 1991; Klaver and Böhme, 1986, 1997; Martin, 1992; Rieppel and Crumly, 1997; Schwenk, 1988.

Iguanidae

Anoles, iguanas, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Acrodonta (= Agamidae and Chamaeleonidae).

Content Eight subfamilies, Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, Phrynosomatinae, Polychrotinae, and Tropidurinae.

Distribution Throughout the Americas, Madagascar, and west-central Pacific islands (Fig. 20.6).

Characteristics Iguanids range from small (30 mm adult SVL, *Anolis ophiolepis*) to large (750 mm adult SVL, *Cyclura nubilia*) lizards, many covered dorsally and ventrally by large, keeled, overlapping scales and others with small, granular scales. No osteoderms occur dorsally or ventrally on the trunk. All species are limbed, and the pectoral girdle has a T-shaped interclavicle and curved rod-shaped clavicles. The tail is usually long to moderately long, and many iguanids have caudal autotomy with fracture planes variously located in the caudal vertebrae. The tongue is covered dorsally with reticular papillae and lacks lingual scales; the foretongue is nonretractable. The skull possesses paired nasals, postorbitals, squamosals, and single (fused) frontal and parietal bones; a parietal foramen is present in most species and perforates the frontal, frontoparietal suture, or parietal. Attachment of the marginal dentition is pleurodont, and teeth are present or absent on the pterygoids.

References Estes et al., 1988; Frost and Etheridge, 1989; Hallermann, 1994, 1998; Macey et al., 1997; Schwartz and Henderson, 1991; Schwenk, 1988, 1994b; Williams, 1988.

Corytophaninae

Sister taxon Uncertain, possibly Polychrotinae.

Content Three genera, *Basiliscus*, *Corytophanes,* and *Laemanctus*, with nine species.

Distribution Southern Mexico to northern South America.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are in broad contact, the parietal foramen perforates the frontal (absent

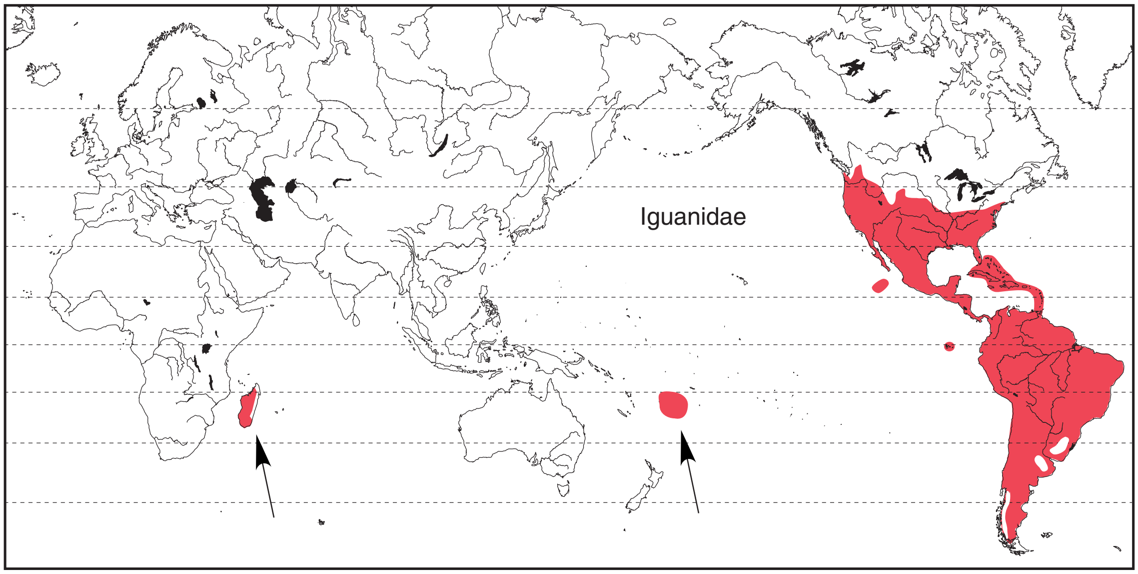


FIGURE 20.6 Geographic distribution of the extant Iguanidae.

in *Laemanctus*), palatine teeth are absent, and pterygoid teeth are present. Meckel's groove in the mandible is usually fused. Males lack femoral pores, and spinuate scale organs are absent.

Biology Corythophanines are largely arboreal lizards (Fig. 20.7), living in dry scrub forest to wet rain forest. They are casque-headed, slender-bodied, long-limbed, and long-tailed lizards, generally ranging from 90 to 200 mm adult SVL. Of the three genera, species of *Corytophanes* and *Laemanctus* are strongly arboreal and rarely ascend to the ground except to lay eggs. They are capable of rapid locomotion, but typically use a slow, methodical gait, reminiscent of chameleons, and although not capable of rapid color change, they are cryptically camouflaged. In contrast, basilisks (*Basiliscus*) are low-level forest inhabitants, foraging largely on the ground but returning to trees to escape predators and to sleep or bask. Basilisks are also capable of running bipedally and are noted for their ability to run across the surface of water. All species with the exception of *Corytophanes pericarinata* are oviparous. Basilisks have 8 to 18 eggs per clutch, whereas the other two genera have fewer eggs (2–8). The viviparous *C. pericarinata* produce an average litter of 7 neonates (3–10). Egg deposition likely occurs year round in equitable habitats and from the early to the middle of the dry season in the more climatically extreme areas. Incubation is about 8 to 12 weeks.

References Frost and Etheridge, 1989; Lang, 1989b; McCoy, 1968; Van Devender, 1982.

Crotaphytinae

Sister taxon Uncertain.

Content Two genera, *Crotaphytus* and *Gambelia*, with 12 species.

Distribution Southwestern United States and northern Mexico.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture, and palatine and pterygoid teeth are present. Meckel's groove in the mandible is open. Males have femoral pores, and spinuate scale organs are absent.

Biology Crotaphytines are moderately large (100–140 mm adult SVL), stout-bodied lizards with long, strong limbs and long tails (Fig. 20.8). They are principally diurnal predators, frequently preying upon other lizards, although arthropods form a significant component of their diet. They occur predominantly in dry open habitats and select a rock or other vantage point from which they can search for prey. When prey is sighted, they jump from their perch and chase their prey. They are fast and capable of bipedal running. They produce clutches of modest size, averaging three to eight eggs per female; clutch size increases as female size and age increase.

References Frost and Etheridge, 1989; McGuire, 1996.

FIGURE 20.7 Representative iguanid lizards. Clockwise from upper left: smooth helmet-head *Corytophanes cristatus*, Corytophaninae (photograph by J. P. Caldwell); Boulenger's dwarf iguana *Enyalioides palpebralis*, Hoplocercinae (L. J. Vitt); Dumeril's Madagascar swift *Oplurus grandidieri*, Oplurinae (H. Uible); and Wied's flathead anole *Enyalius catenatus*, Polychrotinae (L. J. Vitt).

Hoplocercinae

Sister taxon Uncertain, possibly Iguaninae.

Content Three genera, *Enyalioides*, *Hoplocercus,* and *Morunasaurus*, with 10 species.

Distribution Disjunct, from the Isthmus of Panama to northern South America and in upland areas of the Amazon basin. *Hoplocercus* occurs in the Brazilian cerrados, south of the Amazon basin.

Characteristics In the skull, the lacrimal foramen is enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture, palatine teeth are absent, and pterygoid teeth are present. Meckel's groove in the mandible is open.

FIGURE 20.8 Representative iguanid lizards. Clockwise from upper left: collared lizard *Crotaphytus collaris*, Crotaphytinae (photograph by L. J. Vitt); Fijian crested iguana *Brachylophus vitiensis*, Iguaninae (G. R. Zug); greater earless lizard *Cophosaurus texanus*, Phrynosomatinae (L. J. Vitt); and yellow-headed tropidure *Tropidurus flaviceps*, Tropidurinae (L. J. Vitt).

Males have femoral pores, and spinuate scale organs are absent.

Biology Hoplocercines are moderately large lizards (90–150 mm adult SVL), each genus with a different habitus. For example, *Hoplocercus* is a robust lizard, somewhat like a spiny iguana, and *Enyalioides* (Fig. 20.7) is more slender with longer hindlimbs. This difference in body form is associated with more terrestrial habits in open habitats in the former and semiarboreal habits in forest habitats in the latter. All species are insectivorous. Reproductive behavior is little studied.

References Avila-Pires, 1995; Frost and Etheridge, 1989.

Iguaninae

Sister taxon Uncertain, possibly Hoplocercinae.

Content Eight genera, *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana,* and *Sauromalus*, with 29+ species.

Distribution Americas from southwestern United States to Paraguay and southern Brazil, West Indies, Galapagos, and west-central Pacific islands.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture, palatine teeth are absent, and pterygoid teeth are present. Meckel's groove in the mandible is fused. Males have femoral pores, and spinuate scale organs are absent.

Biology Iguanines (the iguanas) are typically large lizards; most species exceed 200 mm adult SVL, although some, such as the Fijian banded iguana (*Brachylophus fasciata*) and the desert iguana (*Dipsosaurus dorsalis*) attain sexual maturity at 140 to 160 mm SVL.

Iguanas are predominantly terrestrial in mesic to xeric habitats. Only *Iguana* and *Brachylophus* (Fig. 20.8) display strong arboreality, rarely descending to the ground. They are predominantly to exclusively herbivores, feeding on a wide variety of plant parts, including flowers and fruits as well as foliage. *Amblyrhynchus cristatus* feeds exclusively on marine algae and grazes beneath the water even though it is not an exceptionally proficient swimmer. All iguanas are oviparous and produce moderately large clutches, ranging from 2 to 8 eggs in the small-bodied *D. dorsalis* and 12 to 88 eggs in the large-bodied *Cyclura* and *Iguana*. Nutrition is a significant factor in clutch size; large-bodied species in resource-poor environments produce fewer eggs. Several of the larger iguanas (e.g., *Iguana iguana*, *Conolophus pallidus*) migrate from their home ranges to special nesting sites to deposit eggs. For most iguanas, incubation is about 10 to 12 weeks, but commonly requires more than 30 weeks in the two Fijian iguanas.

References Burghardt and Rand, 1982; Frost and Etheridge, 1989; Norell and de Queiroz, 1991; Wiewandt, 1982.

Oplurinae

Sister taxon Uncertain, possibly Tropidurinae or Polychrotinae.

Content Two genera, *Chalarodon* and *Oplurus*, with one and six species, respectively.

Distribution Madagascar and the Iles Comores.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture, palatine teeth are present or absent, and pterygoid teeth are present. Meckel's groove in the mandible is variably open or fused. Males lack femoral pores, and spinuate scale organs are present.

Biology In looks and behavior, the Madagascan oplurines share many features with the phrynosomatines and tropidurines. They range from 60 to 90 mm adult SVL (*Chalarodon*) to 90 to 150 mm (*Oplurus*; Fig. 20.7). They include arboreal and terrestrial taxa. *Oplurus* lives mainly on rocks and *Chalarodon* lives in sandy areas. All live in xeric habitats, scrub to desert. All species are oviparous; the smaller *Chalarodon madagascarensis* typically lays two eggs and the somewhat larger *Oplurus* deposits clutches of four to six eggs. Nests are regularly dug and eggs are deposited in the ground, but some rock dwellers deposit eggs in rock crevices.

References Blanc, 1977; Frost and Etheridge, 1989; Glaw and Vences, 1994; Titus and Frost, 1996.

Phrynosomatinae

Sister taxon Uncertain, possibly Tropidurinae.

Content Nine genera, *Callisaurus*, *Cophosaurus*, *Holbrookia*, *Petrosaurus*, *Phrynosoma*, *Sceloporus*, *Uma*, *Urosaurus,* and *Uta*, with 110+ species.

Distribution Southern one-half of North America to western Panama.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture, and palatine and pterygoid teeth are absent. Meckel's groove in the mandible is open. Males have femoral pores, and spinuate scale organs are absent.

Biology Phrynosomatines are the dominant iguanid lizards of North America and Mexico; species diversity of this clade declines southward through Central America. They are largely arid-adapted species (Fig. 20.8) and reach their greatest abundance in the xeric habitats of the southwestern United States and the Mexican Plateau. *Sceloporus* is the most diverse genus with more than 70 species. The moderately robust, spiny-scaled body of many *Sceloporus* epitomizes the spiny-lizard appearance shared with many other iguanid and agamid genera. This body form also largely characterizes a terrestrial–semiterrestrial, sit-and-wait foraging lizard that preys largely on insects and other arthropods. *Urosaurus*, *Holbrookia*, and their relatives are smaller-scaled, slender-bodied, and longer-limbed lizards, and although they and the *Sceloporus* may not look like the pancake-bodied *Phrynosoma* (an ant specialist), they are all closely related. The phrynosomatines are predominantly moderate-sized lizards, and most species range from 50 to 100 mm adult SVL. A few species are larger but none exceeds 200 mm SVL. Phrynosomatines are predominantly oviparous. Clutches consist of 2 to 28 eggs, although most species produce less than 10 eggs per clutch. Several species of *Phrynosoma* and *Sceloporus* are livebearers, producing litters of 6 to 30 neonates. Most species occur in seasonal environments; hence reproduction is strongly seasonal. The first clutch is deposited in middle to late spring and often a second clutch is produced a few weeks later. Incubation times generally range from 6 to 8 weeks.

References Dunham et al., 1988; Fitch, 1970; Frost and Etheridge, 1989; Reeder, 1995; Reeder and Wiens, 1996; Sherbrooke, 1981; Sites et al., 1992.

Polychrotinae

Sister taxon Uncertain, possibly Corytophaninae or Oplurinae.

Content Eight genera, *Anisolepis*, *Anolis*, *Diplolaemus*, *Enyalius*, *Leiosaurus*, *Polychrus*, *Pristiodactylus,* and *Urostrophus*, with 320+ species.

Distribution Southeastern United States through Central America and the West Indies to nearly the southern tip of South America.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen usually perforates the frontoparietal suture (occasionally the parietal), palatine teeth are present or absent, and pterygoid teeth are present. Meckel's groove in the mandible is fused. Males lack femoral pores (except *Polychrus*), and spinuate scale organs are typically present.

Biology Polychrotinae are the most speciose iguanid lizards (Fig. 20.7). One genus, *Anolis* (anoles), has about 200 species. The adaptive radiation of the West Indian *Anolis* within and among islands has provided a theoretical and experimental springboard for numerous evolutionary and ecological studies (e.g., Losos, 1994; Roughgarden, 1995; Schoener, 1974; Williams, 1983). Polychrotines, also known as anolines, are predominately arboreal species as indicated by their specialized foot morphology. They range in size from 30 mm SVL (*Anolis ophiolepis*) to greater than 180 mm SVL (*Anolis equestris* complex), although most species are within 40 to 80 mm SVL. Most species are sexually dimorphic with larger males. All appear to be diurnal, and most are sit-and-wait foragers on arthropod prey. Anoles have a unique reproductive physiology that includes continual egg production. Only one egg is laid at a time—in a terrestrial nest—but another egg is in production. Oogenetic maturation, ovulation, and egg shelling occur alternately between the left and the right ovaries and oviducts, and, under ideal conditions, a female in good condition will lay an egg every 16 to 20 days. Continuous reproduction does not typically occur in the wild because most environments are climatically cyclic; thus food availability and quality are also cyclic. Other polychrotines have a typical lizard reproduction and produce clutches with variable numbers of eggs (range, 2–23) deposited in a terrestrial nest.

Comments *Anolis* is morphologically uniform, and this uniformity has made it difficult to determine relationships among the various species groups. Guyer and Savage (1987; Savage and Guyer, 1989) offered one solution and recognized two major clades, *Anolis* and *Norops*, and several much smaller ones. Their solution has been accepted by some researchers but rejected by others because their proposed taxa are likely paraphyletic (e.g., Jackman et al., 1997b).

References Avila-Pires, 1995; Etheridge and Williams, 1991; Frost and Etheridge, 1989; Guyer and Savage, 1987; Irschick et al., 1997; Jackman et al., 1997b; Losos, 1994; Roughgarden, 1995; Savage and Guyer, 1989; Schoener, 1974; Vitt and Lacher, 1981; Vitt et al., 1995, 1996a; Williams, 1983.

Tropidurinae

Sister taxon Uncertain, possibly Phrynosomatinae.

Content Nine genera, *Ctenoblepharys*, *Leiocephalus*, *Liolaemus*, *Microlophus*, *Phymaturus*, *Plesiomicrolophus*, *Stenocercus*, *Tropidurus,* and *Uranoscodon*, with 175+ species.

Distribution West Indies from the Bahamas to the southern tip of South America.

Characteristics In the skull, the lacrimal foramen is not enlarged, the jugal and squamosal are not in broad contact, the parietal foramen perforates the frontoparietal suture or is absent, palatine teeth are absent, and pterygoid teeth are usually present. Meckel's groove in the mandible is variably fused. Males lack femoral pores, and spinuate scale organs are absent.

Biology Tropidurines are morphologically similar to the sceloporines, and include both spiny (Fig. 20.8) and smooth-scaled forms. They are generally a more diverse group of lizards living in a broader range of habitats from mesic forest to deserts; nonetheless, like phrynosomatines, they occur primarily in open habitats, and many are arid-adapted. Tropidurines show three adaptative radiations: a leiocephalin clade in the West Indies, a tropidurin one in northern and central South America; and a liolaemin clade in the grasslands and deserts of southern South America. The former two clades have larger body sizes (>65 mm adult SVL) and many have the spiny-lizard appearance; they also are typical insectivores. The liolaemins are somewhat smaller and smoother-scaled lizards; many species include significant amounts of vegetable matter in their diets. Most tropidurines are oviparous with clutches ranging from 1 to 14 eggs; generally larger species have larger clutches. Some populations of the southern latitude and high-elevation species, such as *Liolaemus magellanicus*, are viviparous.

References Avila-Pires, 1995; Etheridge, 1995; Frost, 1992; Frost and Etheridge, 1989; Jaksíc and Schwenk, 1983; Vitt, 1991; Vitt and Goldberg, 1983; Vitt and Zani, 1996d; Vitt et al., 1997a.

Nyctisaura

Gekkonidae

Geckos and pygopods

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain; two main hypotheses are Annulata or Scleroglossa/Autarchoglossa.

Content Four subfamilies, Diplodactylinae, Eublepharinae, Gekkoninae, and Pygopodinae.

Distribution Pantropic on all land masses (Fig. 20.9).

Characteristics Geckos are small (16–18 mm adult SVL, *Sphaerodactylus parthenopion*) to large (370 mm SVL, *Hoplodactylus delcourti*) lizards. Most species are covered dorsally and ventrally by small, granular scales that are occasionally interspersed with tubercles. No osteoderms occur dorsally on the trunk; they occur ventrally in some geckos. Most species are distinctly limbed; these taxa have a pectoral girdle with a T-shaped or cruciform interclavicle and angular clavicles. The tail is usually moderately short to long (two-thirds to just longer than SVL). Caudal autotomy is common, and a fracture plane occurs posterior to the transverse processes of each caudal vertebra. The tongue is covered dorsally with peglike papillae and lacks lingual scales; the foretongue is nonretractable. The skull possesses paired nasals and single or paired frontals and parietals; squamosals are present or absent; and postorbitals and a parietal foramen are absent. Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

Comments Eublepharines are regularly given familial status and considered the sister group of the clade containing all other geckos. However, most studies examining the relationships among geckos usually only include one or two outgroups of other lizards, and conversely, studies examining the relationships of squamates seldom treat eublepharines independently of other geckos. See the Overview.

References Bauer, 1994; Donnellan et al., 1999; Estes et al., 1988; Hallermann, 1998; Kluge, 1987, 1991b; Rösler, 1995; Russell et al., 1997; Schwenk, 1988.

Diplodactylinae

Sister taxon Pygopodinae.

Content Fifteen genera, *Bavayia*, *Carphodactylus*, *Crenadactylus*, *Diplodactylus*, *Eurydactylodes*, *Hoplodactylus*, *Naultinus*, *Nephrurus*, *Oedura*, *Phyllurus*, *Pseudothecadactylus*, *Rhacodactylus*, *Rhynchoedura*, *Saltuarius*, and *Strophurus*, with 110+ species.

Distribution Australia, New Caledonia, and New Zealand.

Characteristics Body is not elongate or snakelike; both fore- and hindlimbs are well developed. The skin

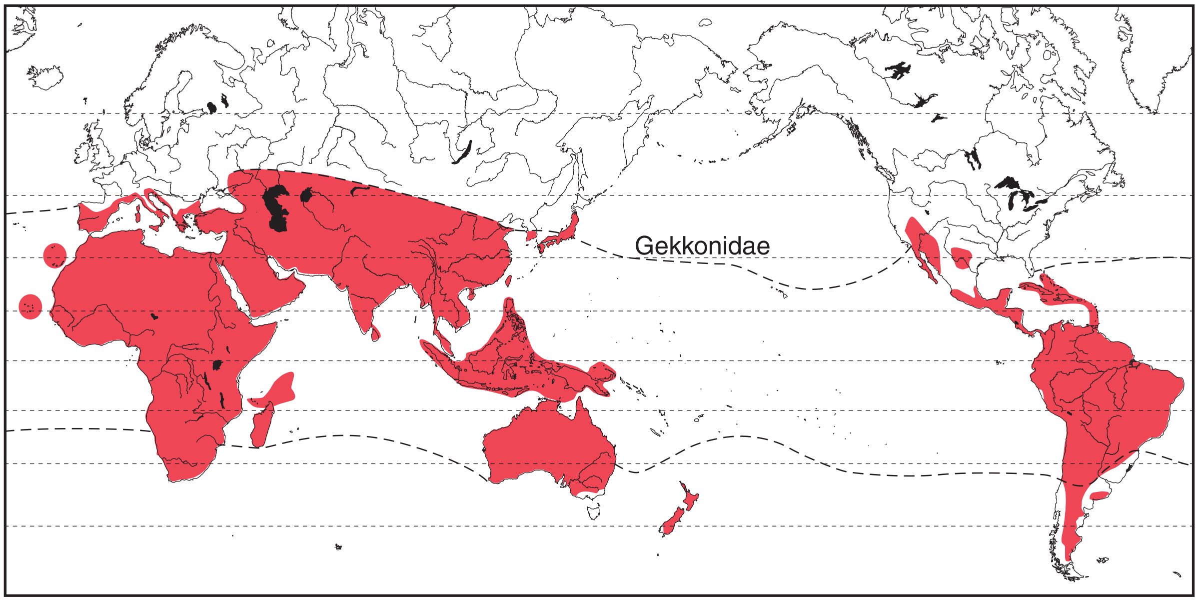


FIGURE 20.9 Geographic distribution of the extant Gekkonidae.

is soft with numerous small, juxtaposed scales. The skull has paired premaxillaries, paired parietals, and an imperforate stapes, except in *Eurydactylodes.* The eye is covered by a spectacle and usually contains 20 or more sclerotic ossicles. The auditory meatus is fully encircled by a closure muscle, and the tectorial membrane is thickened medially.

Biology Diplodactylines are predominately moderate-sized geckos (60–110 mm adult SVL; Fig. 20.10), although *Hoplodactylus delcourti* attains a 370-mm SVL and *Rhacodactylus* adults commonly exceed 100 mm SVL. Diplodactylines occupy a wide range of habitats from cool, moist forest to dry scrub and desert. Most are nocturnal and many are arboreal although a few, such as *Nephrurus,* are distinctly terrestrial, spending the day in burrows and foraging on the surface at night. Most are insectivorous although the prehensile-tailed *Naultinus* and a few others are nectivores, or at least nectar and flowers form a significant portion of their diet. Most are oviparous and typically lay two eggs, which remain leathery through incubation. A few, such as *Hoplodactylus* and *Naultinus*, are viviparous and produce only two neonates.

References Bauer, 1990; Gill and Whitaker, 1996; Greer, 1989; King and Horner, 1993.

Eublepharinae

Sister taxon Uncertain, likely the Gekkoninae–Diplodactylinae–Pygopodinae clade.

Content Six genera, *Aeluroscalabotes*, *Coleonyx*, *Eublepharis*, *Goniurosaurus*, *Hemitheconyx,* and *Holodactylus*, with 25 species.

Distribution Disjunct in southwestern North America and northern Central America, and sub-Saharan Africa and southern Asia.

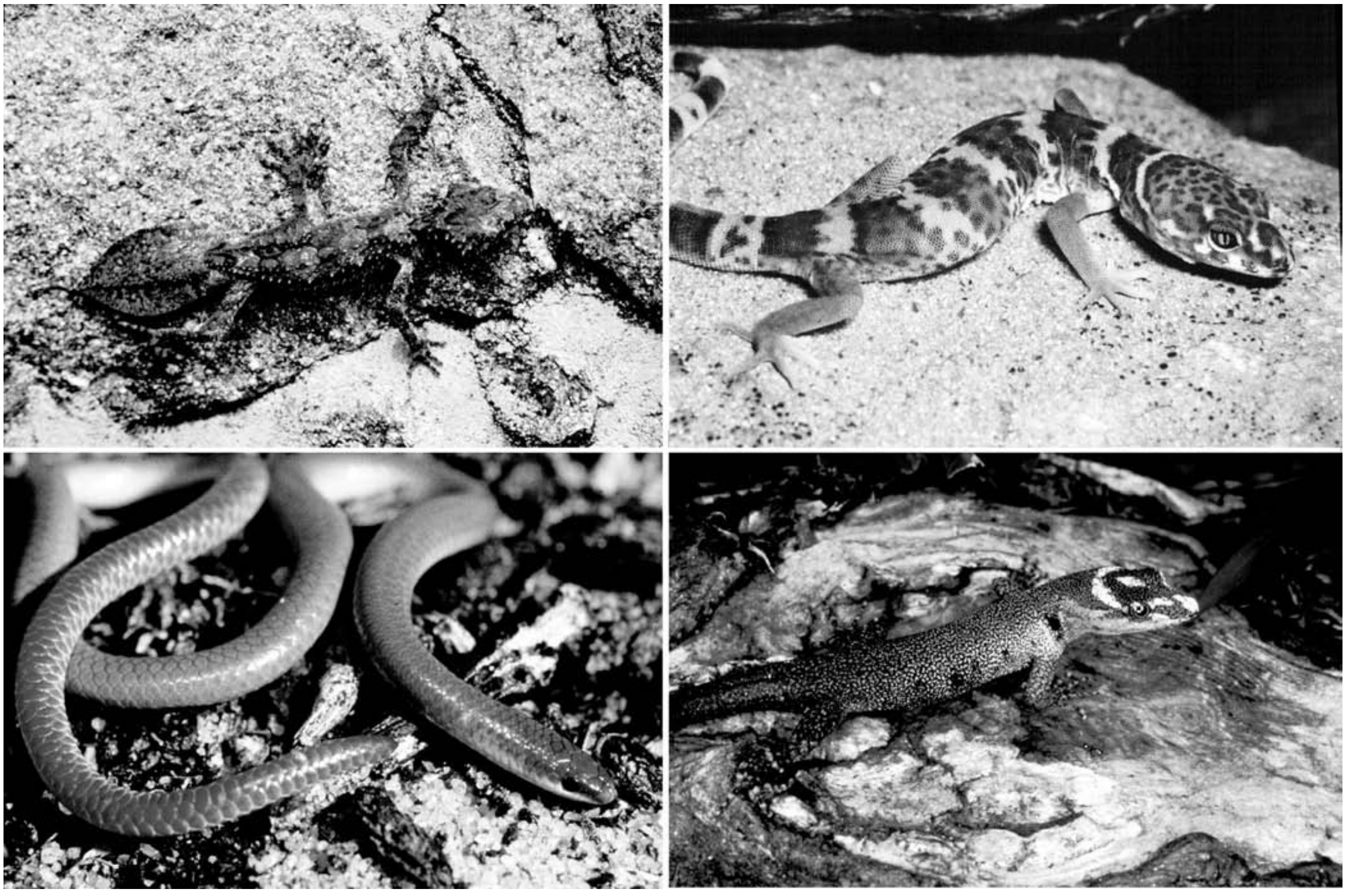


FIGURE 20.10 Representative geckos. Clockwise from upper left: northern leaf-tailed gecko *Phyllurus cornutus*, Diplodactylinae (photograph by G. R. Zug); Texas banded gecko *Coleonyx brevis*, Eublepharinae (R. W. Van Devender); Trinidad gecko *Gonatodes humeralis*, Gekkoninae (J. P. Caldwell); and southern pygopodid *Aprasia inaurita*, Pygopodinae (M. Kearney).

Characteristics Body is not elongate or snakelike; both fore- and hindlimbs are well developed. The skin is soft with numerous small, juxtaposed scales. The skull has paired premaxillaries, a single parietal, and a stapes perforated by a branch of the facial artery. The eye lacks a spectacle cover and usually contains 20 or more sclerotic ossicles. The auditory meatus has a semicircular closure muscle, and the tectorial membrane is uniform.

Biology Eublepharines are moderate to large geckos, ranging from 45 to 155 mm adult SVL. With the exception of Bornean *Aeluroscalabotes*, they are terrestrial geckos with narrow digits, and all are nocturnal insectivores. Their disjunct Northern Hemisphere distribution suggests an ancient lizard clade, and presently each regional occurrence denotes a separate center of diversification. The American radiation produced six species (*Coleonyx*), two living on the floor of mesic tropical forests and four in the Southwest deserts (Fig. 20.10). The Asian *Eublepharis* consists of eight species in the Asian deserts from Iraq to northeastern peninsular India. The other Asian taxa are mainly forest inhabitants; *Goniurosaurus* lives on the forest floor or rock outcrops, and *Aeluroscalabotes* lives above the forest floor on logs and understory shrubs. The African radiation (*Hemitheconyx* and *Holodactylus*, two species each) occurs mainly in scrub and desert habitats. All eublepharines are surface foragers and have a fixed clutch size of two eggs.

References Dial and Grismer, 1992, 1994; Dial and Schwenk, 1996; Grismer, 1988; Grismer et al., 1994; Inger and Lian, 1996.

Gekkoninae

Sister taxon Uncertain, possibly the Diplodactylinae–Pygopodinae clade.

Content Nearly 80 genera, *Afroedura*, *Afrogecko*, *Agamura*, *Ailuronyx*, *Alsophylax*, *Aristelligella*, *Aristelliger*, *Asaccus*, *Asiocolotes*, *Blaesodactylus*, *Bogertia*, *Briba*, *Bunopus*, *Calodactylodes*, *Carinatogecko*, *Chondrodactylus*, *Christinus*, *Cnemaspis*, *Coleodactylus*, *Colopus*, *Cosymbotus*, *Crossobamon*, *Cryptactites*, *Cyrtodactylus*, *Dixonius*, *Ebenavia*, *Euleptes*, *Geckoella*, *Geckolepis*, *Geckonia*, *Gehyra*, *Gekko*, *Goggia*, *Gonatodes*, *Gymnodactylus*, *Haemodracon*, *Hemidactylus*, *Hemiphyllodactylus*, *Heteronotia*, *Homonota*, *Homopholis*, *Lepidoblepharis*, *Lepidodactylus*, *Luperosaurus*, *Lygodactylus*, *Matuatua*, *Microgecko*, *Microscalabotes*, *Nactus*, *Narudasia*, *Pachydactylus*, *Palmatogecko*, *Paragehyra*, *Paroedura*, *Perochirus*, *Phelsuma*, *Phyllodactylus*, *Phyllopezus*, *Pristurus*, *Pseudogekko*, *Pseudogonatodes*, *Ptenopus*, *Ptychozoon*, *Ptyodactylus*, *Quedenfeldtia*, *Rhoptropus*, *Saurodactylus*, *Sphaerodactylus*, *Stenodactylus*, *Tarentola*, *Tenuidactylus*, *Teratolepis*, *Teratoscincus*, *Thecadactylus*, *Tropiocolotes*, *Urocotyledon,* and *Uroplatus*, with 800+ species.

Distribution Pantropic and temperate Eurasia.

Characteristics Body is not elongate or snakelike; both fore- and hindlimbs are well developed. The skin is soft with numerous small, juxtaposed scales, except in *Teratoscincus.* The skull has a single premaxillary, a single parietal (paired in sphaerodactyl geckos), and an imperforate or perforated stapes. The eye is covered by a spectacle and contains 14 sclerotic ossicles. The auditory meatus has a semicircular closure muscle, and the tectorial membrane is uniform.

Biology The gekkonines are the most speciose lizard group and are possibly the most diverse and successful lizards, although lygosomine skinks may be as diverse. Varying greatly in morphology, particularly foot morphology, they nonetheless remain recognizable as geckos and most retain a nocturnal activity pattern, which is considered the ancestral condition for the gekkonids. *Phelsuma, Coleodactylus, Pseudogonatodes, Lepidoblepharis, Lygodactylus,* and most *Gonatodes* (Fig. 20.10) are diurnal. Most geckonines are small to moderate-sized lizards, ranging from 35 to 100 mm adult SVL. A few, such as *Gekko*, commonly exceed 100 mm SVL as adults, and one clade, *Sphaerodactylus*, are typically tiny geckos (most less than 30 mm SVL). Most geckos are rupicolous or arboreal. Aridland species commonly occur on rock outcrops and cliffs, and forest species occupy a variety of elevated sites from low understory to high in the canopy. Other geckos are strictly terrestrial, living on leaf litter, in burrows, or beneath surface detritus. Most are insectivorous; however, larger species commonly eat smaller geckos, and a few species at least supplement their diet with nectar, fruit, and sap. Some small species, such as *Coleodactylus amazonicus*, eat springtails and mites that they capture in the leaf litter. All gekkonines are oviparous, typically depositing two eggs that have flexible shells when laid. The shells quickly harden and become resistant to water loss. The tiny *Sphaerodactylus, Coleodactylus, Pseudogonatodes,* and *Lepidoblepharis* deposit single eggs, which may reflect a morphological constraint on clutch volume because of small body size. One large species, *Thecadactylus rapicauda*, also has a clutch size of a single egg. The gekkonines include about a dozen species that are parthenogenetic, several of which have spread widely throughout the Indo-Australia and Pacific region via accidental transport by humans (e.g., *Hemidactylus garnotii*, *Lepidodactylus lugubris*).

References Greer, 1989; Ineich, 1992; King and Horner, 1993; Schwartz and Henderson, 1991; Vitt and Zani, 1997.

Pygopodinae

Sister taxon Diplodactylinae.

Content Eight genera, *Aclys*, *Aprasia*, *Delma*, *Lialis*, *Ophidiocephalus*, *Paradelma*, *Pletholax,* and *Pygopus*, with 35+ species.

Distribution Australia and southern New Guinea.

Characteristics Body is elongate and snakelike; external evidence of forelimbs is lacking and hindlimbs are flaplike. The skin is composed of large, overlapping scales. The skull has paired premaxillaries, paired parietals (single in *Lialis*), and an imperforate stapes. The eye is covered by a spectacle and contains 11–19 sclerotic ossicles. The auditory meatus is fully encircled by a closure muscle, and the tectorial membrane is uniform.

Biology The snakelike pygopods are moderate (59 mm adult SVL, *Delma australis*) to large (310 mm SVL, *Lialis jicari*) lizards; most species are between 70 and 120 mm SVL as adults. Pygopods are largely but not entirely diurnal. They both search for and ambush prey, and most taxa are insectivorous. They eat a broad variety of arthropods, although a few appear to be dietary specialists, such as *Aprasia,* which feeds on ants. The large species may prey occasionally on small vertebrates, and *Lialis* appears to prey only on lizards, especially skinks. *Lialis* has a highly flexible hinge in the middle of the skull, and this added flexibility permits them to tightly grasp the hard, slippery-scaled skinks. Pygopods typically lay two eggs, although nests of six or more pygopod eggs have been found, indicating communal nesting. The eggs retain a flexible shell throughout an 8- to 10-week incubation period.

References Greer, 1989; Kluge, 1974, 1976; Patchell and Shine, 1986a,b; Shea, 1993.

Nyctisaura–Annulata

Dibamidae

Blindskinks

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain; two main hypotheses suggest Amphisbaenia or Scincomorpha.

Content Two genera, *Anelytropsis* and *Dibamus*, with 1 and 10 species, respectively.

Distribution Disjunct, Mexico and eastern Indochina to the East Indies (Fig. 20.11).

Characteristics Dibamids are small to moderate-sized (50–200 mm adult SVL) snakelike lizards. They lack forelimbs and have only flaplike hindlimbs. The body is cloaked in shiny, smooth, overlapping scales. No osteoderms occur dorsally or ventrally on the trunk. The absence of the forelimb is also internal; neither limb nor pectoral girdle bones are present. The tail is short and autotomic; a fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue is covered dorsally with filamentous papillae and lacks lingual scales; the foretongue is nonretractable. The skull possesses paired nasals and frontals, the postorbitals and squamosals are present or absent, and the parietal bone is single (fused); a parietal foramen is absent. Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

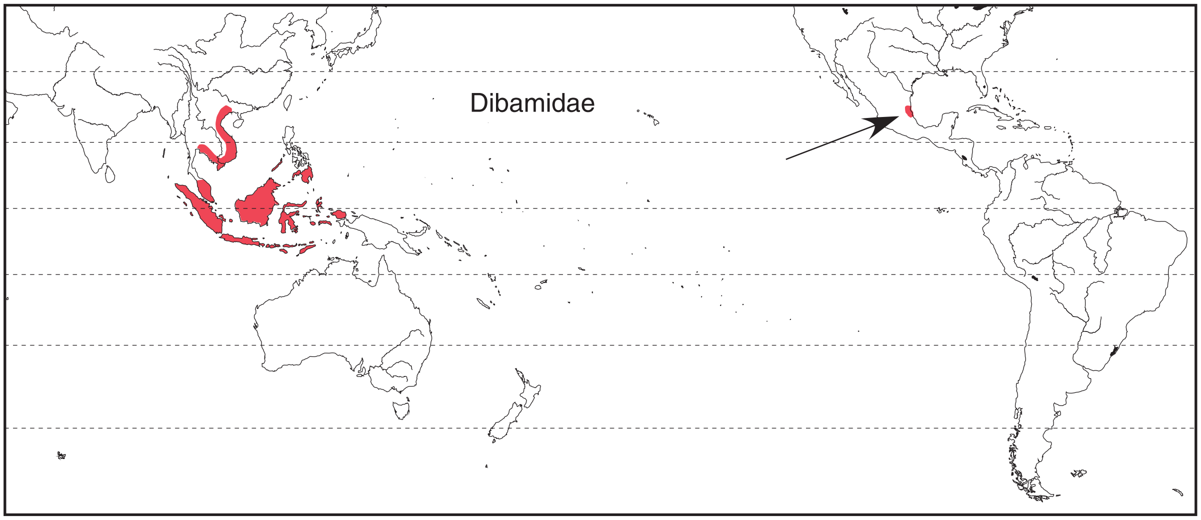


FIGURE 20.11 Geographic distribution of the extant Dibamidae.

Biology Dibamids are predominantly subsurface lizards, living beneath surface detritus and often in burrows and crevices in the ground. They apparently are not strict burrowers but depend upon burrows and other openings in the soil, although they are capable of digging in loose humus or friable soils. *Dibamus* (Fig. 20.12) is a forest-floor inhabitant and requires moist soils; during the dry season, it lives deep in the moisture shadow, beneath rocks and fallen trees. *Anelytropsis* is more arid adapted and dwells in dry upland forest and scrub. They are insectivorous, and all are presumably oviparous. Limited evidence suggests that *Dibamus* lays a single egg but that it may lay multiple sequential clutches. After deposition, the eggshell hardens, forming a barrier to water loss as in gekkonines. Reproductive data are not available for *Anelytropsis*.

References Estes et al., 1988; Greer, 1985; Hallermann, 1998; Schwenk, 1988.

Nyctisaura–Annulata–Amphisbaenia

Amphisbaenidae

Wormlizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Bipedidae or Rhineuridae.

Content Eighteen genera, *Amphisbaena*, *Ancylocranium*, *Anops*, *Aulura*, *Baika*, *Blanus*, *Bronia*, *Cadea*, *Cercolophia*, *Chirindia*, *Cynisca*, *Dalophia*, *Geocalamus*, *Leposternon*, *Loveridgea*, *Mesobaena*, *Monopeltis*, and *Zygaspis*, with ±130 species.

Distribution Greater Antilles, South America, and Africa (Fig. 20.13).

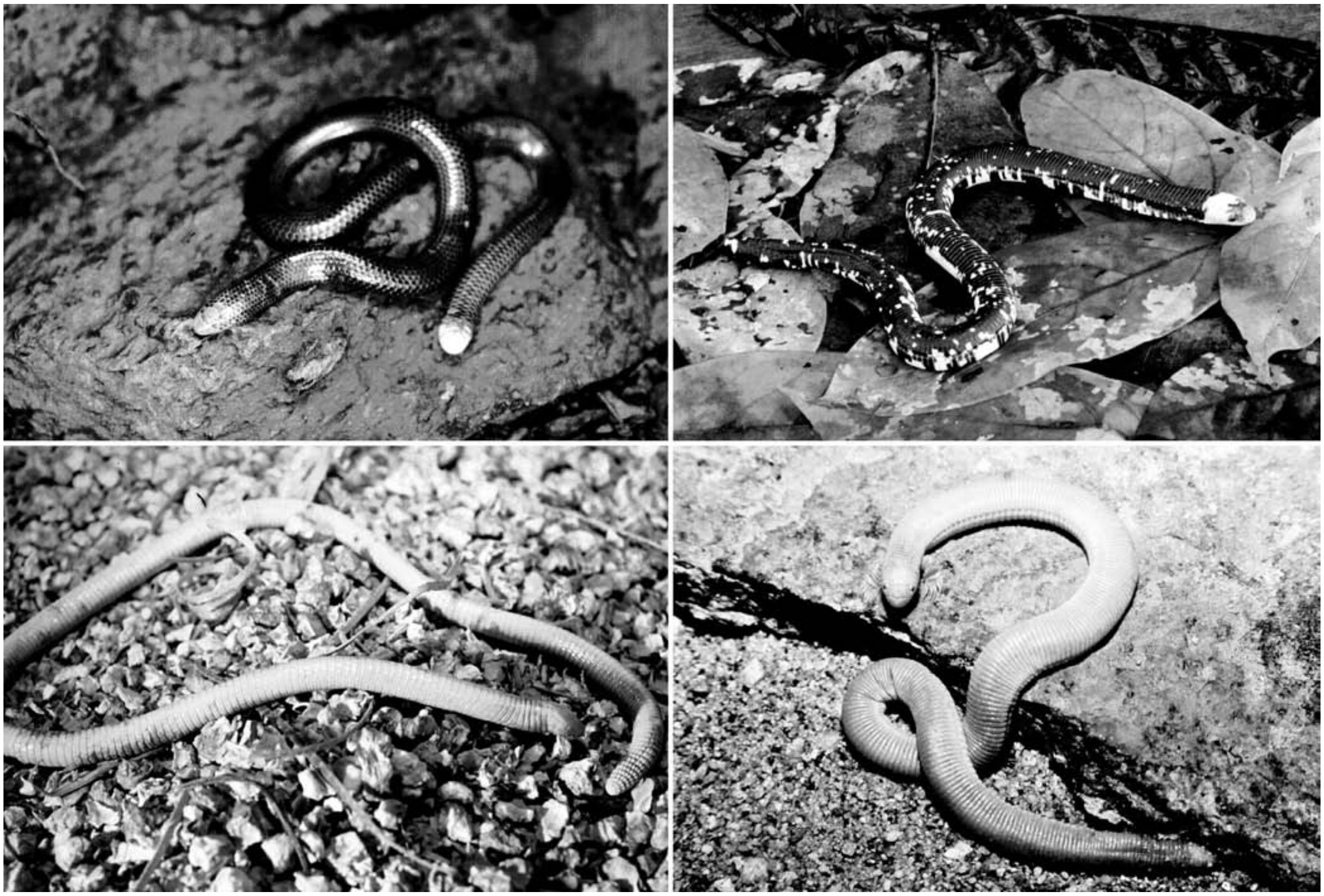


FIGURE 20.12 Representative annulate lizards. Clockwise from upper left: blindskink *Dibamus* sp., Dibamidae (photograph by R. W. Murphy); sooty wormlizard *Amphisbaena fulginosa*, Amphisbaenidae (L. J. Vitt); molelimb wormlizard *Bipes biporus*, Bipedidae (L. L. Grismer); and Florida wormlizard *Rhineura floridana*, Rhineuridae (R. G. Tuck, Jr.).

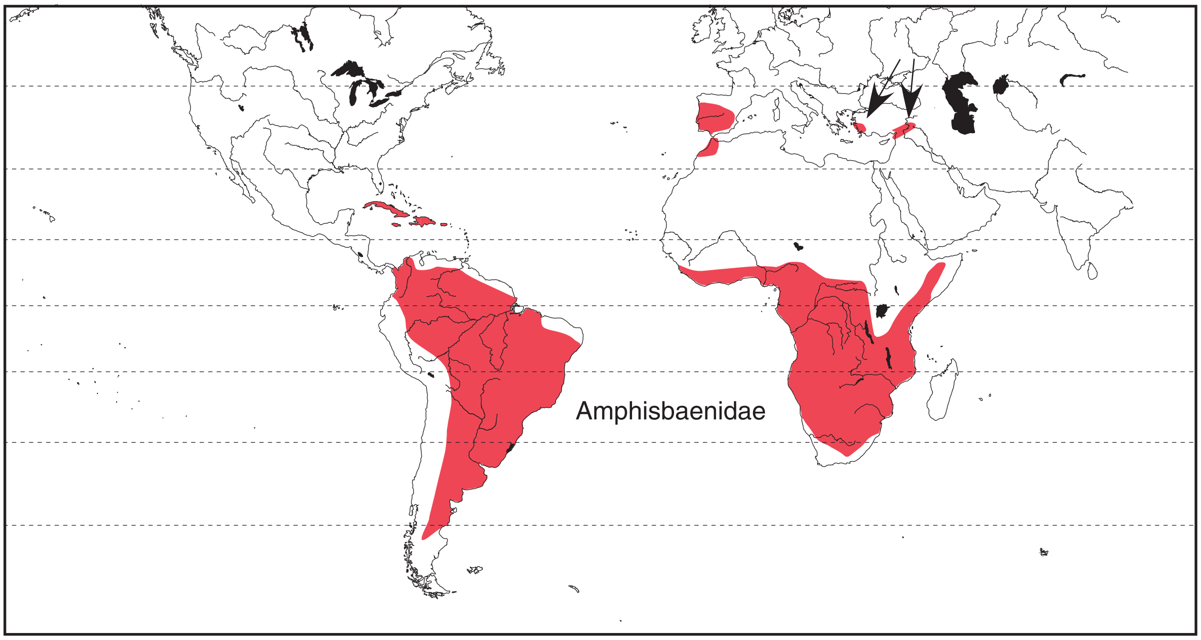


FIGURE 20.13 Geographic distribution of the extant Amphisbaenidae.

Characteristics Amphisbaenids are limbless, wormlike lizards. This annulate appearance results from rings of rectangular, juxtaposed scales encircling the body and tail. No osteoderms occur dorsally or ventrally on the trunk. The external limbless appearance is accompanied by the total absence of fore- and hindlimb skeletons; however, pelvic vestiges and occasionally sternal or pectoral vestiges persist. The tail is short and autotomic, but regeneration may not occur. The fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and is covered dorsally with lingual scales arranged in diagonal rows; the posterior edges of these scales are smooth. The foretongue is nonretractable. The skull possesses paired nasals and frontals, a single, large premaxillary and parietal, and no postorbitals or squamosals; a parietal foramen is absent, except in *Monopeltis.* Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

Biology Amphisbaenids are moderate-sized wormlizards (Fig. 20.12); most range from 250 to 400 mm adult SVL, although a few species are larger or smaller. *Amphisbaena alba* reaches 720 mm TL, whereas a few smaller species, such as *Chirindia rondoensis,* are only 90 to 120 mm SVL as adults. All are burrowers and create their own burrow systems. The blunt-cone or bullethead taxa (e.g., *Amphisbaena*, *Blanus*, and *Zygaspis*) burrow by simple head-ramming. The spade-snouted taxa (e.g., *Leposternon* and *Monopeltis*) tip the head downward, thrust forward, and then lift upward to compress the soil to the roof of the burrow. The laterally compressed keel-headed taxa (e.g., *Anops* and *Ancylocranium*) ram the head forward, and then alternately swing it to the left and right to compress the soil to the sides of the burrow. The ecology and life histories of most amphisbaenians are poorly studied. Among the amphisbaenids, most species appear to be oviparous, although *Loveridgea ionidesi* and *Monopeltis capensis* are live-bearers. Reproductive data are limited; clutch size appears small, typically from two to four elongate eggs, and clutch size may be related to body size.

References Broadley, 1997b; Estes et al., 1988; Gans, 1974, 1978; Gans and Kraklau, 1989; Hallermann, 1998; Schwenk, 1988.

Bipedidae

Mole-limbed wormlizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Amphisbaenidae.

Content One genus, *Bipes*, with three species.

Distribution Coastal southwestern Mexico and southern Baja California (Fig. 20.14).

Characteristics *Bipes* is unique among amphisbaenians by the presence of large molelike forelimbs and forefeet (Fig. 20.12). Their annulate appearance results

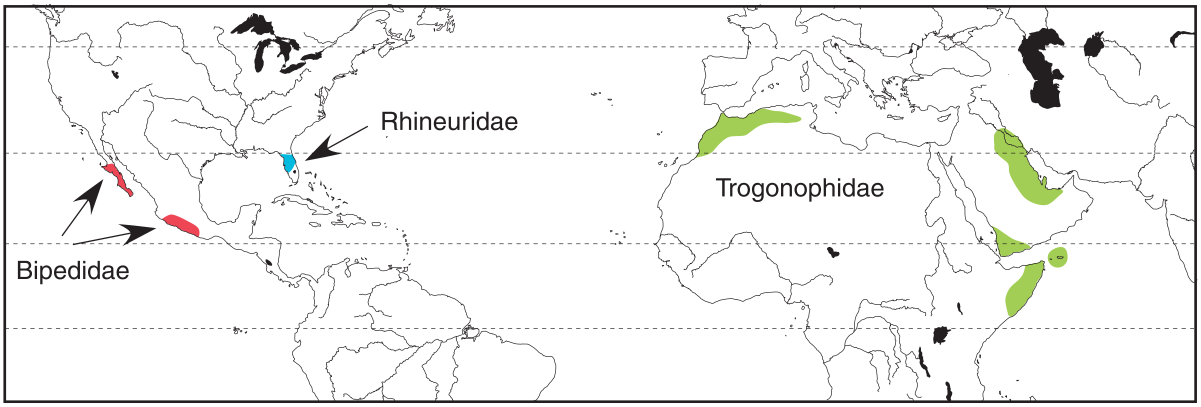


FIGURE 20.14 Geographic distributions of the extant Bipedidae, Rhineuridae, and Trogonophidae.

from rings of rectangular, juxtaposed scales encircling the body and tail. No osteoderms occur dorsally or ventrally on the trunk. Bipedids lack only hindlimb elements; they have unassignable pelvic remnants and robust forelimb and pectoral girdle skeletons, although an interclavicle and clavicles are absent. The tail is short and autotomic, but regeneration may not occur. The fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and is covered dorsally with lingual scales arranged in diagonal rows; the posterior edges of these scales are smooth. The foretongue is nonretractable. The skull possesses paired nasals and frontals, and a single, large premaxillary and parietal. It lacks postorbitals, squamosals, and usually a parietal foramen. Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

Biology *Bipes* are small to moderate-sized wormlizards, ranging from 120 to 240 mm adult SVL. They are blunt-headed and burrow by head-ramming in sandy desert soils. They prey mainly on arthropods, captured presumably in or immediately adjacent to the burrow tunnels. All three species are oviparous and lay small clutches of one to four eggs.

References Estes et al., 1988; Gans, 1978; Hallermann, 1998; Papenfuss, 1982; Schwenk, 1988.

Rhineuridae

Florida wormlizard

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Amphisbaenidae.

Content Monotypic, *Rhineura floridana*.

Distribution Central Florida (Fig. 20.14).

Characteristics Rhineurids are limbless, wormlike lizards. The annulate appearance results from rings of rectangular, juxtaposed scales encircling the body and tail. No osteoderms occur dorsally or ventrally on the trunk. The external limbless appearance is accompanied by the total absence of fore- and hindlimb skeletons; however, pelvic vestiges and occasionally sternal or pectoral vestiges persist. The tail is short and lacks autotomy. The tongue bears filamentous papillae and is covered dorsally with lingual scales arranged in diagonal rows; the posterior edges of these scales are smooth. The foretongue is nonretractable. The skull possesses paired nasals and frontals, and a single, large premaxillary and parietal. It lacks postorbitals, squamosals, and a parietal foramen. Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

Biology *Rhineura floridana* is a moderate-sized, burrowing lizard that ranges from 240 to 380 mm adult SVL. Although confined to sandy soils, it occurs in mesic hammock forest to xeric scrub forest. It preys largely on invertebrates, which it captures within the burrow system or on the surface near burrow openings. It is oviparous and usually lays a clutch of two eggs.

References Estes et al., 1988; Gans, 1978; Hallermann, 1998; Schwenk, 1988.

Trogonophidae

Spade-headed wormlizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly clade containing Amphisbaenidae, Bipedidae, and Rhineuridae.

Content Four genera, *Agamodon*, *Diplometopon*, *Pachycalamus,* and *Trogonophis*, with six species.

Distribution North Africa, Horn of Africa, and eastern Arabian Peninsula (Fig. 20.14).

Characteristics Trogonophids are limbless, wormlike lizards. The annulate appearance results from rings of rectangular, juxtaposed scales encircling the body and tail. No osteoderms occur dorsally or ventrally on the trunk. The external limbless appearance is accompanied by the total absence of limb and girdle skeletons. The tail is short and lacks caudal autotomy. The tongue bears filamentous papillae and is covered dorsally with lingual scales arranged in diagonal rows; the posterior edges of these scales are smooth. The foretongue is nonretractable. The skull possesses paired nasals and frontals, a large premaxillary, and a large parietal; it lacks postorbitals, squamosals, and a parietal foramen. Attachment of the marginal dentition is acrodont, and the pterygoid lacks teeth.

Biology The trogonophids are the most divergent amphisbaenians. Accentuating the peculiarity of a wormlike habitus, they have shorter, heavier bodies and strongly flattened snouts with slightly upturned edges. They are inhabitants of dry sandy soils. Unlike the other amphisbaenians, they dig with an oscillating head movement followed by an upward or side-to-side sweep. They create their burrows by an alternating rotational movement of the head that simultaneously shaves off the sides of the tunnel and compacts the walls. Feeding apparently occurs mainly in the burrow or immediately adjacent to it. All trogonophids are small to moderate in size, ranging from 80 to 240 mm SVL. They are oviparous, except the live-bearing *Trogonophis wiegmanni*, which produces about five neonates in a litter.

References Estes et al., 1988; Gans, 1974, 1978; Hallermann, 1998; Schwenk, 1988.

Nyctisaura

Xantusiidae

Night lizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, two main hypotheses suggest Annulata or Lacertiformes.

Content Three genera, *Cricosaura*, *Lepidophyma*, and *Xantusia*, with ±20 species.

Distribution Western United States and eastern Mexico through Central America to northern South America. *Cricosaura typica* occurs at Cabo Cruz, Cuba (Fig. 20.15).

Characteristics Xantusiids are small lizards, less than 100 mm adult SVL. Dorsally, they bear small, granular scales, and ventrally large, juxtaposed scales (Fig. 20.16). No osteoderms occur dorsally or ventrally on the trunk. All species are limbed, and the pectoral girdle has a cruciform interclavicle and angular clavicles. The tail is usually long and autotomic. A fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue is covered dorsally with peglike

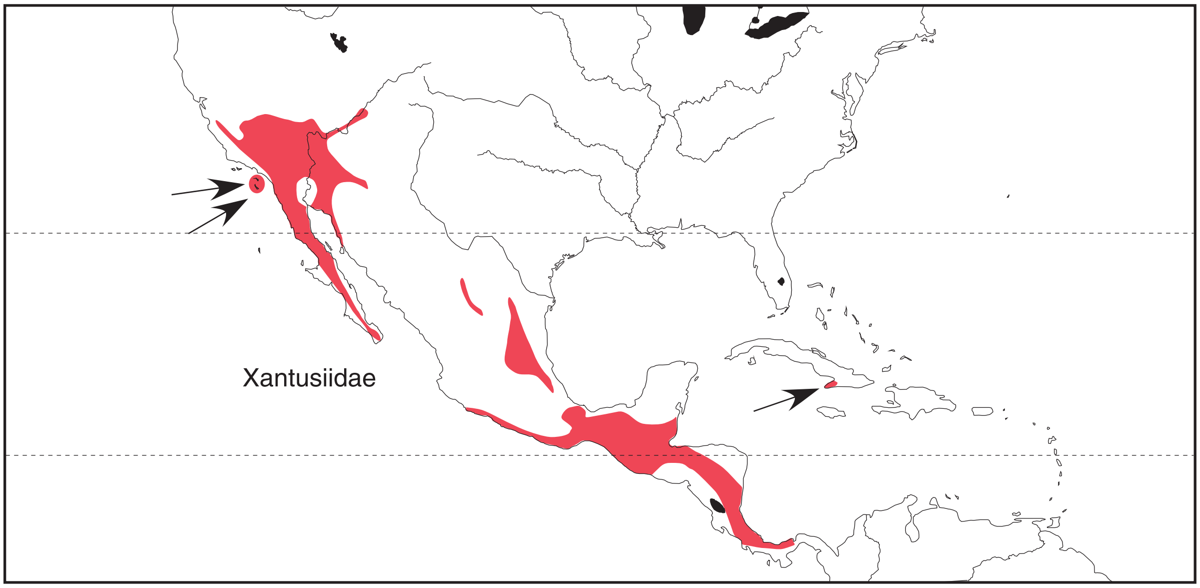


FIGURE 20.15 Geographic distribution of the extant Xantusiidae.

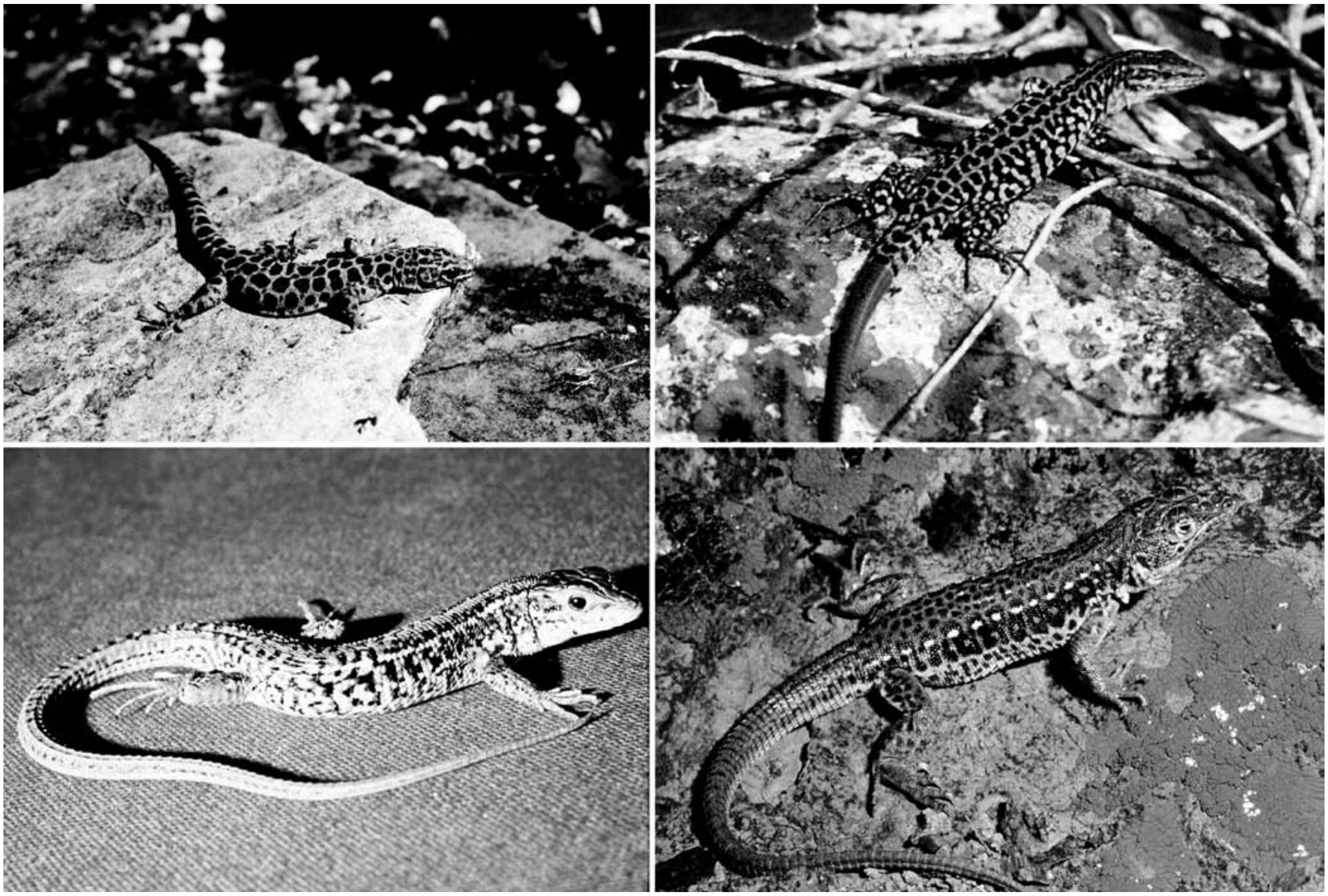


FIGURE 20.16 Representative xantusiid and lacertid lizards. Clockwise from upper left: granite night lizard *Xantusia henshawi*, Xantusiidae (photograph by L. J. Vitt); Italian wall lizard *Podarcis sicula*, Lacertidae (D. Bauwens); lined racerunner *Eremias lineolata*, Lacertidae (L. L. Grismer); and snake-eyed lizard *Ophisops elegans*, Lacertidae (R. G. Tuck, Jr.).

papillae and lacks lingual scales; the foretongue is nonretractable. The skull possesses paired nasals, squamosals, and either single or paired frontal and parietal bones. Postorbitals are absent, but if present, a parietal foramen perforates the parietal bone. Attachment of the marginal dentition is pleurodont, and the pterygoid lacks teeth.

Biology Night lizards are extremely secretive lizards. Although their elliptical pupils suggest that they are nocturnal, they are diurnal to crepuscular but seldom venture into the open; instead they forage slowly in and under ground litter, in rock crevices, or beneath a canopy of low, dense vegetation. Whether desert or forest inhabitants, all are probably sedentary and may have home ranges of only a few square meters. All appear to be insectivores and to consume a large variety of arthropods. *Cricosaura typica* has reduced limbs, and its movements are predominantly serpentine. Although the limbs of the other taxa are also short, they use walking and running gaits. All xantusiids are live-bearers, producing one to eight young each year or biennially. The tropical forest-dwelling *Lepidophyma* consists of unisexual (parthenogenetic) and bisexual species; otherwise, little is known of their biology, although one cave-dwelling species, *Lepidophyma smithii*, feeds mainly on figs that fall into their retreats.

References Bezy, 1988, 1989; Crother and Presch, 1994; Estes et al., 1988; Fellers and Drost, 1991a,b; Hallermann, 1998; Hedges et al., 1991; Schwartz and Henderson, 1991; Schwenk, 1988.

Lacertiformes

Lacertidae

Wall lizards, rock lizards, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Teioidea.

Content Twenty-seven genera, *Acanthodactylus*, *Adolfus*, *Algyroides*, *Australolacerta*, *Eremias*, *Gallotia*, *Gastropholis*, *Heliobolus*, *Holaspis*, *Ichnotropis*, *Lacerta*, *Latastia*, *Meroles*, *Mesalina*, *Nucras*, *Omanosaura*, *Ommateremias*, *Ophisops*, *Pedioplanis*, *Philochortus*, *Podarcis*, *Poromera*, *Psammodromus*, *Pseuderemias*, *Rhabderemias*, *Takydromus,* and *Tropidosaura*, with 220+ species; see Comments below.

Distribution Most of Africa, Europe, and Asia, southward into the northern East Indies (Fig. 20.17).

Characteristics Lacertids are small to large lizards, ranging from 40 to 260 mm adult SVL. Body scalation is variable. Dorsal and lateral body scales range from large, overlapping smooth or keeled scales to small, granular scales; rectangular ventral scales are juxtaposed or overlapping (Fig. 20.16). No osteoderms occur dorsally or ventrally on the trunk. All species are limbed; the pectoral girdle has a cruciform interclavicle and angular clavicles. The tail is autotomic, usually long, and is more than two times longer than SVL in *Takydromus.* Each caudal vertebra has a fracture plane anterior to the transverse processes. The tongue bears filamentous papillae and lingual scales, arranged in alternating rows dorsally. The posterior edges of the lingual scales are smooth, and the foretongue is nonretractable. The skull possesses paired nasals, postorbitals, squamosals, and most often a parietal and a frontal; a parietal foramen is absent. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

Biology The lacertids and teiids are sometimes referred to as Old and New World ecological equivalents. This generality roughly fits the behavioral, ecological, and reproductive similarities between *Lacerta* and *Cnemidophorus*, which are terrestrial, occur in arid landscapes, and have some parthenogenetic populations. The elongate, whiptail habitus is common to most other lacertids as well. Most lacertids are terrestrial, although a few are arboreal, such as *Holaspis guentheri*, which is known for its parachuting behavior even though it appears similar morphologically to other taxa. Lacertids range in size from less than 40 mm adult SVL (*Algyroides fitzingeri*) to nearly 260 mm SVL (*Gallotia stehlini*); adults of most species are less than 120 mm SVL. Lacertids are largely insectivores and forage on the ground or low in shrubs and on bases of trees. *Meroles anchietae* regularly eats seeds, an uncommon food for

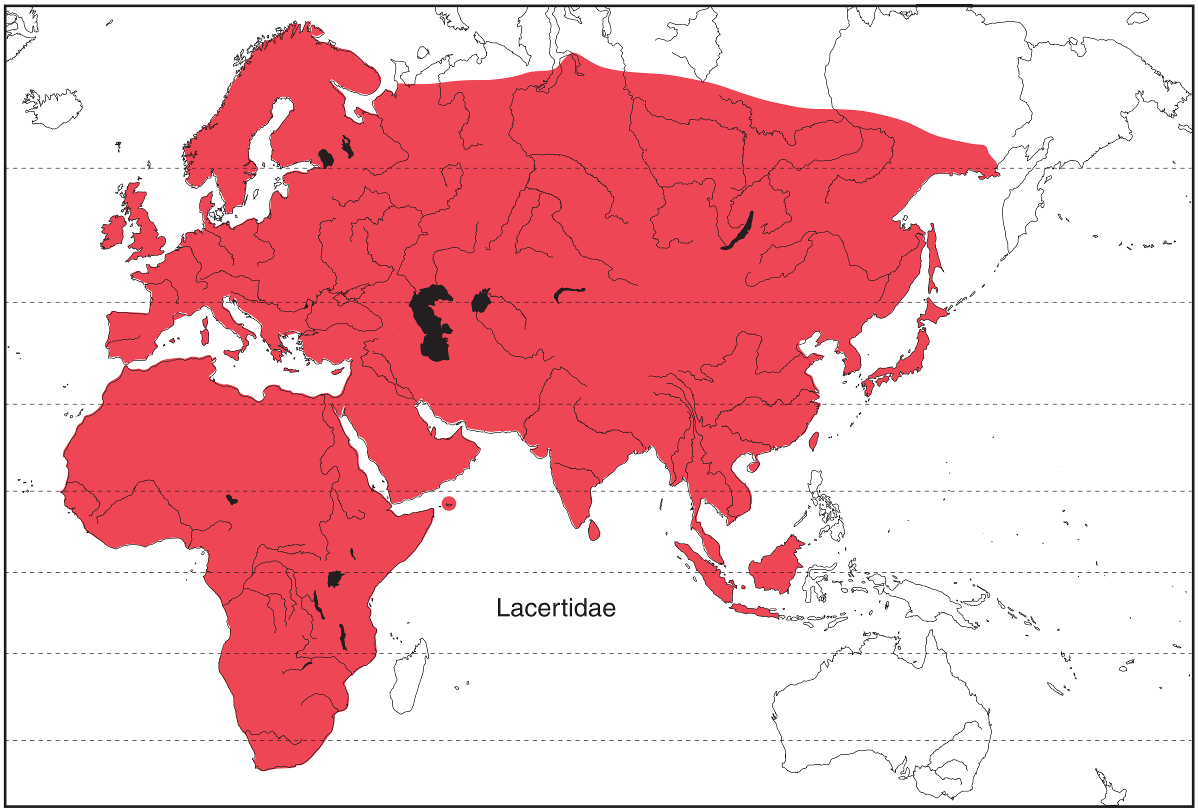


FIGURE 20.17 Geographic distribution of the extant Lacertidae.

lizards. Some *Lacerta* and *Australolacerta* are strongly saxicolous and are efficient, speedy climbers of rock surfaces; some *Takydromus* spend more time off the ground than on, usually in thick grass or shrubs; and *Gastropholis* and *Holaspis* are strongly arboreal, often high in trees and seldom on the ground. Most lacertids are oviparous and produce modest clutches, usually less than 10 eggs; however, clutch size is related to body size and large species, such as *L. lepida* (180–200 mm SVL), lay 20 or more eggs. Populations of the viviparous *L. vivipara* occur in areas of northern Europe, which has 6 months of freezing temperatures. Females carry from 4 to 11 embryos for 3 or 4 months; birth occurs from late July to early October. Spanish *L. vivipara* reportedly are oviparous.

Comments No subfamilies are recognized among the lacertids, although the "tropical" Afroasian taxa form a clade (Arnold, 1989, 1998). The relationships of the Palearctic genera are less easily resolved, and "*Lacerta*" is clearly a paraphyletic group. One study suggested that several subgenera (*Omanosaura*, *Teira*, *Timon*, and *Zootoa*) should be elevated to generic status; this recommendation has not received wide support (Mayer and Bishoff, 1996).

References Arnold, 1989, 1993, 1998; Braña and Bea, 1987; Darevskii, 1978; Engelmann et al., 1986; Estes et al., 1988; Hallermann, 1998; Mayer and Benyr, 1994; Mayer and Bishoff, 1996; Schwenk, 1988.

Teioidea

Gymnophthalmidae

Microteiids

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Teiidae.

Content Thirty-six genera, *Alopoglossus*, *Amapasaurus*, *Anadia*, *Anotosaura*, *Arthrosaura*, *Bachia*, *Calyptommatus*, *Cercosaura*, *Colobodactylus*, *Colobosaurus*, *Colobosauroides*, *Echinosaura*, *Ecpleopus*, *Euspondylus*, *Gymnophthalmus*, *Heterodactylus*, *Iphisa*, *Leposoma*, *Macropholidus*, *Micrablepharus*, *Neusticurus*, *Nothobachia*, *Opipeuter*, *Pantodactylus*, *Pholidobolus*, *Placosoma*, *Prionodactylus*, *Procellosaurinus*, *Proctoporus*, *Psilophthalmus*, *Ptychoglossus*, *Riolama*, *Stenolepis*, *Teuchocercus*, *Tretioscincus,* and *Vanzosaura*, with 160+ species.

Distribution Southern Central America to southern South America east of the Andes (Fig. 20.18).

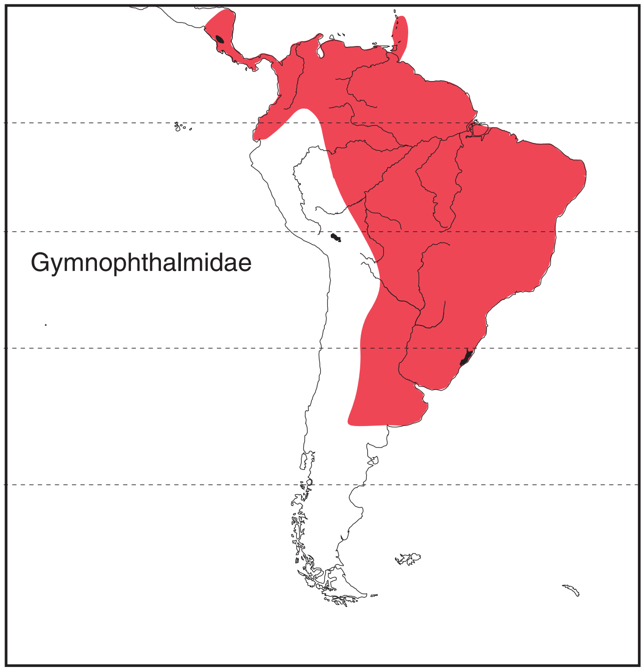


FIGURE 20.18 Geographic distribution of the extant Gymnophthalmidae.

Characteristics Gymnophthalmids are mostly small lizards, less than 60 mm adult SVL. Their scalation is variable; dorsal and lateral scales are small (*Prionodactylus*) to large (*Iphisa*), and smooth (*Bachia*) to strongly keeled (*Arthrosaura*). Occasionally small and large scales are interspersed and usually overlapping; ventral scales are usually larger than dorsal scales and smooth or keeled. No osteoderms occur dorsally or ventrally on the trunk. Most species have limbs, and the limbs are usually small but well developed (reduced in *Bachia*, absent in *Calyptommatus*). The pectoral girdle has a cruciform interclavicle and angular clavicles. The tail varies from moderately short to long and is autotomic. A fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and lingual scales arranged in diagonal rows on the dorsal surface. The posterior edges of the lingual scales are smooth, and the foretongue is nonretractable. The skull possesses paired nasals, postorbitals, squamosals, and single (fused) frontal and parietal bones; the parietal foramen is absent. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

Biology Microteiids, as their vernacular name implies, are generally small lizards (Fig. 20.19). Most are terrestrial species, and forage and rest within the forest-floor detritus. *Alopoglossus angulatus* and *Neusticurus* reside in swampy areas and readily escape into water. Presumably, all are insectivores; none appears to be dietary specialists, although some species occur

FIGURE 20.19 Representative teioid lizards. On left, top to bottom: ocellated lizard *Cercosaura ocellata*, Gymnophthalmidae (photograph by L. J. Vitt); Schreiber's many-fingered microteiid *Pantodactylus schreibersii*, Gymnophthalmidae (J. P. Caldwell); and Amazon keeled junglerunner *Kentropyx altamazonica*, Teiinae (L. J. Vitt). Right: striped tegu *Tupinambis longilineus*, Tupinambinae (J. P. Caldwell and L. J. Vitt).

regularly in association with termite nests. Reproductive biology is known only for a few species; these taxa are oviparous. Average clutch size is likely two eggs for most species. Occasionally, nests are found with more than two eggs, suggesting communal nesting (e.g., *Proctoporus raneyi*). Populations of most species have both females and males, although *Gymnophthalmus* and *Leposoma* have all-female (parthenogenetic) populations.

References Avila-Pires, 1995; Cole et al., 1990; Estes et al., 1988; Hallermann, 1998; Kizirian, 1996; Schwenk, 1988; Vitt and Avila-Pires, 1998; Vitt et al., 1998b.

Teiidae

Whiptail lizards, tegus, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Gymnophthalmidae.

Content Two extant clades, Teiinae and Tupinambinae, and two extinct clades, Chamopsiinae and ‘‘Polyglyphanodontinae.’’

Distribution Americas, from northern United States to Chile and Argentina (Fig. 20.20).

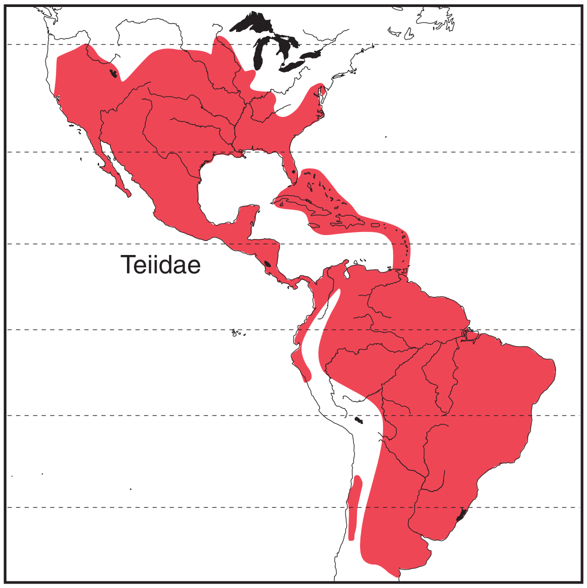


FIGURE 20.20 Geographic distribution of the extant Teiidae.

Characteristics Teiids are small (55 mm adult SVL, *Cnemidophorus inornatus*) to large (400 mm adult SVL, *Tupinambis merianae*) lizards. The dorsal and lateral body scales are usually small and granular, whereas the rectangular ventral scales are larger, juxtaposed, and arranged in transverse rows. No osteoderms occur dorsally or ventrally on the trunk. All species are limbed; the pectoral girdle has a T-shaped interclavicle and angular clavicles. The tail is autotomic and usually long, and a fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and dorsal lingual scales, arranged in diagonal rows. The posterior edges of the lingual scales are smooth, and the foretongue is nonretractable. The skull possesses paired nasals, postorbitals, squamosals, and single frontal (occasionally paired) and parietal bones; a parietal foramen is often present and perforates the parietal. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

References Denton and O'Neill, 1995; Estes et al., 1988; Hallermann, 1998; Presch, 1974, 1988; Schwenk, 1988.

Teiinae

Sister taxon Tupinambinae.

Content Five genera, *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius*, with 110+ species.

Distribution Southern North America to northern Argentina.

Characteristics The skull has the anteromedial edge of the supratemporal fenestra formed by the postfrontal and/or postorbital bones, a medially expanded quadrate with sliding articulation with the pterygoid, and a nasal process on the maxillary. The retroarticular process of the mandible bears a dorsal pit or sulcus.

Biology *Ameiva* (ca. 45–200 mm adult SVL) and *Cnemidophorus* (55–150 mm) are the best known teiines because of their widespread occurrence and often moderately high population densities. Both taxa are active at high body temperatures. Nearctic species of *Cnemidophorus* remain inactive and in their burrows until environmental temperatures reach about 24°C; once active, they maintain body temperatures at 36°C or higher. Their thermal physiology generally limits the amount of time spent active each day and determines their total yearly activity period. They and most other teiine genera forage mainly on the ground for arthropods. Two species, *Cnemidophorus arubensis* and *Dicrodon guttulatum*, are herbivorous. *Cnemidophorus* is predominantly a temperate-zone, aridland taxon, although the *lemniscatus* species group occurs from Central America to northern Argentina; *Ameiva* and others are predominantly tropical, wet to dry forest taxa. The large-bodied *Ameiva ameiva* and the smaller-bodied *Cnemidophorus lemniscatus* are abundant in Amazonian areas where disturbance of the forest provides open habitats that facilitate colonization. All teiines are oviparous, and clutch size is associated with lizard body size. *Cnemidophorus* has clutches ranging from two to six eggs, but one species, *Cnemidophorus arubensis*, produces a single egg; *Ameiva* tends to be slightly larger and its average clutch size is slightly larger (four to seven eggs). *Dicrodon*, *Kentropyx* (Fig. 20.19), and *Teius* share body and clutch size with *Cnemidophorus*. *Cnemidophorus* contains unisexual and bisexual species, and nearly one-third of the ±45 species is parthenogenetic. Parthenogenesis has been confirmed in only two species of the other genera, *Kentropyx borckiana* and *Teius suquiensis*.

References Avila et al., 1992; Avila-Pires, 1995; Cole et al., 1995; Sartorius et al., 1999; Schwartz and Henderson, 1993; Vitt and Breitenbach, 1993; Vitt and Zani, 1996c; Vitt et al., 1995a; Wright, 1993; Wright and Vitt, 1993.

Tupinambinae

Sister taxon Teiinae.

Content Four genera, *Callopistes*, *Crocodilurus*, *Dracaena*, and *Tupinambis*, with eight species.

Distribution South America, east of the Andes to central Argentina and Chile, and northward in inter-Andean valleys.

Characteristics The skull has the anteromedial edge of the supratemporal fenestra formed by the parietal, an unexpanded quadrate without a pterygoid articulation, and a maxillary without a nasal process. The retroarticular process of the mandible is smooth dorsally.

Biology Tupinambines are a much less speciose group than the teiines, but overall they are more diverse in habits and habitat preference. They range in size from the smaller *Callopistes maculatus* (120–170 mm adult SVL) to the larger tupinambines, *Crocodilurus* (to 220 mm SVL), *Dracaena* (to 360 mm), and *Tupinambis* (250–420 mm). These larger taxa occupy the forest and grasslands in eastern South America. *C. maculatus* lives in the arid habitats of coastal and piedmont Chile; it preys largely on other lizards. *Crocodilurus lacertinus* is semiaquatic; it always lives by streams, lagoons, or lakes that are bordered by forest. *C. lacertinus* basks on trees above the water and forages on river banks and in the water. It appears to be largely carnivorous, eating a variety of arthropods and small vertebrates. When approached from land, it escapes into the water by swimming in a serpentine fashion. *Dracaena guianensis* is also a semiaquatic resident of forest streams and lakes. It is caimanlike in appearance and spends more time in the water than *C. lacertinus.* Its head is broad and heavily muscled, and its molariform teeth crush snails, its major food. The five tegu species (*Tupinambis*; Fig. 20.19) occur in a wide range of habitats from forest to grasslands. As adults, tegus are usually assumed to prey mainly on small vertebrates; however, dietary studies indicate that they are opportunistic omnivores that include vegetable matter in their diets as a common if not voluminous item. Reproductive data are generally unavailable; as for teiines, clutch size undoubtedly is associated with body size, although *D. guianensis* apparently has small clutches of 2 to 4 eggs. Tegus have large clutches, from 4 to 32 eggs for *Tupinambis tequixin*, and presumably the incubation period is moderately long, from 3 to 4 months. Parthenogenesis has not been reported in tupinambines.

References Avila-Pires, 1995; Cei, 1993; Colli et al., 1998; Donoso-Barros, 1966; Sullivan and Estes, 1997.

Diploglossa

Cordylidae

Crag, girdled, and plated lizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Scincidae.

Content Two subfamilies, Cordylinae and Gerrhosaurinae; see Comments below.

Distribution Sub-Saharan Africa and Madagascar (Fig. 20.21).

Characteristics Cordylids are small to moderately large lizards that range in adult SVL from 60 to 300 mm and are typically heavily armored. The scales may abut or overlap and frequently are strongly keeled. Rectangular osteoderms underlie the scales dorsally and ventrally on the trunk; they are thicker and stronger dorsally. Typically, the dorsal and ventral scale armor is separated by a longitudinal ventrolateral groove or fold. All species are limbed; the pectoral girdle has a T-shaped or cruciform interclavicle and either curved, rodlike or angular clavicles. The tail is moderately short to long and autotomic; a fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and dorsal lingual scales arranged in alternating rows. The posterior edges of the lingual scales are serrate, and the foretongue is nonretractable. The skull possesses paired nasals, postorbitals, and squamosals, and a single parietal and frontal (occasionally paired); there is no evidence of a parietal foramen. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

Comments Lang (1991) showed that the cordylids consist of two clades; however, subsequent studies of lizard phylogeny continue to treat them as a single clade, and we follow that usage here.

References Estes et al., 1988; Lang, 1991; Hallermann, 1998; Schwenk, 1988.

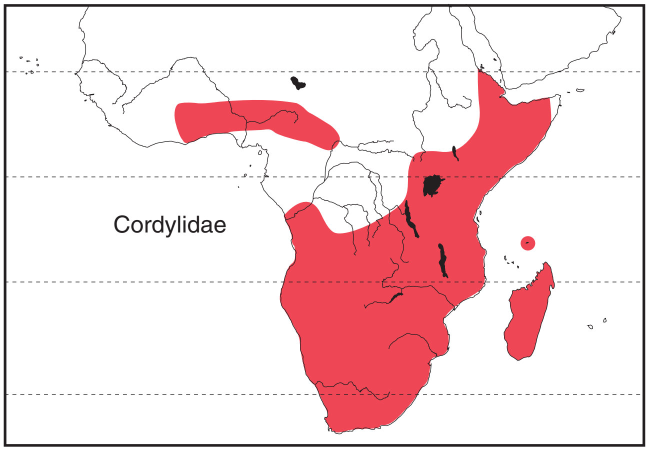


FIGURE 20.21 Geographic distribution of the extant Cordylidae.

Cordylinae

Sister taxon Gerrhosaurinae.

Content Four genera, *Chamaesaura*, *Cordylus*, *Platysaurus,* and "*Pseudocordylus*," with ±40 species.

Distribution Sub-Saharan Africa.

Characteristics The head has four parietal scales, and each nostril is enclosed in nasal or nasal and postnasal scales; cycloid scales are present on the throat. The skull has a slitlike supratemporal fossa on each side, the anteroventral border of the orbit is formed by the maxillary and jugal, and lacrimals are not visible externally. The zygosphene and zygantra of opposing vertebrae form a strong articulation.

Biology Cordylines, the girdled lizards, live in semiarid and arid habitats, and not unexpectedly, all are diurnal and heliophilic. *Cordylus* (Fig. 20.22), *Pseudocordylus*, and *Platysaurus* are mainly rock dwellers that forage in the surrounding grassland or scrub. They are agile climbers of rock surfaces and typically use rock crevices for rest and safety. They wedge themselves in rock cracks, and their rough scaly bodies armor them from predator attacks in these crevices as well as when they are exposed. *Chamaesaura* is a clade of elongate, reduced-limb lizards. They live in grasslands and use undulatory locomotion, an especially effective locomotor pattern in thick grass. Although somewhat snakelike because of small limbs, elongate body, and tail, which may be two times body length, *Chamaesaura* retains the cordyline armored appearance. All cordylines are predominantly insectivores, although small vertebrates and plant material can be regular dietary items. Cordylines are viviparous, except for the oviparous *Platysaurus* species. The larger taxa typically give birth to litters of one to four neonates, and somewhat surprisingly, the smaller-bodied *Chamaesaura* commonly has four to nine young in a litter. *Platysaurus* produces only two-egg clutches.

FIGURE 20.22 Representative cordylids and skinks. Clockwise from upper left: black spiny-tail lizard *Cordylus niger*, Cordylinae (photograph by D. Bauwens); black-lined plated lizard *Gerrhosaurus nigrolineatus*, Gerrhosaurinae (L. J. Vitt); Schmidt's helmet skink *Tribolonotus schmidti,* Lygosominae (G. R. Zug); and broadhead skinks *Eumeces laticeps*, Scincinae (L. J. Vitt).

References Branch, 1988; Lang, 1991; Mouton, 1997.

Gerrhosaurinae

Sister taxon Cordylinae.

Content Six genera, *Angolosaurus*, *Cordylosaurus*, *Gerrhosaurus*, *Tetradactylus*, *Tracheloptychus,* and *Zonosaurus*, with 30+ species.

Distribution Sub-Saharan Africa and Madagascar.

Characteristics The head has two parietal scales, and each nostril is enclosed in three or four scales, including an infralabial scale; cycloid scales are lacking. The skull has lost the supratemporal fossae; the anteroventral border of the orbit is formed by the jugal, and the lacrimals are visible externally. The zygosphene and zygantra of opposing vertebrae do not articulate.

Biology Gerrhosaurines, the plated lizards, are more diverse ecologically than the cordylines. Although predominantly residents of semiarid and arid habitats, some Madagascan taxa are forest residents, and *Zonosaurus maximus* is possibly semiaquatic. All are diurnal and most are heliothermic. *Gerrhosaurus* (Fig. 20.22) and *Cordylosaurus* are stout, scale-armored, mainly rock-dwelling lizards. *Tetradactylus* has a variety of body forms from a strong-limbed habitus to an elongate, reduced-limb body form, and in some species, the forelimbs are lost and the hindlimbs are tiny. The elongate taxa live in grasslands and use lateral undulation locomotion. *Angolosaurus skoogi* is a sand diver or swimmer, living largely in sand-dune habitats. It is also an omnivore and regularly eats foliage. The Madagascan *Tracheloptychus* and *Zonosaurus* are less heavily armored and appear skinklike; they live in habitats from sand dunes to dry forest. Plated lizards are generally omnivores; insects and other arthropods are the major prey, but plant matter is commonly eaten. The larger species often prey on small vertebrates. Gerrhosaurines are oviparous. Clutch size is small but not fixed, ranging from two to six eggs per clutch. Clutch size is not associated with body size; the largest gerrhosaurine, *Gerrhosaurus validus*, averages four eggs (range, two to five) per clutch.

References Branch, 1988; Glaw and Vences, 1994; Lang, 1991; van Dyke, 1997.

Scincidae

Skinks

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, likely Cordylidae.

Content Four clades, Acontinae, Feyliniinae, Lygosominae, and Scincinae.

Distribution Worldwide (Fig. 20.23).

Characteristics Skinks are small to large lizards (27–350 mm adult SVL). They are almost always

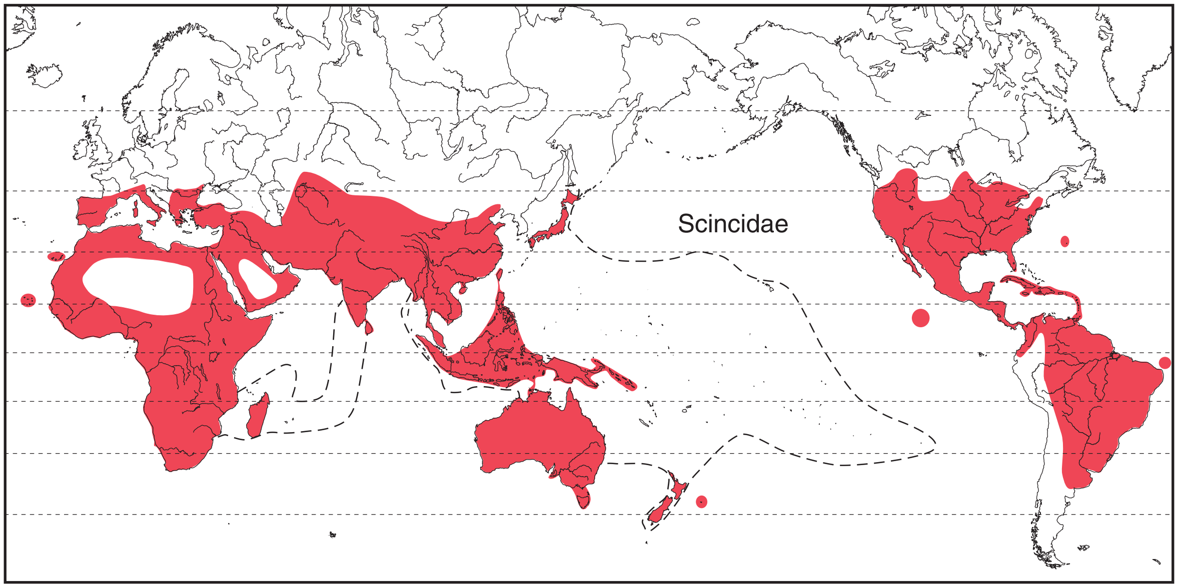


FIGURE 20.23 Geographic distribution of the extant Scincidae.

covered dorsally and ventrally by overlapping scales. Osteoderms underlie the scales dorsally and ventrally on the trunk. Body form ranges from strong limbed to no external limbs; in strongly reduced limb taxa, the interclavicle is absent or cruciform; the clavicles are angular. Tails are long to moderately long. Caudal autotomy is common but not universal in skinks; autotomic caudal vertebrae have a fracture plane anterior to the transverse processes. The tongue bears filamentous papillae and dorsal lingual scales arranged in alternating rows. The posterior edges of the lingual scales are serrate, and the foretongue is nonretractable. The skull possesses paired nasals and squamosals, either single or paired postorbitals and frontals, and a single fused parietal. A parietal foramen is present or absent, and when present, perforates the parietal. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

References Estes et al., 1988; Greer, 1970b, 1974, 1989; Hallermann, 1998; Schwenk, 1988.

Acontinae

Sister taxon "Scincinae."

Content Three genera, *Acontias*, *Acontophiops*, and *Typhlosaurus*, with 17 species.

Distribution Southern Africa.

Characteristics The skull has paired frontal bones, left and right palatines not touching medially on the palate, a complete supratemporal arch, and a small post-temporal fenestra. Limbs are absent.

Biology Acontines are limbless, fossorial skinks. Unlike the feylines, these skinks retain large head scales and the general limbless anguimorph habitus. All are large skinks, ranging from about 110 mm in the smaller species to about 550 mm TL in *Acontias plumbeus*. They are predominantly aridland species, burrowing in sandy soils or living within bunchgrass. All are viviparous and produce litters of 1 to 4 neonates in the smaller species and 10 to 14 young in the larger species.

References Branch, 1988; Broadley, 1997a.

Feyliniinae

Sister taxon "Scincinae."

Content One genus, *Feylinia*, with six species.

Distribution Tropical West and Central Africa.

Characteristics The skull has paired frontal bones, left and right palatines nearly touching medially on the palate, an incomplete supratemporal arch, and no post-temporal fenestra. Limbs are absent.

Biology Feyliniines are moderate to large, limbless skinks, ranging from 60 to 300 mm adult SVL. In general appearance, they are typhlopid like although the mouth is larger, and the head is somewhat more elongate. They appear to be largely fossorial in forest or forest-edge habitats. The diet remains unconfirmed, and all species are presumably viviparous.

References Brygoo and Roux-Estève, 1983.

Lygosominae

Sister taxon "Scincinae."

Content Over 82 genera, *Ablepharus*, *Afroblepharus*, *Anomalopus*, *Apterygodon*, *Ateuchosaurus*, *Bartleia*, *Bassiana*, *Caledoniscincus*, *Calyptotis*, *Carinascincus*, *Carlia*, *Clairescincus*, *Coeranoscincus*, *Coggeria*, *Cophoscincopus*, *Corucia*, *Cryptoblepharus*, *Ctenotus*, *Cyclodina*, *Dasia*, *Egernia*, *Emoia*, *Eremiascincus*, *Eroticoscincus*, *Eugonglyus*, *Eulamprus*, *Eulepis*, *Eumecia*, *Fojia*, *Geomyersia*, *Geoscincus*, *Glaphyromorphus*, *Gnypetoscincus*, *Graciliscincus*, *Haackgreerius*, *Harrisoniascincus*, *Hemiergis*, *Isopachys*, *Lacertaspis*, *Lacertoides*, *Lamprolepis*, *Lampropholis*, *Lankascincus*, *Larutia*, *Leiolopisma*, *Leptoseps*, *Leptosiaphos*, *Lerista*, *Lioscincus*, *Lipinia*, *Lobulia*, *Lygisaurus*, *Lygosoma*, *Mabuya*, *Marmorosphax*, *Menetia*, *Morethia*, *Nannoscincus*, *Niveoscincus*, *Notoscincus*, *Ophioscincus*, *Panaspis*, *Papuascincus*, *Paralipinia*, *Parvoscincus*, *Phoboscincus*, *Prasinohaema*, *Proablepharus*, *Pseudemoia*, *Saiphos*, *Saproscincus*, *Scincella*, *Sigaloseps*, *Simiscincus*, *Sphenomorphus*, *Tachygyia*, *Techmarscincus*, *Tiliqua*, *Tribolonotus*, *Tropidophorus*, *Tropidoscincus*, *Typhlosaurus*, and *Vietnascincus*, with 760+ species.

Distribution Worldwide, although limited occurrence in North and Central America.

Characteristics The skull has a single frontal, left and right palatines that usually touch medially on the palate, a complete supratemporal arch, and usually a post-temporal fenestra. Limbs are usually present, although they are regularly reduced in some species groups.

Biology Lygosomines occupy most lizard niches from highly arboreal to strongly fossorial, from tropical desert and forest to cool–temperate grassland and forest, from littoral and streamside to desert, from insectivorous or carnivorous to herbivorous, and from small (27–33 mm adult SVL, *Menetia greyi*) to large (350 mm SVL, *Corucia zebrata*). Behavior is equally diverse, from diurnal to nocturnal (uncommon), from solitary to communal, from sedentary to migratory, and from territorial to nonterritorial. Reproductive mode varies from oviparity to viviparity. The degree of development within eggs prior to hatching in oviparous species and the degree of placentation in viviparous species vary greatly. Eggs are laid as single clutches and guarded or abandoned, or, infrequently, eggs are deposited communally. Clutch size is typically low (<6 eggs) and is limited to one or two eggs in some species groups (e.g., *Tribolonotus*, Fig. 20.22, and *Emoia*, respectively). Viviparous taxa range from those that retain large-yolked eggs in the oviducts (e.g., *Saiphos equalis*) to those with an elaborately and fully developed placenta (e.g., *Mabuya*, *Pseudemoia*).

References Blackburn, 1993b; Broadley, 1997a; Greer, 1989; M. Hutchinson, 1992, 1993; Stewart and Thompson, 1996.

"Scincinae"

Sister taxon Paraphyletic, thus presumably to all other scincid subfamilies.

Content Thirty genera, *Amphiglossus*, *Androngo*, *Barkudia*, *Brachymeles*, *Chalcides*, *Chalcidoseps*, *Cryptoscincus*, *Davewakeum*, *Eumeces*, *Gongylomorphus*, *Janetaescincus*, *Macroscincus*, *Melanoseps*, *Neoseps*, *Nessia*, *Ophiomorus*, *Pamelaescincus*, *Paracontias*, *Proscelotes*, *Pseudacontias*, *Pygomeles*, *Scelotes*, *Scincopus*, *Scincus*, *Scolecoseps*, *Sepsina*, *Sepsophis*, *Sphenops*, *Typhlacontias,* and *Voeltzkovia*, with 210+ species.

Distribution North America and Africa eastward through Southwest Asia; absent throughout much of South Asia with some species in east Asia and the Philippines.

Characteristics The skull has paired frontal bones, left and right palatines usually separated medially on the palate, a complete supratemporal arch, and a posttemporal fenestra. Limbs are usually present, although they are regularly reduced in some species groups.

Biology Scincines share some of the diversity seen in the lygosomines, but this group has only one-third as many species. They range in size from 32 mm adult SVL in some of the smaller species to 220 mm SVL in large species such as *Amphiglossus.* Most have a cylindrical body and tail, a more or less conical head, well-developed moderately short limbs, and shiny, smooth scales (Fig. 20.22). Limb reduction and body elongation occur in some genera, including *Scelotes* and *Neoseps*, and external limbs are absent in a few species (e.g., *Typhlacontias*). No scincines are strongly arboreal, although some taxa are good climbers and forage and sleep in trees, and a few deposit eggs in tree hollows or epiphytes. Most species are terrestrial or semifossorial. All are predominantly carnivorous; insects and other small arthropods are the major prey. Larger species eat small vertebrates, and some species occasionally eat plant matter. Scincines are both oviparous and viviparous (e.g., *Chalcides*). Clutch and litter size is generally modest, and 1 to 2 eggs or neonates are produced in the smaller species, whereas 12 to 18 are produced in the larger species.

Comment Greer (1970b), when partitioning the Scincidae, noted that the scincines represented a grade and were associated largely on shared ancestral characters.

References Blackburn, 1993b; Branch, 1988; Glaw and Vences, 1994; Greer, 1970b.

Anguimorpha

Anguidae

Alligator lizards, galliwasps, glass lizards, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly clade containing Xenosauridae and Varanoidea.

Content Four subfamilies, Anguinae, Anniellinae, Diploglossinae, and Gerrhonotinae.

Distribution Disjunct, Americas, Europe, Southwest Asia, and southern Asia (Fig. 20.24).

Characteristics Anguids are small (55–70 mm adult SVL, *Elgaria parva*) to very large (500–520 mm SVL and 1.4 m maximum TL, *Ophisaurus apodus*) limbed to limbless lizards. All are heavily armored with largely nonoverlapping scales. Osteoderms underlie these scales dorsally and ventrally on the trunk, and a longitudinal ventrolateral groove or fold separates this dorsal and ventral scale armor in some taxa. The fold allows body expansion for breathing, feeding, and reproduction, yet maintains the shield effect of the scale armor. Body form ranges from strong limbed to no external limbs; in strongly reduced limb taxa, the interclavicle is absent or cruciform; the clavicles are angular. Tails are short to very long. Caudal autotomy is common but not universal among anguids; autotomic caudal vertebrae have a fracture plane anterior to the transverse processes. The tongue bears filamentous papillae and lacks lingual scales. The foretongue retracts into the hindtongue. The skull possesses paired nasals and postorbitals, present or absent paired squamosals, single or paired frontals, and a single (fused) parietal. A parietal foramen is present and perforates the parietal. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

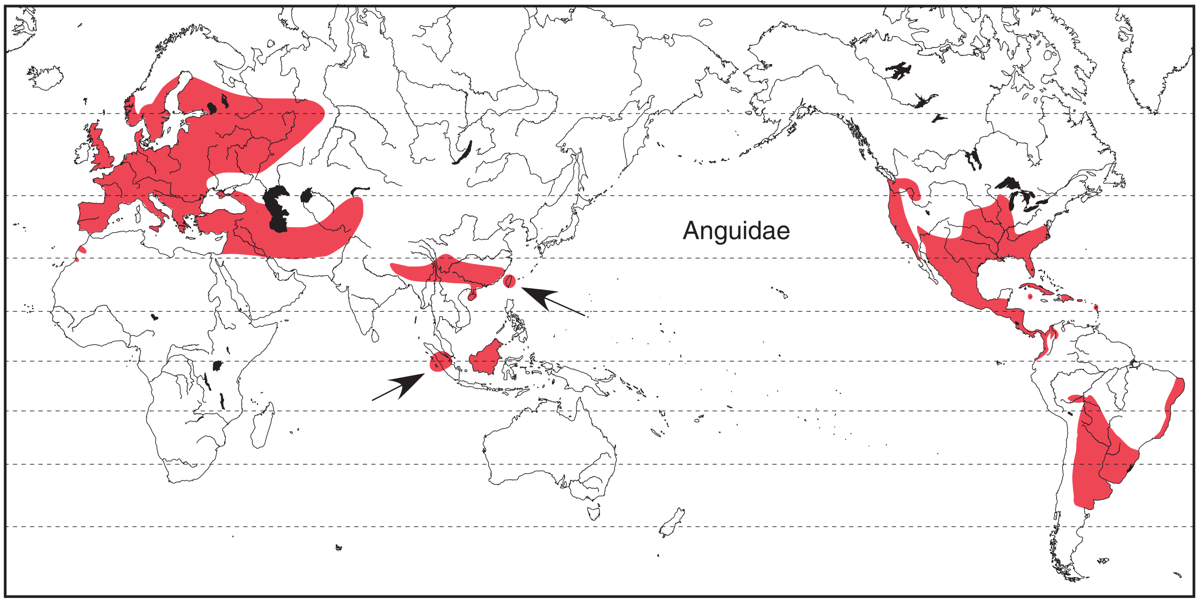


FIGURE 20.24 Geographic distribution of the extant Anguidae.

References Estes et al., 1988; Gauthier, 1982; Hallermann, 1998; Schwenk, 1988.

Anguinae

Sister taxon Uncertain, possibly clade containing Diploglossinae and Gerrhonotinae.

Content Two genera, *Anguis* and *Ophisaurus*, with 1 and 16 species, respectively.

Distribution North America and Eurasia.

Characteristics Anguines are robust, elongate, limbless lizards. The tail is long, typically twice the length of the body. A ventrolateral fold is well developed in *Ophisaurus* (Fig. 20.25) but indistinct in *Anguis*. The skull possesses paired frontals, pterygoid teeth, more than 15 teeth on the dentaries, and unicuspid posterior teeth. The frontoparietal scales are very small and widely separated.

Biology *Anguis fragilis,* the slowworm, is a moderately abundant resident of scrub and open habitats with dense ground coverage. Slowworms are largely diurnal, occasionally basking. They are most often observed in a slow search for their primary prey, snails and slugs. They also eat arthropods and small vertebrates. They are generally active from early spring to late fall; mating occurs in late spring and fetuses are carried for 8 to 12 weeks. Litters of 4 to 28, but usually less than 12, young are born in late August and early September. If mating occurs late or if a cool summer occurs, females retain the embryos over the winter. *Ophisaurus* is more speciose with a broader size range (150–400 mm adult SVL) and lives in more different habitats; however, general behavior and habitat preference are similar to those of *A. fragilis*, that is, a slow, methodical prey-search behavior and a preference for open habitats with heavy ground cover. *Ophisaurus* preys more heavily on arthropods, although it eats a broad array of small semifossorial and terrestrial animals. In contrast to *Anguis*, all *Ophisaurus* are oviparous and deposit clutches of 4 to 20 eggs; females appear to remain with the eggs during the 8- to 10-week incubation period.

References Frazer, 1989; Gauthier, 1982; Mitchell, 1994.

Anniellinae

Sister taxon Uncertain, possibly Anguinae.

Content One genus, *Anniella*, with two species.

Distribution California and Baja California.

Characteristics Anniellines are small, elongate, limbless lizards. The tail is short, less than two-thirds body length. A ventrolateral fold is absent. The skull possesses paired frontals, pterygoid teeth, fewer than 15 teeth on the dentaries, and unicuspid posterior teeth. The frontoparietal scales are small and separated.

Biology The slender snakelike *Anniella* are 150 to 180 mm adult SVL. They inhabit coastal sand dunes and valleys from sea level to 1600 m in elevation, and are largely confined to friable soils that retain some

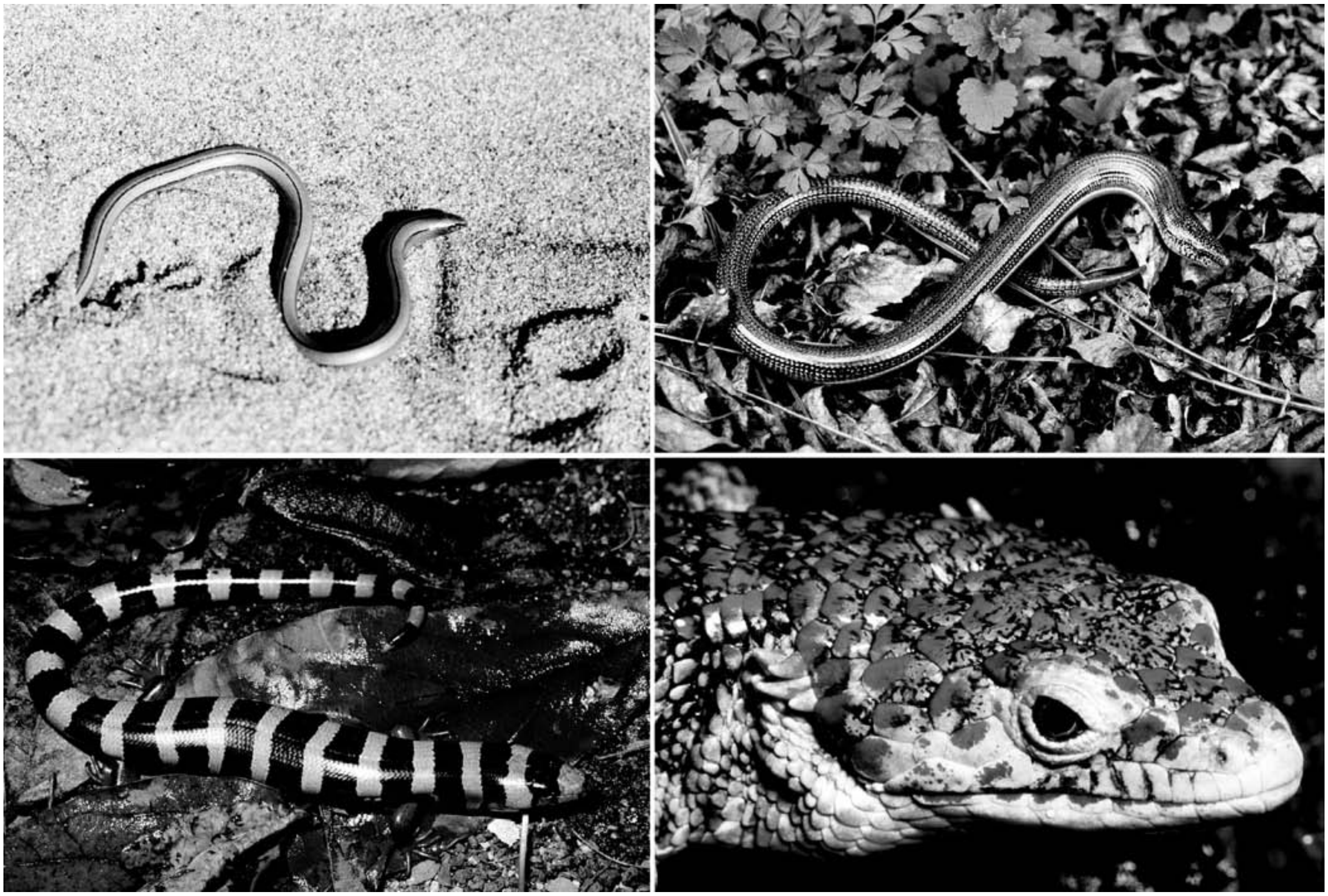


FIGURE 20.25 Representative anguid lizards. Clockwise from upper left: California legless lizard *Anniella pulchra*, Anniellinae (photograph by L. J. Vitt); eastern glass lizard *Ophisaurus ventralis*, Anguinae (J. M. Howland); Bocourt's arboreal alligator lizard *Abronia aurita*, Gerrhonotinae (J. A. Campbell); and banded galliwasp *Diploglossus fasciatus*, Diploglossinae (O. A. V. Marques).

moisture. They obtain their highest abundance in sandy soils with moderate plant cover. Typically, they are nocturnal, resting below the soil's surface during the day and foraging on the surface at night, commonly in the detritus beneath bushes. They are susceptible to desiccation and are able to "drink" interstitial water from the soil when soil moisture content exceeds 7%. They eat a broad variety of small arthropods. Mating occurs in early fall, and the female usually carries one or two fetuses for a 3- to 4-month gestation.

References Bell et al., 1995; Fusari, 1985; Gauthier, 1982; Goldberg and Miller, 1985; Stebbins, 1954.

Diploglossinae

Sister taxon Gerrhonotinae.

Content Five genera, *Celestus*, *Diploglossus*, *Ophiodes*, *Sauresia*, and *Wetmorena*, with 40+ species.

Distribution West Indies, Central America, and central South America.

Characteristics Diploglossines are elongate lizards that generally have small, but well-developed limbs. The limbs may be greatly reduced in some taxa (e.g., *Ophiodes*). The tail is usually less than the body length. A ventrolateral fold is generally lacking. The skull possesses paired frontals, no pterygoid teeth, more than 15 teeth on the dentaries, and bicuspid posterior teeth. The frontoparietal scales are small and separated.

Biology Galliwasps contain some of the smallest anguid taxa (60 mm adult SVL, *Celestus macrotus*) and some large taxa (280 mm SVL, *Diploglossus anelpistus*). Diploglossines are terrestrial to fossorial lizards; most live in forested habitats, although some live in more arid grassland or scrub habitats. Diploglossines include both diurnal and nocturnal members; all prey mainly on arthropods. Both oviparity (some *Diploglossus*) and viviparity (*Celestus* and some species of *Diploglossus*) occur; clutch and litter number are correlated with body size. Small species such as *Diploglossus delasagra* lay 2 eggs; others such as *Celestus curtissi* give birth to 2 to 5 neonates. Larger taxa such as *Diploglossus warreni* bear 8 to 27 neonates.

References Cei, 1993; Gauthier, 1982; Savage and Lips, 1993; Schwartz and Henderson, 1991.

Gerrhonotinae

Sister taxon Diploglossinae.

Content Five genera, *Abronia*, *Barisia*, *Elgaria*, *Gerrhonotus,* and *Mesaspis*, with 42+ species.

Distribution Northwestern United States southward to western Panama.

Characteristics Gerrhonotines are stout-bodied lizards with short, well-developed limbs; the tail is usually less than the body length. A well-developed ventrolateral fold occurs on the trunk. The skull possesses a frontal, pterygoid teeth, more than 15 teeth on the dentaries, and bicuspid posterior teeth. The frontoparietal scales are nearly or barely touching on the dorsal midline.

Biology The alligator lizards derive their name from the heavy armoring on the head, body, and tail, and the strong broad jaws. None is aquatic, although most prefer moist habitats from tropical upland forests to the coastal and montane forests of western North America; a few species live in oak savannas and deserts. The tropical *Abronia* (Fig. 20.25) is the most speciose of the gerrhonotines; it is strongly arboreal, even possessing a prehensile tail. The gerrhonotines are mostly moderate-sized lizards, less than 110 mm adult SVL, although the Texan *Gerrhonotus liocephalus* attains 200 mm SVL. They are carnivorous, feeding mainly on arthropods but also on small vertebrates. Reproductively, gerrhonotines are both oviparous and viviparous. Oviparous taxa usually lay 2 to 40 eggs, and viviparous species bear 2 to 15 young. Incubation normally requires at least 8 to 10 weeks, and gestation 8 to 12 weeks.

References Campbell and Frost, 1993; Fitch, 1970; Gauthier, 1982; Good, 1994; Stebbins, 1954.

Xenosauridae

Knob-scaled lizards

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, with two main hypotheses-Anguidae or the varanoid–thecoglossan clade.

Content Two genera, *Shinisaurus* and *Xenosaurus*, with one and four species, respectively.

Distribution Disjunct, southern China and eastern Mexico into Guatemala (Fig. 20.26).

Characteristics Xenosaurids are moderate-sized lizards (100–150 mm adult SVL). They are covered dorsally and ventrally by granular, juxtaposed scales and large keeled tubercles. Ventrally the trunk contains small, nonarticulate osteoderms, but none is present dorsally. The limbs are well developed; the pectoral girdle has a T-shaped or cruciform interclavicle and angular clavicles. The tail is moderately long, about 1.2 times body length. Caudal autotomy is present or absent; when present, a fracture plane occurs anterior to the transverse processes of each caudal vertebra. The tongue bears filamentous papillae and lacks lingual scales. The foretongue retracts into the hindtongue. The skull possesses paired nasals,

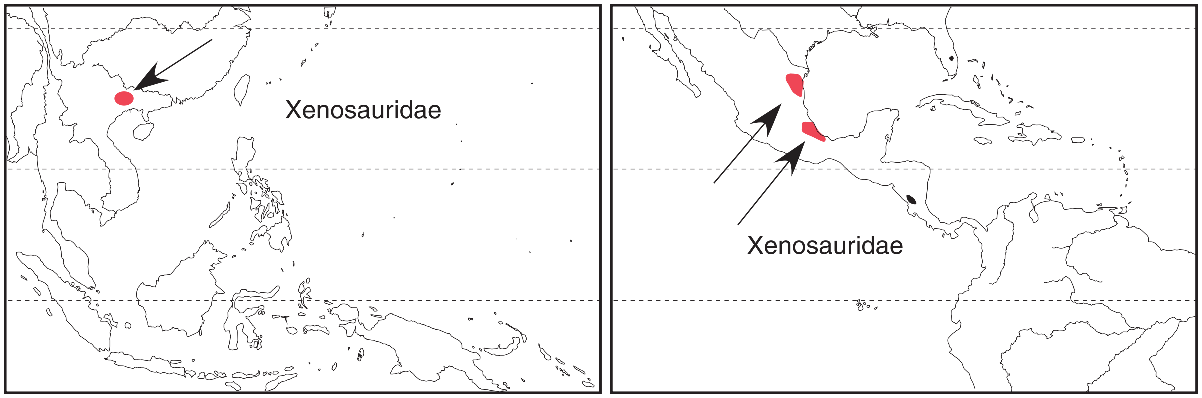


FIGURE 20.26 Geographic distribution of the extant Xenosauridae.

postorbitals and squamosals, single or paired frontals, and a parietal. A parietal foramen is present and perforates the frontoparietal suture. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

Biology Both the Asian and the American taxa appear stenohydric, generally requiring moist surroundings and losing water rapidly in dry conditions. The Asian *Shinisaurus crocodilurus* occurs in moist montane forests along streams. It is semiaquatic and during the day forages in mountain streams for fish, tadpoles, and other animal prey. At night, the lizards rest on branches overhanging water. Knob-scaled lizards were previously reported to be nocturnal, but field observations in China and Mexico show them to be diurnal. The American *Xenosaurus* (Fig. 20.27) contains terrestrial residents that occur in moist cloud to dry scrub forest, most commonly associated with rock outcrops. *Xenosaurus* preys mainly on arthropods. Xenosaurids are live-bearers. *S. crocodilurus* may produce litters of 15 neonates, usually many fewer, and has a gestation period of 8 to 14 months. *Xenosaurus* bears litters of 2 to 8 young, most often 2, and gestation requires 11 to 12 months. Postnatal parental care possibly occurs in *Xenosaurus newmanorum*.

References Ballinger et al., 1995; Estes et al., 1988; Hallermann, 1998; Lemos-Espinal et al., 1997a,b; Mägdefrau, 1997; Schwenk, 1988.

Varanoidea

Helodermatidae

Gila monster and Mexican beaded lizard

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

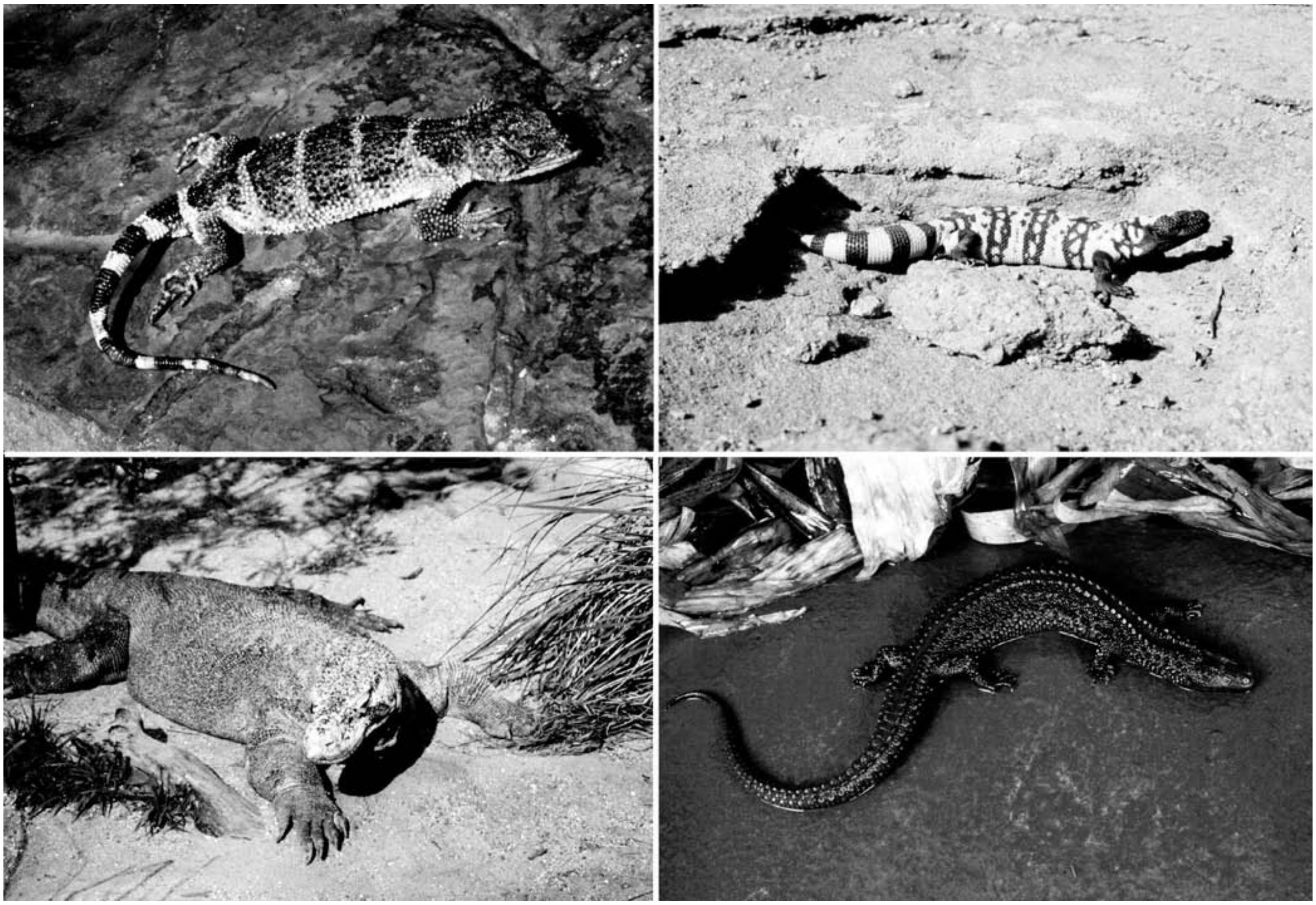


FIGURE 20.27 Representative xenosaurid and varanoid lizards. Clockwise from upper left: flathead knob-scaled lizard *Xenosaurus platyceps*, Xenosauridae (photograph by L. J. Vitt); Gila monster *Heloderma suspectum*, Helodermatidae (L. J. Vitt); earless monitor *Lanthanotus borneensis*, Lanthanotinae (L. W. Porras); and Komodo dragon *Varanus komodoensis,* Varaninae (G. R. Zug).

Sister taxon Thecoglossa or Varanidae.

Content One genus, *Heloderma*, with two species.

Distribution Southwestern North America, from the Sonoran Desert southward along the Mexican Pacific coast to Guatemala (Fig. 20.28).

Characteristics Helodermatids are large lizards (300–500 mm adult SVL). They are the only lizards with venom glands. They have broad, somewhat flattened heads, robust bodies, short well-developed limbs, and heavy tails. They have a thick skin with rows of rounded scales circling the body; scales are somewhat tuberculated dorsally and laterally and are slightly larger and squarish ventrally. Ventrally the trunk contains small, nonarticulate osteoderms, but none are present dorsally. The pectoral girdle has a T-shaped interclavicle and angular clavicles. The tail is moderately short, about two-thirds body length. Caudal autotomy does not occur. The tongue bears filamentous papillae and lacks lingual scales. The foretongue retracts into the hindtongue. The skull possesses paired nasals, frontals, and squamosals, no postorbitals, and a parietal. A parietal foramen is absent. Attachment of the marginal dentition is pleurodont, and pterygoid teeth occur.

Biology *Heloderma* is a slow-moving, diurnal lizard. Nestling rodents and lagomorphs are the main prey of *Heloderma suspectum*, and lizard and bird eggs for *Heloderma horridum*. These solitary predators have good vision and hearing. They methodically search for prey above and below ground throughout their home ranges of several hectares, and they are strong diggers and good climbers. Though *H. suspectum* (Fig. 20.27) is active throughout the warm months, individuals forage most intensely in late winter and early spring. When not foraging, they rest in underground burrows and similar retreats. Courtship and mating occur from late April to early June. Two to 12 eggs are laid in mid-July to mid-August. The eggs overwinter, hatching after about 10 months in May.

References Beck and Lowe, 1991; Bogert, 1993; Estes et al., 1988; Hallermann, 1998; Lowe et al., 1986; Norell and Gao, 1997; Pregill et al., 1986; Schwenk, 1988.

Thecoglossa

Varanidae

Monitors, goannas, and earless monitor

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Helodermatidae or clade containing Serpentes and extinct thecoglossans.

Content Two subfamilies, Lanthanotinae and Varaninae.

Distribution Warm temperate and tropical Africa, Asia, and Australia (Fig. 20.28).

Characteristics Varanids are generally large lizards. They have thick skin with numerous rows of small, rounded scales circling the body; the ventral scales are slightly larger. Dorsally the trunk lacks osteoderms; ventrally small, nonarticulate osteoderms are present in some taxa. Monitors have well-developed limbs; the pectoral girdle has a T-shaped or cruciform interclavicle and angular clavicles. The tail is long to very long and lacks caudal autotomy. The tongue bears filamentous papillae and lacks lingual scales. The foretongue retracts into the hindtongue. The skull possesses paired frontals and squamosals, no postorbitals, and a nasal and a parietal. A parietal foramen is usually present and perforates the parietal. Attachment of the marginal dentition is pleurodont, and pterygoid teeth are present or absent.

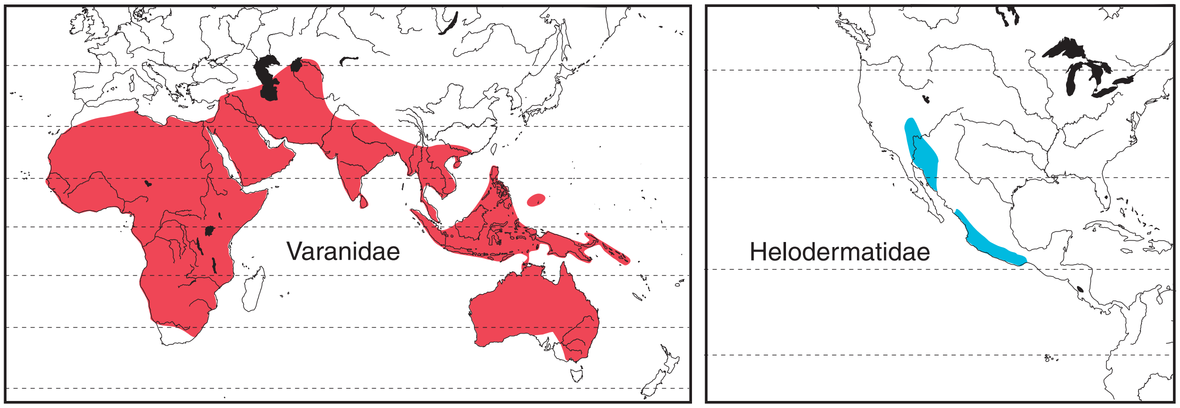


FIGURE 20.28 Geographic distributions of the extant Helodermatidae and Varanidae.

References Baverstock et al., 1993; Estes et al., 1988; Hallermann, 1998; Schwenk, 1988;

Lanthanotinae

Sister taxon Varaninae.

Content Monotypic, *Lanthanotus borneensis.*

Distribution Borneo.

Characteristics *Lanthanotus borneensis*, the earless monitor, has pterygoid teeth and lacks a parietal eye and a hemibaculum (i.e., a cartilaginous strut in each hemipenis).

Biology *L. borneensis* is poorly studied, partially owing to its preferred habitat and habits. Most information derives from captive individuals. Adults (309–440 mm TL) appear to be restricted to forested habitats. Presumably, adults and juveniles are semiaquatic and live in or adjacent to forest streams and swamps. They forage at night on land and in the water; they eat invertebrates and small vertebrates. During the day, they rest in burrows that can be partially flooded. They are oviparous and produce small clutches (two to six eggs).

References Manthey and Grossman, 1997; Proud, 1978.

Varaninae

Sister taxon Lanthanotinae.

Content One genus, *Varanus*, with about 50 species.

Distribution Sub-Saharan Africa eastward through Asia to Australia and islands in the southwestern Pacific (Fig. 20.28).

Characteristics The varanines have no pterygoid teeth, possess a parietal eye, and have a hemibaculum (a cartilaginous strut in each hemipenis).

Biology Monitors are distinct lizards; they have small heads and long necks, long and robust bodies, well-developed limbs, and long, muscular tails. They range in size from the pygmy goanna *Varanus brevicauda* at a maximum 120 mm adult SVL (230 mm TL) to the largest known lizard *Varanus komodoensis* (3.1 m maximum TL) weighing more than 200 kg (Fig. 20.27). All monitors are active predators and have strong jaws and sharp, conically recurved teeth. The smaller species prey mainly on arthropods and small vertebrates. With increasing body size, prey preference shifts to larger vertebrates, emphasizing mammals. They catch live prey but also are scavengers. The Philippine butaan (*Varanus olivaceus*) seasonally eats fruit. Most species are terrestrial to semiarboreal, although a few species (e.g., *Varanus doreanus*) are strongly arboreal. The Australian bulliwallah (*Varanus mertensi*) is seldom more than a meter from water and commonly feeds and escapes into the water. All varanids are oviparous, and none shows evidence of parental care. Clutch size is generally associated with body size. The smaller Australian species have 2 to 4 eggs in a clutch, and the larger species, such as *Varanus bengalensis*, deposit 5 to 42 eggs, although clutches of the largest monitor (*V. komodoensis*) average only 16 eggs (range, 2–30). Eggs are typically buried and have a moderately long incubation—seldom less than 100 days to nearly 1 year.

Comments The taxon *Varanus* contains nine morphologically distinct subgroups that contain one or more species. These subgroups have formal subgeneric names that are occasionally used as generic names.

References Auffenberg, 1981, 1988, 1994; Bennett, 1998; Greer, 1989; King and Green, 1993; Pianka, 1994b, 1995; Ziegler and Böhme, 1997.

Chapter

21

Snakes

OVERVIEW

Snakes are the second most speciose group of living reptiles with over 2900 species (Uetz, 1999). Like lizards, they occur on all continents except Antarctica. They have had a more successful marine radiation than lizards, yet they have been less successful than lizards in dispersing onto the world’s oceanic islands. All possess the elongate, ‘‘limbless’’ habitus, but within this standard serpentine body form, they display a multitude of shapes, sizes, and surface textures. This diversity in morphology reflects diverse behavioral, ecological, and physiological adaptations, but all are carnivores. As a group, snakes eat a wide variety of prey, but the diets of many species are highly specialized.

Snakes (Serpentes; Ophidia, stem-based name) are limbless or nearly so. The pectoral girdle and forelimbs are totally absent; where present, the pelvic girdle and hindlimbs are rudimentary and visible externally as small horny ‘‘spurs,’’ one on each side of the cloaca opening. Elongation of the body is accomplished by an increase in number of vertebrae, which typically range between 120 and 240, although the number can be more than 500. The numerous vertebrae, each with a pair of ribs in the neck and trunk, create a marvelously flexible body, and this flexibility permits extremely efficient undulatory locomotion in water, on and under ground, and in bushes and trees. The body is covered with epidermal scales, the number, size, and arrangement of which are often species specific. In most snakes, the venter (underside) has a series of large, transversely rectangular scales that extend from the throat onto the tail. In many snakes, the number of large ventral scales equals the number of vertebrae.

Without limbs, snakes capture, manipulate, and consume their prey using only the body and mouth. This necessity has led to major modifications of cranial anatomy. Some of these adaptations are unique to snakes, including the exclusion of the supraoccipital from the margin of the foramen magnum by exoccipitals and a flexible ligamentous symphysis between the dentaries. Other unique traits have no apparent connection to feeding, such as the absence of ciliary-body muscles in the eyes and the presence of a tracheal lung. Some characters occur in both snakes and one or more taxa of reduced-limbed or limbless lizards; these features include no squamosal; no epipterygoid; no sclerotic ossicles in the eyes; each eye covered by a transparent scale (spectacle); and the absence of the tympanum and the eustachian tube. The limbless condition results in body modifications as well, including the presence of more than 30 presacral (trunk and neck) vertebrae, and the left lung absent or greatly reduced and the right lung dominant.

The early classification of snakes "was based completely on living forms but approached . . . entirely as specimens in museum jars" (McDowell, 1987, p. 3). External appearance dominated. In 1758, Linnaeus recognized snakes as Serpentes, a class distinct from reptiles, with three genera and nearly 200 species. His successors recognized additional species and began to divide them into groups on similarity of external form. Only in the mid-19th century did C. Duméril (1853) depart from tradition and base his classification additionally on the skull and its dentition. Subsequently, E. D. Cope began the search for snake relationships by examining a greater variety of internal structures, including vertebral, lung, and hemipenial morphology. His posthumously published classification (1900) recognized five suborders: Epanodonta (Typhlopidae), Catodonta (Leptotyphlopidae), Tortricina (Aniliidae, Cylindrophiidae, Uropeltidae), Colubroidea (all other snakes, exclusive of vipers, divided into four divisions), and Solenoglypha (Viperidae). Cope's groups were well defined by a variety of characteristics in addition to the aforementioned ones. While Cope's was an innovative classification, Boulenger's classification (1893) was simpler and won wide acceptance, being used into the middle of the 20th century. The Boulenger classification began at the familial level with no higher level groupings; however, it did divide the Colubridae into series (Aglypha, Opisthoglypha, and Proteroglypha), each with one or more subfamilies.

Hoffstetter's classification (1955, 1962, and earlier) began the effort to reflect evolution by incorporating fossils; however, our modern approach to snake classification owes much to G. Underwood's controversial *A Contribution to the Classification of Snakes* (1967). His broad selection and intimate examination of characters and his willingness to cleave the larger poly- and paraphyletic taxa into monophyletic ones provide the foundation for most modern studies. His classification is the only recent one to broadly survey the morphological spectrum of representatives of all groups of snakes. It uses Hoffstetter's groups and divides snakes into three major groups (Scolecophidia, Henophidia, and Caenophidia) and most suprageneric taxa currently recognized, although not necessarily now at the same taxonomic level. His study just preceded the use of cladistic analysis in herpetology and lacks dendrograms of snake relationships.

One cladogram and its classification indicate that snakes diverged early into the scolecophidians (blindsnakes) and the alethinophidians (Fig. 21.1, Table 3.7). The blindsnakes contain three major clades: Anomalepididae, Leptotyphlopidae, and Typhlopidae. The monophyly of the scolecophidians has strong support (Wallach, 1998) and is based on numerous derived characters that are shared, including the absence of an artery through the trigeminal foramen; a mandible less than one-half the length of the jaw; a vestigial pelvis and hindlimb within the body wall; thymus paired; epidermal lipid glands on the anteriormost head shields; undifferentiated smooth, glossy, cycloid body scales; and the absence of enlarged ventral scales. Within the scolecophidians, anomalepidids and typhlopids are each other's closest relatives and the sister clade to the leptotyphlopids.

The branching pattern and sister-group relationships are less certain in the alethinophidians, although some sister-group and clade relationship hypotheses appear regularly from different data sets and analyses. Three robust clades are represented by boas (Boidae) and pythons (Pythonidae); a colubroid clade of atractaspidids, colubrids, elapids, and viperids; and a colubroid-*Acrochordus* sister group (Caenophidia). The proposed relationships among the other clades and to these robust clades are much more variable. The henophidian (primitive snakes, excluding caenophidians) and booid (boids, pythonids, bolyerids, tropidophiids) groups of Underwood and earlier systematists are paraphyletic. Alethophidians consist of a grade of primitive snakes that apparently arose prior to the boas, pythons, and caenophidians (Fig. 21.1). The glossy snakes of this grade (Aniliidae, Anomochilidae, Cylindrophiidae, Loxocemidae, Uropeltidae, and Xenopeltidae) are tropical species, predominantly Asian, fossorial, and display low diversity. The relationships among these snakes is uncertain. Skeletal data alone indicate an early divergence in the alethophidians with one lineage giving rise to the glossy snakes and the other to the boas, pythons, and caenophidians (Cundall et al., 1993). Morphological data also suggest that Aniliidae is the sister group to the *Cylindrophis*–Uropeltidae clade. The uncertainties of relationships occur in part because most studies do not include all or most representatives of these "primitive" snakes; therefore, it is difficult to compare the results and interpretations arising from different sets of taxa.

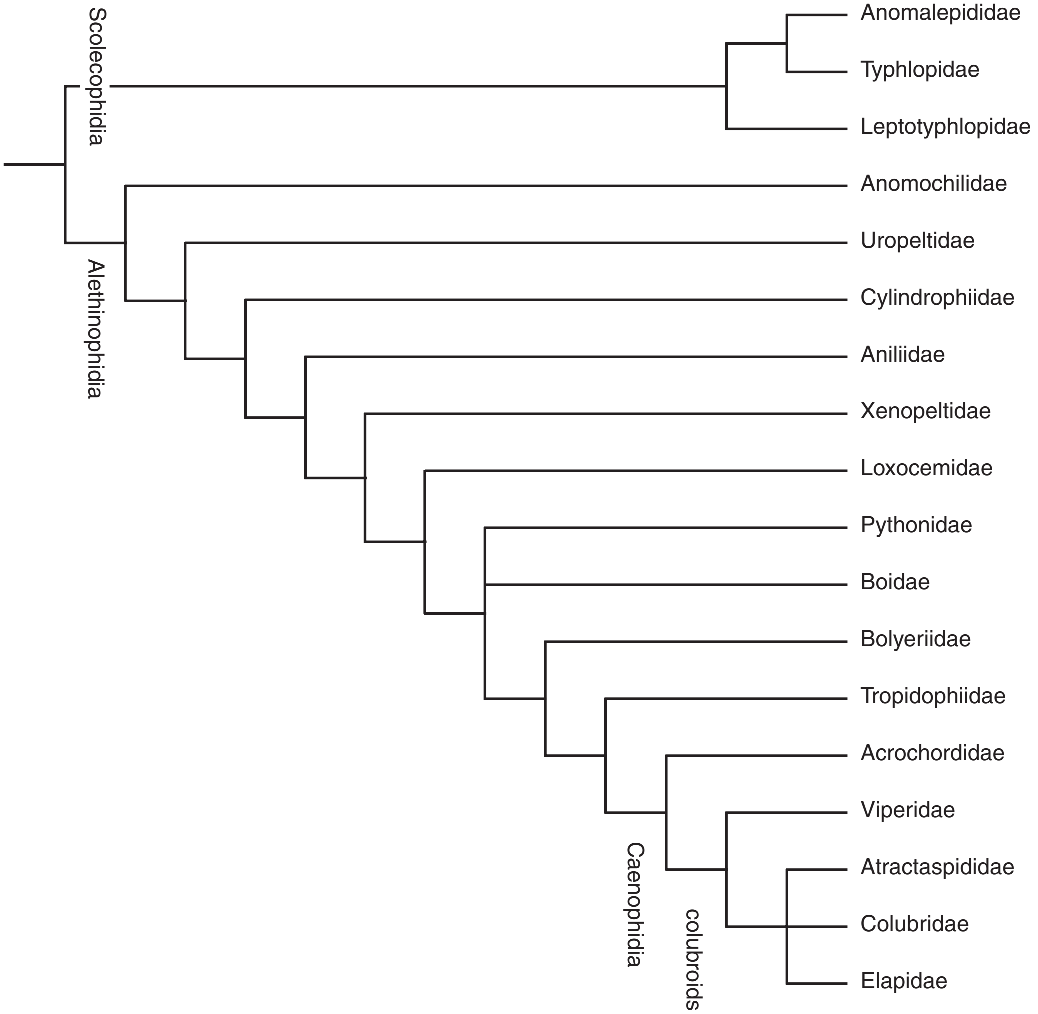


FIGURE 21.1 A cladogram depicting relationships among the families of extant snakes. The cladogram derives from Cundall et al. (1994, Fig. 2) with colubroid relationships from Cadle (1987, Fig. 3.1C). Cladogram redrawn from original for uniformity.

Similar difficulties occur as well in the more "advanced" snakes. Our knowledge of snake relationships is improving; nonetheless, interpretations are varied so all relationships should be considered putative or presumptive. As noted above, the present consensus considers boids and pythonids as sister groups (Kluge, 1991a), and each represents an ancient clade. In turn, these two taxa are often placed as the sister-group clade for the bolyeriids, caenophidians, and tropidophiids; however, the relationships among these three are best considered unresolved (Fig. 21.1). Certainly, no cladistic analysis links the bolyeriids and/or tropidophiids directly to the boas and pythons. Arguments exist that the tropidophiids consist of two groups which might not be closely related to one another (Zaher, 1994a). Whether one clade or two independent clades, the tropidophiids, as represented by *Tropidophis*, is the probable sister group of the caenophidians. Recently, an examination of the enigmatic *Xenophidion*, a presumed colubrid, suggested instead that it is the sister group to the tropidophiids (Wallach and Günther, 1998).

With rare exception, *Acrochordus* is considered to be a caenophidian and usually the sister group to the colubroids Viperidae (Atractaspididae, Colubridae, Elapidae). With similar strong support, vipers are the sister group to the other colubroids (Fig. 21.1). The relationships among the other three clades are much less certain, and this uncertainty yields multiple interpretations. The atractaspidids have been placed as a clade within the Colubridae, as the sister group to "aparallactine" colubrids or included with them, or more recently as a separate clade containing the fanged *Atractaspis* and the nonfanged aparallactines. The atractaspidids appear to be the sister group of elapids (McDowell, 1987; Underwood and Kochva, 1993), although viperids and other African colubrids have been proposed as sister groups. The elapids have long been recognized as a monophyletic group (McCarthy, 1985), although the placement of a few African snakes (e.g., *Homoroselaps*) in elapids remains unclear. McDowell (1969) was the first to recognize and document that seasnakes and terrestrial elapids were not separate clades; instead, seasnakes arose from within the Australian radiation of terrestrial elapids. The present interpretation suggests that the terrestrial elapids of Africa, the Americas, and Asia (i.e., Elapinae) represent a grade, and the seasnakes, seakraits, and terrestrial Papua–Australian elapids (i.e., Hydrophiinae) form a monophyletic group (Keogh, 1998). Further, *Bungarus* is the likely sister group to the hydrophiine clade. *Laticauda* has affinities to a divergent group of Papuan elapids, and affinities of the viviparous seasnakes (i.e., formerly hydrophiines) are within the Australian elapids. Not all these relationships have been confirmed by independent study.

Viperidae also has been proposed as the sister group of the Atractaspididae; however, most evidence points to viperids as the sister group to the other three colubroid clades (e.g., Cadle, 1992; but see Kraus and Brown, 1998). Within this clade, *Azemiops* appears to be the sister group to two other clades, the true vipers (Viperinae) and the pitvipers (Crotalinae). The relationships in and among the colubrids are far less resolved and seemingly change with each new data set and analysis. Because the elapids and atractaspidids, and possibly the viperids, likely arose within the colubrids, the colubrid group is paraphyletic and perhaps even polyphyletic. A few groups appear to be robustly monophyletic, such as Homalopsinae, Pareatinae, and Xenodermatinae. Others, for example, Colubrinae and Xenodontinae, are also likely clades (when membership is restricted), and a few groups, for example, Lamprophiinae (= lycodontines or boodontines) and Natricinae, are clearly paraphyletic. A growing dilemma within colubrid systematics is the constant redefinition of groups so that the species content of one author's group usually is different from the same-named group of another author. Also, owing to the high species diversity of many of the colubrid genera and higher taxa, it is difficult for researchers to include all representatives of ingroups and appropriate outgroups in their studies. These absences can skew the results and lead to different interpretations because different researchers are comparing similar, but not identical, sets of taxa (OTUs).

General References Ananjeva et al., 1988; Bauchot, 1994; Cogger and Zweifel, 1998; Ernst and Zug, 1996; Grandison, 1977; Greene, 1997; Greer, 1997; Shine, 1991b.

Systematic References Cadle, 1987, 1992; Cundall et al., 1993; David and Ineich, 1999; Dowling et al., 1996; Heise et al., 1995; Hoffstetter, 1955, 1962; Keogh, 1998; Kluge, 1991a; Kraus and Brown, 1998; Liem et al., 1971; McCarthy, 1985; McDiarmid et al., 1999; McDowell, 1969, 1974, 1981; Rieppel, 1988; Smith et al., 1977; Underwood, 1967; Underwood and Kochva, 1993; Wallach and Günther, 1998; Zaher, 1994a,b.

TAXONOMIC ACCOUNTS

Scolecophidia

Anomalepididae

Early blindsnakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Typhlopidae.

Content Four genera, *Anomalepis*, *Helminthophis*, *Liotyphlops,* and *Typhlophis* (Fig. 21.2), with 15 species.

Distribution Disjunct in Central and South America (Fig. 21.3).

Characteristics Anomalepidids are slender blindsnakes; most range in adult TL between 150 and 300 mm, and none is larger than 400 mm. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontals. The mandible has a coronoid bone, and each dentary has one to three teeth. They lack cranial infrared receptors in pits or surface indentations. No limb vestiges are evident externally, although pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is absent, a tracheal lung is present, and the left oviduct is usually well developed, although variously reduced in *Anomalepis.*

Biology The anomalepidids are fossorial snakes and live mainly in forests. We know little of their biology owing to their secretive lifestyle. Presumably, they are like other scolecophidians and prey on soft-bodied invertebrates and the larvae and eggs of these animals; termites are likely a major food. One species, *Typhlophis squamosus* (Fig. 21.2), is commonly found in termite nests inside of rotted logs on the forest floor. Based on the limited reproductive data available, all are

FIGURE 21.2 Representative scolecophidian snakes. Clockwise from upper left: Trinidad blindsnake *Typhlophis squamosus*, Anomalepididae (photograph by L. J. Vitt); reticulated blindsnake *Typhlops reticulatus*, Typhlopidae (L. J. Vitt); Jamaican blindsnake *Typhlops jamaicensis*, Typhlopidae (R. G. Tuck, Jr.); and seven-line threadsnake *Leptotyphlops septemstriatus*, Leptotyphlopidae (L. J. Vitt).

oviparous and lay small clutches that consist of 2 to 13 eggs.

References Dixon and Kofron, 1983; Kofron, 1988; Lancini and Kornacker, 1989; McDiarmid et al., 1999; Underwood, 1967; Wallach, 1998.

Leptotyphlopidae

Threadsnakes or wormsnakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Anomalepididae and Typhlopidae clade.

Content Two genera, *Leptotyphlops* and *Rhinoleptus*, with 90+ species.

Distribution Tropics and subtropics of Africa and the Americas, and Southwest Asia (Fig. 21.4).

Characteristics Of the scolecophidians, leptotyphlopids are typically the thinnest-bodied members (Fig. 21.2). They reach a maximum of 400 mm adult SVL, but most are 150 to 250 mm SVL. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries lacking teeth, and optic foramina that perforate the frontals. The mandible has a coronoid bone, and each dentary has four or five teeth. They lack cranial infrared receptors in pits or surface indentations. No limb vestiges are evident externally, although pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. They lack a left lung, a tracheal lung, and a left oviduct.

Biology Threadsnakes are fossorial and occur in a variety of habitats from semidesert to forest. They feed on soft-bodied invertebrates, although termites appear to be the primary food of some species. Unlike many termite predators, they are capable of living in termite

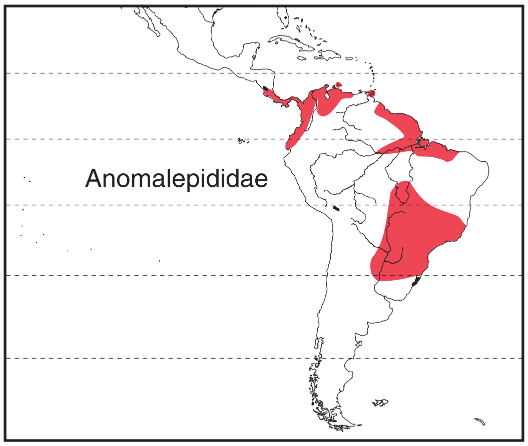


FIGURE 21.3 Geographic distribution of the extant Anomalepididae.

nests and are permanent residents within termite galleries. They have evolved a secretion that averts the attack of the soldier termites and ants, possibly by deceiving the potential attackers into considering them as nestmates. Because they can move freely through termite tunnels, they are occasionally observed high above the ground, for example, in screech owl nests. Some species, such as *Leptotyphlops macrolepis* in the Amazon rain forest, have been observed on rainy nights nearly 2 m above ground, wrapped around small tree trunks with the head and neck extending perpendicular to the trunk and moving back and forth. They may climb trees to locate termite nests by detecting airborne chemical cues associated with the release of termite alates. Leptotyphlopids are oviparous, laying 1 to 12 small, elongate eggs. The Texas threadsnake, *Leptotyphlops dulcis*, exhibits parental care by coiling around its eggs; perhaps this behavior also occurs in other species.

References McDiarmid et al., 1999; Underwood, 1967; Wallach, 1998.

Typhlopidae

Blindsnakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Anomalepididae.

Content Six genera, *Acutotyphlops*, *Cyclotyphlops*, *Ramphotyphlops*, *Rhinotyphlops*, *Typhlops*, and *Xenotyphlops*, with 210+ species.

Distribution Cosmopolitan in tropical regions (Fig. 21.5).

Characteristics Blindsnakes range from small (140–180 mm TL, *Ramphotyphlops braminus*) to large (950 mm maximum TL, *Rhinotyphlops schlegelii*). Cranially,

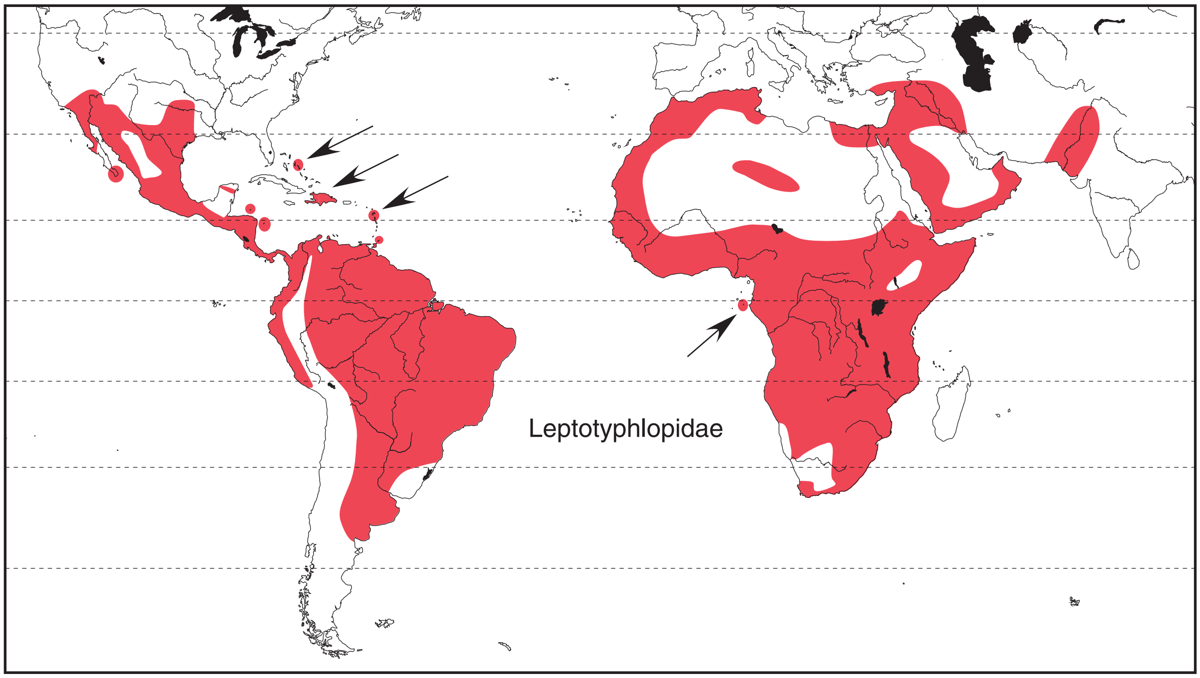


FIGURE 21.4 Geographic distribution of the extant Leptotyphlopidae.

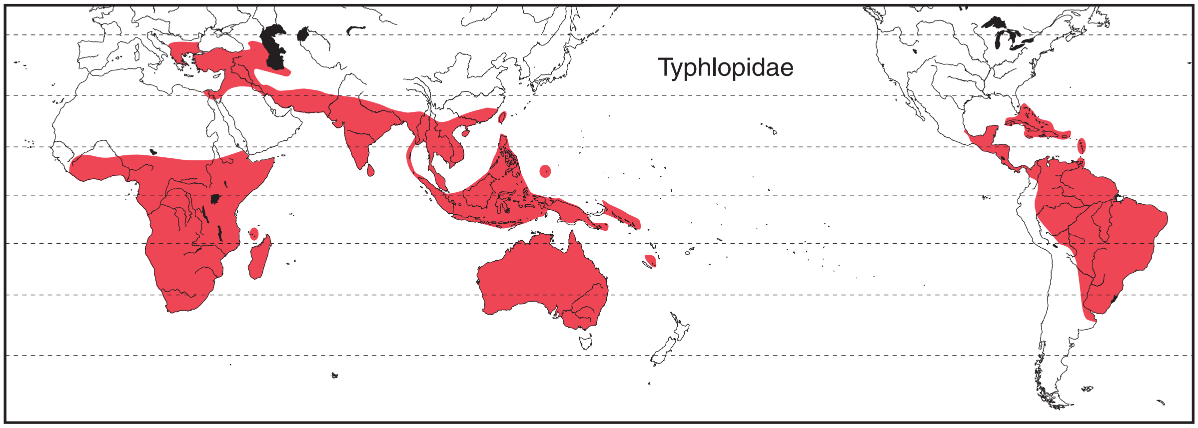


FIGURE 21.5 Geographic distribution of the extant Typhlopidae.

these snakes have two common carotid arteries, edentulous premaxillaries, transversally oriented maxillaries with solid teeth, and optic foramina that perforate the frontals. The mandible has a coronoid bone and lacks teeth on the dentary. They lack cranial infrared receptors in pits or surface indentations. No limb vestiges are evident externally although pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is vestigial or absent, and the tracheal lung is multichambered; the left oviduct is absent.

Biology Typhlopids are the most speciose blindsnakes (Fig. 21.2) and occupy a variety of habitats from near desert to rain forest. All are fossorial, but some have been observed in arboreal situations, presumably having followed a termite trail or a termite gallery tunnel to climb a tree. Termites, ants, and their larvae and eggs appear to be the major food, although blindsnakes consume other soft-bodied arthropods. Reproductive data are unavailable for most species. Of the known species, all are oviparous, with the possible exception of one report in which embryos were observed in *Typhlops diardii*; however, this observation may represent delayed egg deposition, not viviparity. Clutch size varies with body size, ranging from 2 to 7 eggs (*Ra. braminus*) to 40 to 60 eggs (*Rh. schlegelii*). Eggs are deposited shortly after fertilization and incubated typically for 6 to 10 weeks, or they can be held within the oviducts and laid only a week or so before hatching (*Typhlops bibronii*). To date, the brahminy blindsnake (*Ra. braminus*) is the only known unisexual species of snake. Its parthenogenetic reproduction has allowed it to become the most widely dispersed snake species; it now occurs in all continental and many insular tropical areas, apparently arriving as a stowaway in the root mass of exotic "potted" plants. A single female, immature or adult, is all that is required to establish a new population.

References Branch, 1988; Broadley, 1983; Ehmann and Bamford, 1993; Fitch, 1970; Greer, 1997; McDiarmid et al., 1999; Underwood, 1967; Wallach, 1993, 1998; Wynn et al., 1987.

Alethinophidia

Anomochilidae

False blindsnakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing all other alethinophidians.

Content One genus, *Anomochilus*, with two species (Fig. 21.6).

Distribution Malay Peninsula, Sumatra, and Borneo (Fig. 21.7).

Characteristics Anomochilids are small snakes (250–350 mm adult SVL) with short tails. Their blunt heads and smooth, shiny scales give them a blindsnake appearance, and the barely enlarged ventral scales add to this blindsnake disguise. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, diagonally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The mandible has a coronoid bone, and the dentary has teeth. They lack cranial infrared receptors in pits or surface indentations. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is reduced but present, and a tracheal lung is absent; both left and right oviducts are well developed.

FIGURE 21.6 Representative snakes. Clockwise from upper left: false blindsnake *Anomochilus leonardi*, Anomochilidae (photograph by I. Das); red-tailed pipe snake *Cylindrophis ruffus*, Cylindrophiidae (R. W. Murphy); Drummond–Hays shieldtail *Rhinophis drummondhayi*, Uropeltidae (I. Das); and false coralsnake *Anilius scytale*, Aniliidae (L. J. Vitt).

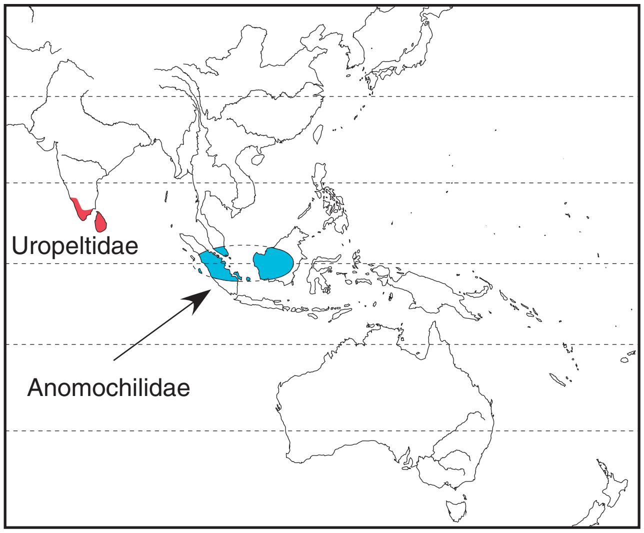


FIGURE 21.7 Geographic distributions of the extant Anomochilidae and Uropeltidae.

Biology *Anomochilus* is known from fewer than 10 specimens, none of which is accompanied by detailed observations, so the biology of these species is largely conjecture. Head and body morphology suggests fossorial habits. The snakes likely use preexisting tunnels or burrow through forest-floor detritus or friable soils. The mouth is small and the unique upper and lower jaw apparatus suggests a diet of small, generally soft-bodied prey. *Anomochilus* appears to be oviparous.

References Cundall and Rossman, 1993; Cundall et al., 1993; McDiarmid et al., 1999; Underwood, 1967; Wallach, 1998.

Uropeltidae

Shieldtail snakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing all alethinophidians except Anomochilidae; alternatively, only Cylindrophiidae (Cadle et al., 1990).

Content Nine genera, *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Pseudoplectrurus*, *Pseudotyphlops*, *Rhinophis*, *Teretrurus,* and *Uropeltis*, with 45+ species.

Distribution Sri Lanka and southern India (Fig. 21.7).

Characteristics Shieldtails have cone-shaped heads, often with a strongly keratinized tip and a uniquely enlarged and roughened scale on the end of a short tail. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontals. The mandible has a coronoid bone, and the dentary bears teeth. Shieldtails lack cranial infrared receptors in pits or surface indentations. Girdle and limb vestiges do not occur externally or internally. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is usually present but small, and a tracheal lung is absent; both left and right oviducts are well developed.

Biology The shieldtails are fossorial snakes. Much of their morphology, from head to tail and the smooth, glossy scale covering, appears associated with burrowing (Fig. 21.6). They are almost exclusively forest inhabitants, occurring in open areas only where the soil is friable, permitting them to burrow deeply and avoid high soil-surface temperatures. They seldom appear on the surface unless uncovered by surface predators (e.g., jungle fowl) or forced to the surface by flooded soils. When exposed, uropeltids hide their heads beneath body coils or debris and present the armored tail to the attacking predator; this behavior allows them to begin burrowing. The conical head and heavily muscled anterior one-quarter of the body facilitates digging. Digging begins with the head embedded in the tunnel wall and the muscular body folded into a series of loops within the skin envelope. The head is driven forward by straightening the body loops; the head then anchors the body and the trunk is pulled forward as well as formed into loops within the skin. This concertina-style burrowing is effective in moist and friable soils, and shieldtails quickly disappear within a self-created hole while the tail shield plugs the hole and protects the escaping snake.

Shieldtails range in size from the very small *Platyplectrurus trilineatus* (100 to 130 mm adult SVL) to the moderate-sized *Uropeltis* (e.g., 420 mm maximum TL, *Uropeltis myhendrae*). Diet is unknown, but because the snakes are totally subterranean, their diet likely consists principally of earthworms and other soft-bodied invertebrates, and perhaps small burrowing vertebrates. Uropeltids appear to be exclusively viviparous, but data are limited. Litter size is small, three to nine embryos (usually four), and pregnancy may be confined to a single oviduct-uterus.

References Cadle et al., 1990; Gans, 1976, 1979, 1986; McDiarmid et al., 1999; Rajendran, 1985; Underwood, 1967; Wallach, 1998.

Cylindrophiidae

Pipe snakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing all alethinophidians except Anomochilidae and Uropeltidae; alternatively, only Uropeltidae (Cadle et al., 1990).

Content One genus, *Cylindrophis*, with eight species.

Distribution Disjunct, Sri Lanka and Southeast Asia through the East Indies (Fig. 21.8).

Characteristics Pipe snakes are moderate to large, thick-bodied, short-tailed snakes. They have smooth, shiny scales, and the ventral scales are only slightly larger than the dorsal ones. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The mandible has a coronoid bone, and teeth are present or absent on the dentary. They lack cranial infrared receptors in pits or surface indentations. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The small left lung is present, and a tracheal lung is absent; both left and right oviducts are well developed.

Biology *Cylindrophis* species range in adult size from about 300 to 900 mm TL. All are fossorial snakes. The two best-known species, *Cylindrophis maculatus* (Sri Lanka) and *Cylindrophis ruffus* (Indochina; Fig. 21.6) are moderately abundant and occur widely from suburban gardens to forest, and occasionally even in mats of floating vegetation. They prefer moist, friable soils, and apparently they dig and create their own burrow systems. *Cylindrophis* regularly uses a head-mimicry display with the tail as a defense mechanism and uncommonly a death-feigning behavior. The pipe snakes are principally nocturnal foragers, searching on the surface for a variety of invertebrate and vertebrate prey, from earthworms to eels and other snakes. All are viviparous and produce litters of 2 to 12 neonates.

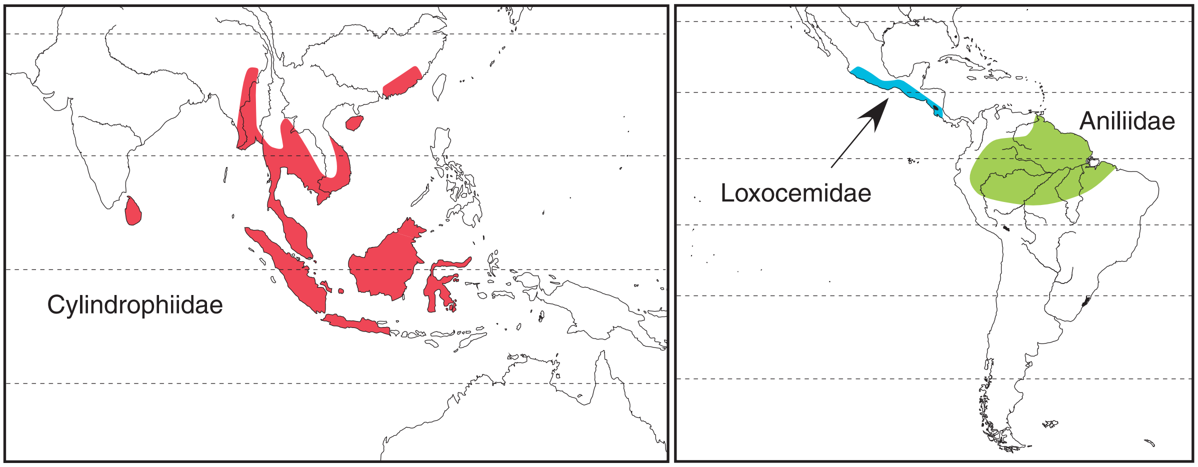


FIGURE 21.8 Geographic distributions of the extant Cylindrophiidae, Aniliidae, and Loxocemidae.

References Adler et al., 1992; Cadle et al., 1990; Cox et al., 1998; Cundall, 1995; McDiarmid et al., 1999; Nanayakkara, 1988; Smith, 1943; Steubing, 1994; Underwood, 1967; Wallach, 1998.

Aniliidae

False coralsnake

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing all alethinophidians except Anomochilidae, Uropeltidae, and Cylindrophiidae.

Content Monotypic, *Anilius scytale.*

Distribution Northern South America (Fig. 21.8).

Characteristics *Anilius scytale* is another smooth, shiny-scaled snake (Fig. 21.6) with a very short tail and ventral scales barely larger than the dorsal ones. Cranially, *A. scytale* has two common carotid arteries, teeth on the premaxillaries, short longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The mandible has a coronoid bone, and the dentary bears teeth. *A. scytale* lacks cranial infrared receptors in pits or surface indentations. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is reduced but present, and a tracheal lung is absent; both left and right oviducts are well developed.

Biology The false coralsnake receives it names from its striking red and black ringed pattern. Adults are typically less than 600 mm TL, although occasionally they exceed 1 m TL. This species is fossorial or at least spends the daylight hours beneath forest-floor litter; apparently, it forages on the surface at night. Although predominantly a forest inhabitant, it occasionally occurs in cultivated areas and other human-disturbed habitats. Adults prey largely on other snakes and amphisbaenians. Sexual maturity occurs at about 350 mm TL, and females give birth to 7 to 15 neonates, typically early in the wet season.

References McDiarmid et al., 1999; Starace, 1998; Underwood, 1967.

Xenopeltidae

Sunbeam snakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon All alethinophidians except Anomochilidae, Uropeltidae, Cylindrophiidae, and Aniliidae.

Content One genus, *Xenopeltis*, with two species (Fig. 21.9).

Distribution Southeast Asia, from Burma through the East Indies to the Philippines (Fig. 21.10).

Characteristics Sunbeam snakes obtain their name from the iridescent glow reflected from their smooth, shiny scales. They have blunt heads, cylindrical bodies, and short tails, but large ventral scales. Cranially, these snakes have two common carotid arteries, teeth on the premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal-parietal sutures. The mandible lacks a coronoid bone, and the dentary bears numerous small teeth. They lack cranial infrared receptors in pits or surface indentations.

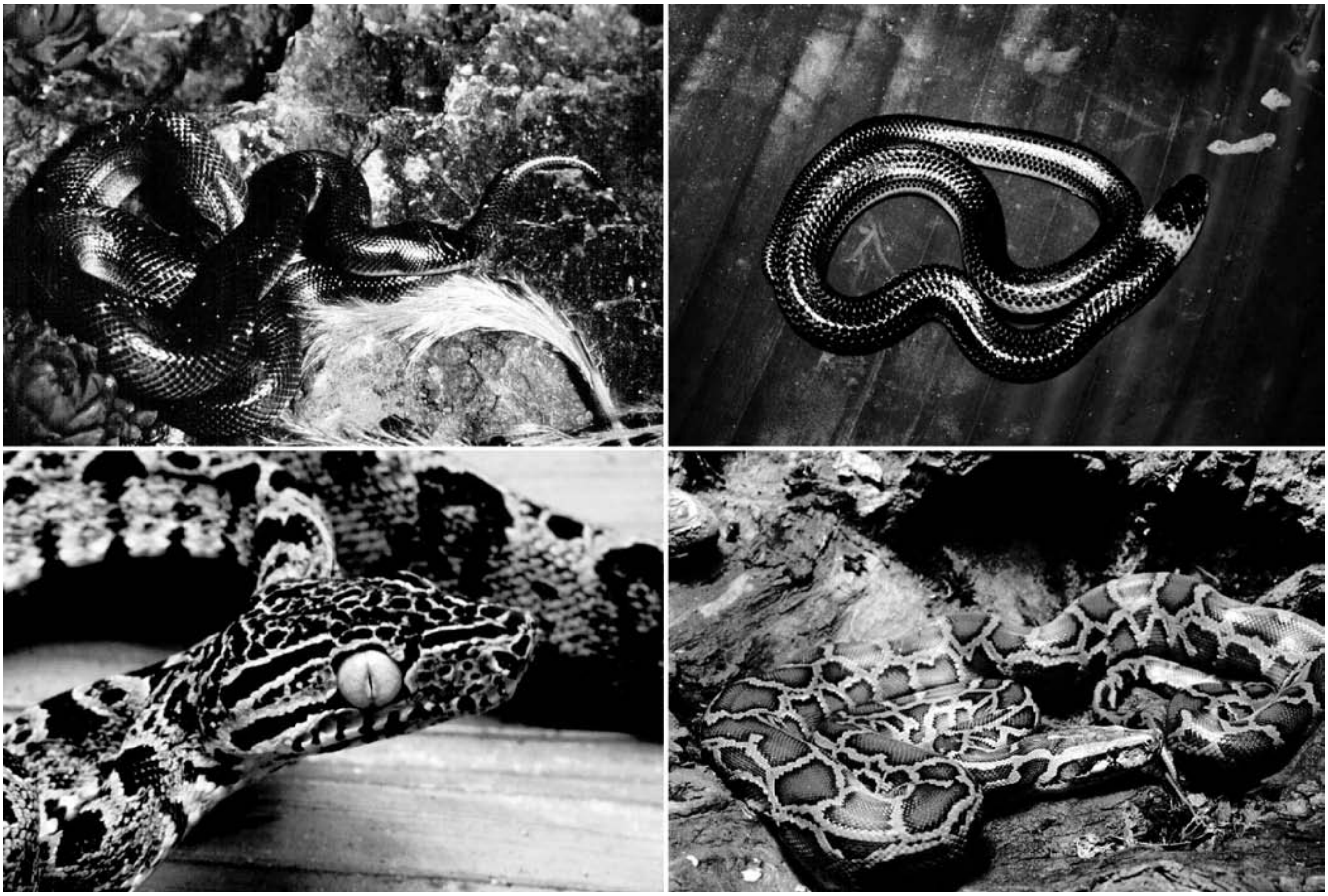


FIGURE 21.9 Representative snakes. Clockwise from upper left: Mesoamerican python *Loxocemus bicolor*, Loxocemidae (photograph by J. A. Campbell); sunbeam snake *Xenopeltis unicolor*, Xenopeltidae (G. R. Zug); Burmese python *Python molurus*, Pythonidae (R. W. Murphy); and garden tree boa *Corallus hortulanus*, Boinae (L. J. Vitt).

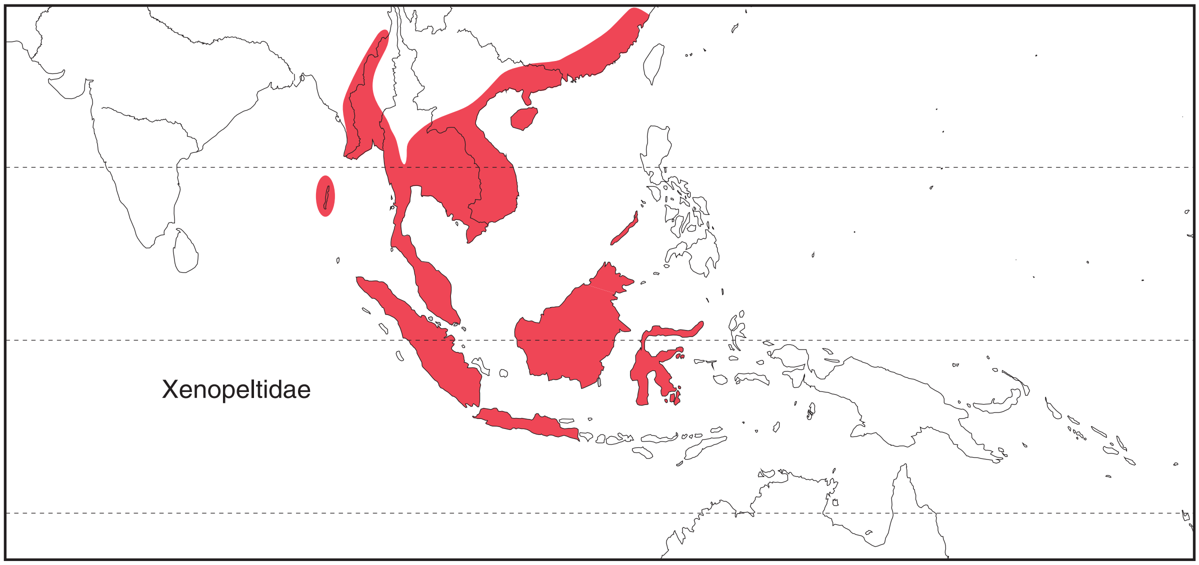


FIGURE 21.10 Geographic distribution of the extant Xenopeltidae.

Girdle and limb vestiges are absent. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is large, and the tracheal lung is absent; both left and right oviducts are well developed.

Biology Of the two species, *Xenopeltis unicolor* (Fig. 21.9) has the widest distribution, and because it is moderately abundant, its biology is reasonably known. Adult *X. unicolor* attain total lengths to 1.3 m; however, most individuals do not exceed 800 mm TL. They are semifossorial snakes, apparently dependent upon the tunnels of other animals. Even though often described as nocturnal, they appear to forage during the day also or at least diurnally during some seasons. The diet is broad and includes a variety of small vertebrates from frogs to mammals. They have a broad ecological tolerance and although commonly associated with water, they occur widely from urban gardens to low montane forest and scrub forest. They are oviparous and can lay as many as 17 eggs in a clutch, but clutch size is usually smaller.

References Cox et al., 1998; David and Vogel, 1996; McDiarmid et al., 1999; Underwood, 1967; Wallach, 1998.

Loxocemidae

Mesoamerican python

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing Pythonidae, Boidae, Bolyeriidae, Tropidophiidae, and Caenophidia.

Content Monotypic, *Loxocemus bicolor.*

Distribution Southern Mexico to Costa Rica (Fig. 21.8).

Characteristics *Loxocemus bicolor* has supraorbital (postfrontal) bones, a cranial feature of primitive snakes. In addition, this taxon has two common carotid arteries, teeth on the premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The mandible has a coronoid bone, and the dentary bears teeth. They lack cranial infrared receptors in pits or surface indentations. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is large, but no tracheal lung occurs; both left and right oviducts are well developed.

Biology *L. bicolor* (Fig. 21.9) attains an adult SVL of 1.4 m, although most adults are less than 1 m. They are relatively uncommon or infrequently seen throughout their distribution; hence, their biology is incompletely known. Although labeled as burrowers, they appear to be more secretive than fossorial, and they generally live in forested habitats. Apparently, they forage only at night, eating a variety of small terrestrial vertebrates (reptiles and mammals) and even seaturtle and iguana eggs. They are oviparous, laying small clutches of four relatively large eggs.

References McDiarmid et al., 1999; Odinchenko and Latyshev, 1996; Underwood, 1967; Wallach, 1998.

Boidae

Boas

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Pythonidae or a clade containing Bolyeriidae, Tropidophiidae, and Caenophidia.

Content Two subfamilies, Boinae and Erycinae.

Distribution Western North America to southern subtropical South America, West Indies, Central Africa to South Asia, Madagascar, and southwest Pacific islands (Fig. 21.11).

Characteristics The "true" boas are small to large snakes. Cranially, they share two common carotid arteries, edentulous premaxillaries with ascending processes, longitudinally oriented maxillaries with solid teeth, optic foramina that perforate the frontal–parietal sutures, and a strongly developed supraoccipital crest. The mandible has a coronoid bone. Most boids have cranial infrared receptors in interlabial pits. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is moderately to well developed, and a tracheal lung is absent; both left and right oviducts are well developed.

References Kluge, 1991a, 1993b; McDiarmid et al., 1999; McDowell, 1987; Underwood, 1967.

Boinae

Sister taxon Erycinae.

Content Six genera, *Boa*, *Candoia*, *Corallus*, *Epicrates*, *Eunectes,* and *Sanzinia*, with 25+ species.

Distribution Disjunct, tropical Americas including the West Indies, Madagascar, and islands of the Southwest Pacific.

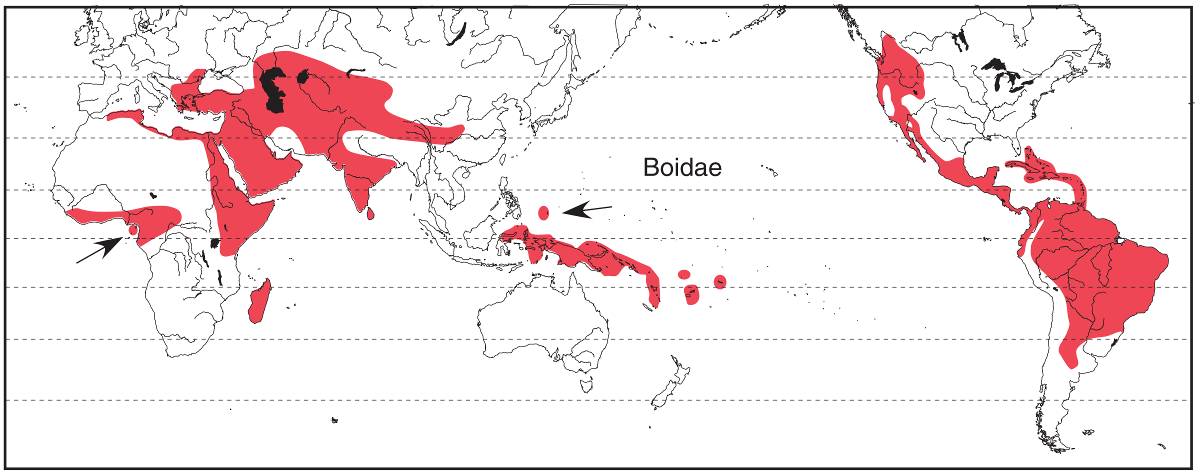


FIGURE 21.11 Geographic distribution of the extant Boidae.

Characteristics Prefrontals touch medially or nearly so; labial sensory pits occur; and caudal vertebrae have simple neural arches.

Biology Boines (Fig. 21.9) range from moderate-sized species (e.g., 600–900 mm adult SVL, *Candoia aspera*) to truly giant snakes (e.g., *Eunectes*, at least to 8 m maximum TL and possibly to 11.5 m). The small to large species are mostly arboreal snakes, although they are regularly found on the ground; the largest-bodied clade, *Eunectes*, is aquatic. Many are bird and mammal predators and are largely nocturnal; they use their infrared sense to locate sleeping prey. Others, such as *Candoia*, capture endotherms but appear to eat mostly lizards and frogs. All are viviparous. Litter size is highly variable; for example, different populations within the *Candoia carinata* complex have litters ranging from 4 to 6 neonates in some, to 40 to 50 neonates in others. Thus, litter number is not strongly associated with body size. The large *Boa constrictor* and *Eunectes* can produce as many as 60 to 70 young, but they usually produce many fewer.

Comment The karyotypic differences between American *Boa* and Madagascan boids, as well as their long independent evolutionary histories, argue for the recognition of *Sanzinia* as distinct from *Boa*.

References Fitch, 1970; Henderson, 1993; Kluge, 1991a; O'Shea, 1996; Tolson and Henderson, 1993.

Erycinae

Sister taxon Boinae.

Content Two genera, *Charina* and *Eryx*, with 3 and 11 species, respectively.

Distribution Disjunct, western North America and Central Africa eastward through Asia to western China.

Characteristics Prefrontals are widely separated medially; labial sensory pits are absent; and caudal vertebrae have forked neural arches.

Biology The sand boas (*Eryx*), rosy boas, and rubber boas (*Charina*; Fig. 21.12) are semifossorial snakes, usually living in semiarid to arid habitats; *Charina bottae* is an exception with its preference for moist, montane conifer forests. All are moderate-sized snakes, typically less than 700 mm TL; they have robust, cylindrical bodies, short tails, blunt heads, and small eyes. They are predominantly nocturnal or crepuscular foragers, and prey mainly on small reptiles and mammals. All are viviparous with litter size usually less than 10 neonates.

Comment Kluge's analysis (1993b) argues for an erycine clade with a resolved divergence from other alethinophidians; other analyses show the traditional erycine–boine sister relationship (Cundall et al., 1994) or show the erycines as an even more basal divergence (Dowling et al., 1996; Heise et al., 1995). Tokar (1989, 1996) recognizes two groups (*Eryx*, *Gongylophis*) of sand boas, but Kluge's analysis does not support this divergence.

References Kluge, 1993b; Tokar, 1989, 1996.

Pythonidae

Pythons

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

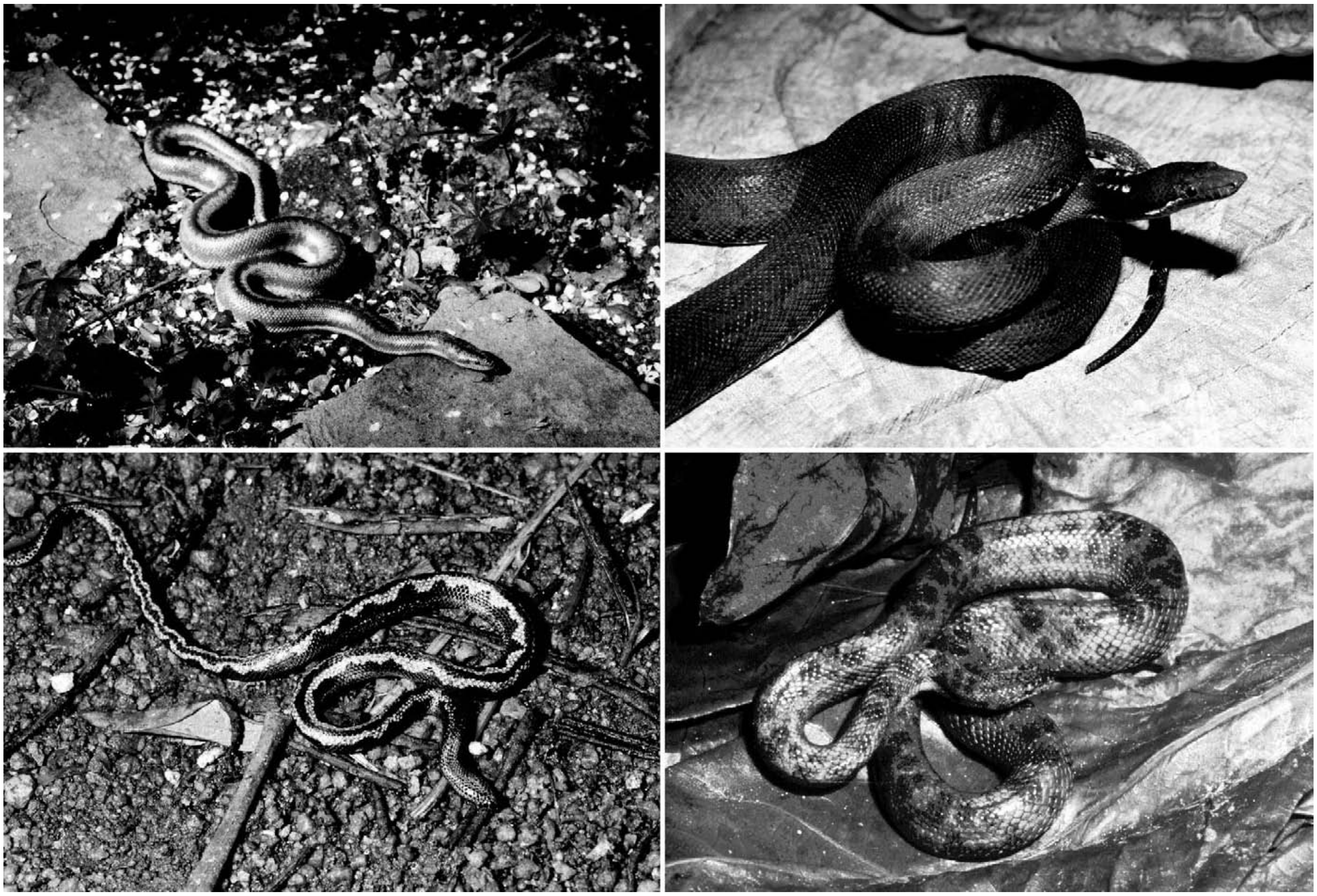


FIGURE 21.12 Representative snakes. Clockwise from upper left: rosy boa *Charina trivirgata*, Erycinae (photograph by L. J. Vitt); Dussumier's splitjaw boa *Casarea dussumieri*, Bolyeriidae (Suzanne L. Collins, The Center for North American Amphibians and Reptiles); Haitian dwarf boa *Tropidophis haetianus*, Tropidophiinae (L. L. Grismer); and spinejaw snake *Xenophidion schaeferi*, Xenophidioninae (Wolfgang Grossman).

Sister taxon Uncertain, possibly Boidae or a clade containing Bolyeriidae, Tropidophiidae, and Caenophidia.

Content Four genera, *Aspidites*, *Liasis*, *Morelia*, and *Python*, with 25+ species.

Distribution Sub-Saharan Africa, and South and Southeast Asia to Australia (Fig. 21.13).

Characteristics Pythons are large to giant snakes (Fig. 21.9). Cranially, they have two common carotid arteries, teeth on the premaxillaries (except in *Aspidites*) without ascending processes, longitudinally oriented maxillaries with solid teeth, paired supraorbitals, optic foramina that perforate the frontal–parietal sutures, and a low or nonexistent supraoccipital crest. The mandible has a coronoid bone. Many pythonines have cranial infrared receptors in interlabial pits. Hindlimb vestiges appear externally as cloacal spurs, and pelvic remnants occur in the trunk musculature. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is usually large and a tracheal lung is absent; both left and right oviducts are well developed.

Biology Adult pythons range from the Australian pygmy python *Liasis childreni* (350–600 mm adult TL) to the giant reticulated python *Python reticulatus* (2.5–10 m TL); adults of most species are less than 4 m. Pythons occur in a wide range of habitats from desert to rain forest. Forest and scrub species forage on and above the ground for vertebrate prey; mammals and birds become the food of the larger individuals. Some species are semiaquatic, for example, *Liasis fuscus,* but birds and mammals are still the major prey. All pythons are oviparous, and in most (if not all) species, females coil about the eggs. In some, such as *Python molurus*, parental care is true brooding; the female maintains an

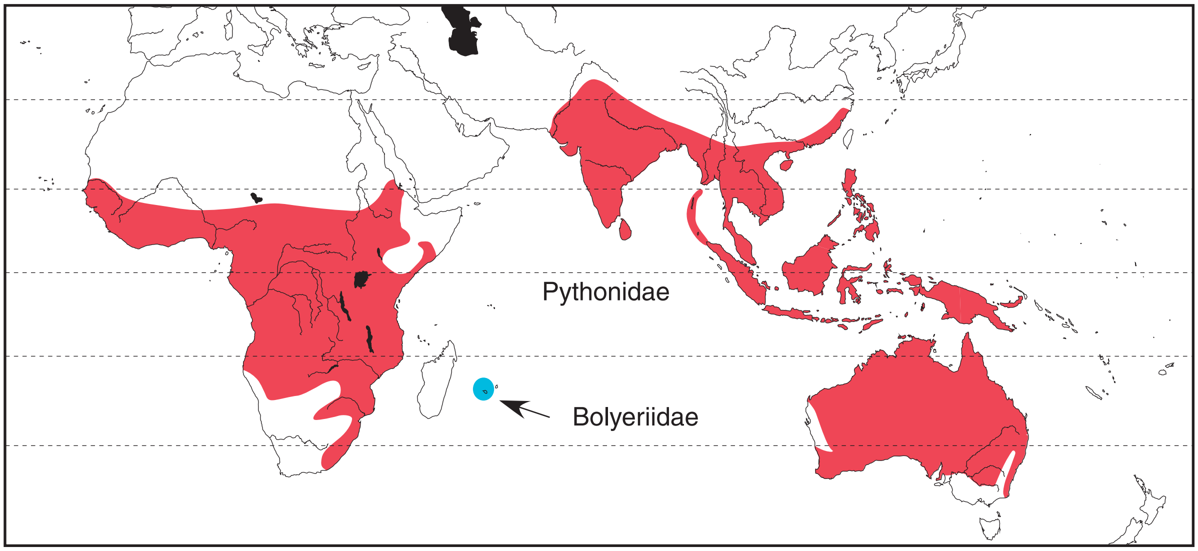


FIGURE 21.13 Geographic distribution of the extant Pythonidae and Bolyeriidae.

elevated body temperature to aid incubation (see Chapters 5 and 7). Clutch size is associated with body size. Smaller and/or the more slender species have clutches of about 5 to 16 eggs, and the larger-bodied species have clutches of 30 to 60 eggs—occasionally over 100 eggs, as reported for *P. reticulatus*.

Comment The generic arrangement follows the clades displayed in Kluge's morphological dendrogram (1993a, Fig. 23).

References Barker and Barker, 1994; Ehmann, 1993; Ernst and Zug, 1996; Kluge, 1993a; McDiarmid et al., 1999; O'Shea, 1996; Shine, 1991b; Shine and Slip, 1990; Underwood, 1967; Underwood and Stimson, 1990.

Bolyeriidae

Mascarene or splitjaw boas

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Clade containing Tropidophiidae and Caenophidia.

Content Two monotypic genera, *Bolyeria multocarinata* and *Casarea dussumieri*.

Distribution Mauritius and islets north of it (Fig. 21.13).

Characteristics Bolyerines are unique among snakes because they possess a maxillary that is divided and hinged into anterior and posterior elements. They are slender boalike snakes (800 mm to 1.38 m TL) without cloacal spurs. Cranially, these snakes have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The mandible has a coronoid bone, and the dentary lacks teeth. They lack cranial infrared receptors in pits or surface indentations. Girdle and limb elements are entirely absent. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment. The left lung is greatly reduced, and there is no tracheal lung; both left and right oviducts are well developed.

Biology The bolyeriids consist of two Recent taxa. *Bolyeria multocarinata* was known from the northern islets near Mauritius, but it is now presumably extinct, as none has been seen since 1975 in spite of extensive searching. *Casarea dussumieri* previously occurred on Mauritius and still occurs today on Round Island. The hinged lower jaw appears to be an adaptation to catch and hold hard, slippery-scaled skinks. Other squamates have evolved similar cranial adaptations for durophagous prey. Field observations indicate that *C. dussumieri* is nocturnal and approaches prey slowly with a raised head and anterior trunk and strikes only when within a few millimeters of the prey. Once grasped, the skink or gecko might be constricted. *C. dussumieri* is oviparous; reproduction in *B. multocarinata* is unknown.

References Bullock, 1986; Cundall and Irish, 1986, 1989; Grandison, 1977; McDiarmid et al., 1999; Underwood, 1967; Wallach and Günther, 1998.

Tropidophiidae

Dwarf boas

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Caenophidia.

Content Three subfamilies, Tropidophiinae, Ungaliophiinae, and Xenophidioninae.

Distribution Malaysia and tropical America (Fig. 21.14).

Characteristics These small to moderate-sized snakes share traits with both "booid" and colubroid snakes. Cranially, they have two common carotid arteries, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the frontal–parietal sutures. The coronoid is reduced or absent, and the dentary bears numerous teeth. Tropidophiids lack cranial infrared receptors in pits or surface indentations. Hindlimb vestiges appear externally as cloacal spurs in males, and pelvic remnants occur in the trunk musculature, except in *Xenophidion*. Intracostal arteries arise from the dorsal aorta at nearly every trunk segment or at intervals of several segments. The left lung is absent (occasionally vestigial in *Ungaliophis*), and a tracheal lung is well developed; both left and right oviducts are well developed.

References McDiarmid et al., 1999; Underwood, 1967; Wallach, 1998; Wallach and Günther, 1998; Zaher, 1994a.

Tropidophiinae

Sister taxon Likely Ungaliophiinae.

Content Two genera, *Trachyboa* and *Tropidophis*, with 2 and 16 species, respectively.

Distribution West Indies, and Central and South America.

Characteristics The dentary lacks an anterior caninelike tooth; the hyoid horns are parallel; and pelvic remnants are present.

Biology *Trachyboa* and *Tropidophis* range in adult TL from 200 mm to 1 m, but most species and individuals are less than 600 mm. They are mainly forest inhabitants and are terrestrial to semiarboreal foragers. They feed mainly on small vertebrates, predominantly lizards. All are viviparous, and litter size is typically 10 or fewer young.

References Schwartz and Henderson, 1991; Tolson and Henderson, 1993.

Ungaliophiinae

Sister taxon Likely Tropidophiinae, but not within a tropidophioid clade according to Zaher (1994b).

Content Two genera, *Exiliboa* and *Ungaliophis*, with one and two species, respectively.***Distribution*** - Disjunct, from southern Mexico to northern Columbia.

Characteristics The dentary lacks an anterior caninelike tooth; the hyoid horns are semiparallel; and pelvic remnants are present.

Biology Ungaliophiines are moderately small snakes (< 760 mm adult TL) that occur in wet to dry forested habitats. *Ungaliophis* is purportedly arboreal or semiarboreal; *Exiliboa placata* is terrestrial, preferring rocky areas. They are secretive snakes, likely nocturnal foragers, and they prey mainly on amphibians and lizards. Ungaliophiines are live-bearers, and *E. placata* bears 8 to 13 neonates in September and October.

References Campbell and Camarillo, 1992; Villa and Wilson, 1990.

Xenophidioninae

Sister taxon Clade containing Ungaliophiinae and Tropidophiinae.

Content One genus, *Xenophidion*, with two species.

Distribution Malaysia.

Characteristics The dentary has a large, anterior caninelike tooth; the hyoid horns are strongly divergent; and pelvic remnants are absent.

Biology Presently, the two species of *Xenophidion* are each known from a single specimen. Both are rain forest-floor inhabitants. They are small snakes, likely not exceeding 300 mm SVL as adults. The single mature female contained several large shelled eggs.

References Manthey and Grossmann, 1997; Wallach, 1998; Wallach and Günther, 1998.

Caenophidia

Acrochordidae

Wart snakes or file snakes

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

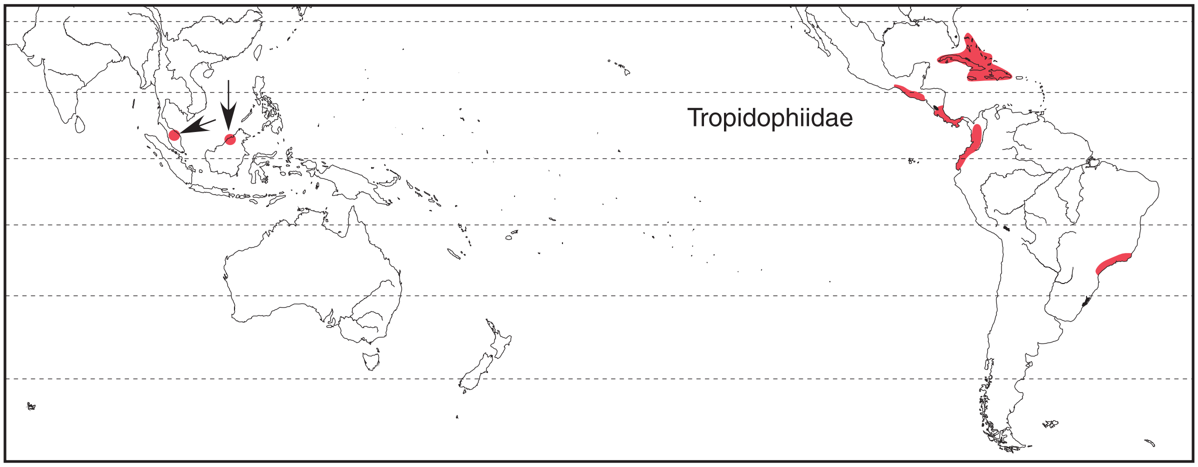


FIGURE 21.14 Geographic distribution of the extant Tropidophiidae.

Sister taxon Clade containing Viperidae, Atractaspididae, Colubridae, and Elapidae.

Content One genus, *Acrochordus*, with three species.

Distribution South and Southeast Asia to the Philippines and northern Australia (Fig. 21.15).

Characteristics Acrochordids are small-headed and thick-bodied snakes; the skin is baggy, appearing several sizes too large for the body. The skin is covered dorsally and ventrally by numerous small, non overlapping, granular scales that have numerous bristle-tipped tubercles arising from the interscalar skin. Cranially, acrochordids have only a left carotid artery, edentulous premaxillaries, longitudinally oriented maxillaries with solid teeth, and optic foramina that perforate the parietal. The mandible lacks a coronoid bone, and the dentary bears numerous teeth. No cranial infrared receptors occur in pits or surface indentations. Girdle and limb elements are absent externally and internally. Intracostal arteries arise from the dorsal aorta at intervals of several trunk segments. The left lung is absent, and a tracheal lung is well developed; the left and right oviducts are well developed.

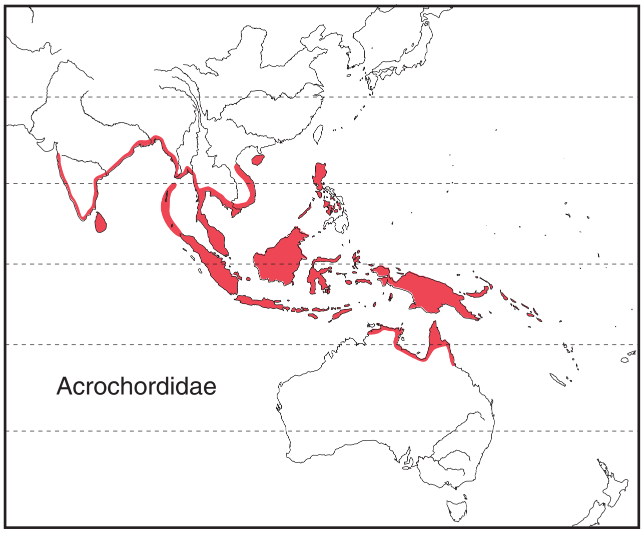


FIGURE 21.15 Geographic distribution of the extant Acrochordidae.

Biology Acrochordids are large snakes, ranging in adult TL from about 800 mm to 1 m (*Acrochordus granulatus*; Fig. 21.16) to 1.9 to 2.7 m (*Acrochordus javanicus*); adult males are always significantly smaller than females. All three species are aquatic and largely incapable of terrestrial locomotion. *A. granulatus* is a brackish and marine species, *Acrochordus arafurae* is a freshwater resident, and *A. javanicus* occurs in both fresh and salt water. All three feed principally on fish, and *A. arafurae* apparently exclusively so. Prey capture usually requires the fish to touch the anterior part of the snake's body, which triggers the snake to trap the fish in body loops and coils using the bristly tubercles for adhesion. The snake quickly shifts the fish forward in a wave-like action of the skin folds and rapidly swallows it. Acrochordids are viviparous, and litters range from 4 to 40 young, all born in the water. Clutch size is correlated with body size, and *A. arafurae* and *A. javanicus* are the most fecund.

References Cox et al., 1998; Manthey and Grossmann, 1998; McDiarmid et al., 1999; Shine, 1986a,b; Shine and Houston, 1993; Shine and Lambeck, 1985; Underwood, 1967; Wallach, 1998; Wallach and Günther, 1998.

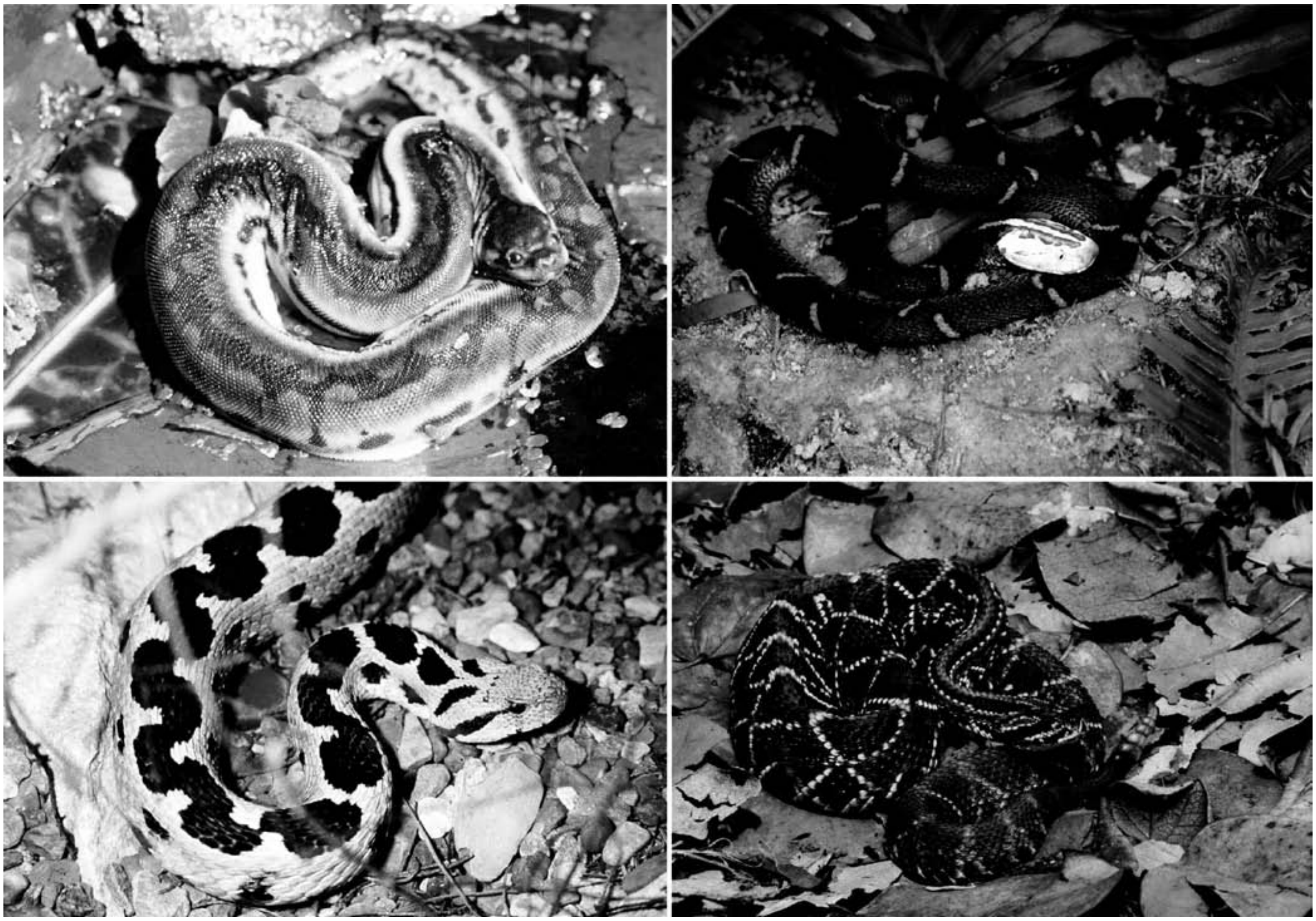


FIGURE 21.16 Representative caenophidian snakes. Clockwise from upper left: little filesnake *Acrochordus granulatus*, Acrochordidae (photograph by K. Nemuras); Fea's viper *Azemiops feae*, Azemiopinae (R. W. Murphy); Neotropical rattlesnake *Crotalus durissus*, Crotalinae (L. J. Vitt); and Ottoman viper *Vipera xanthina*, Viperinae (R. W. Barbour).

Viperidae

Vipers and pitvipers

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly a clade containing Atractaspididae, Colubridae, and Elapidae.

Content Three subfamilies, Azemiopinae, Crotalinae, and Viperinae.

Distribution Worldwide, except Papua-Australia and oceanic islands (Fig. 21.17).

Characteristics Viperids are venomous snakes; a rotating fang apparatus allows the development of long fangs that are erected when biting and folded against the palate when the mouth is closed. Most viperids have robust bodies and distinctly triangular heads. Cranially, viperids have only a left carotid artery, edentulous premaxillaries, blocklike, rotating maxillaries with tubular teeth, and optic foramina that perforate the frontal–parietal or frontal–parietal–parasphenoid sutures. The mandible lacks a coronoid bone and the dentary bears teeth. Cranial infrared receptors occur in loreal pits in crotalines or beneath scale surfaces in other taxa. Girdle and limb elements are absent externally and internally. Intracostal arteries arise from the dorsal aorta at intervals of several trunk segments. The left lung is usually absent or vestigial when present, and a tracheal lung is usually present; left and right oviducts are well developed.

References McDiarmid et al., 1999; Thorpe et al., 1997; Underwood, 1967; Wallach, 1998.

Azemiopinae

Sister taxon Clade containing Crotalinae and Viperinae.

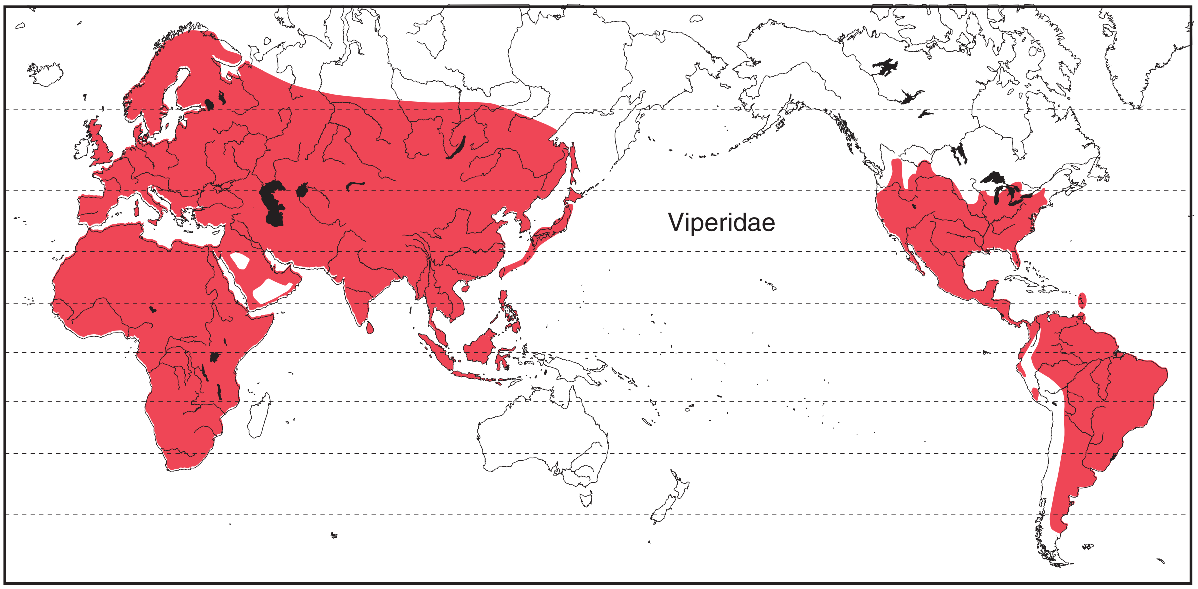


FIGURE 21.17 Geographic distribution of the extant Viperidae.

Content Monotypic, *Azemiops feae.*

Distribution South-central China and adjacent areas of Burma and Vietnam.

Characteristics *Azemiops* lacks a loreal pit, has a distinct choanal process on the palatine, has a large posteromedial orbital process on the prefrontal, and lacks a tracheal lung.

Biology Fea's vipers are moderate-sized snakes (600–720 mm adult TL). They live at midelevations (800–1000 m) in moist montane forest, particularly among clumps of bamboo and tree ferns. *Azemiops feae* appears to be semifossorial and lives in the forest litter in high-humidity localities. The snakes spend the day beneath objects, often in wet situations, and emerge late at night to forage on and in the surface litter; mammals are likely the major prey. These snakes appear to dehydrate rapidly even in moderately dry conditions. Whether reproduction is oviparous or viviparous remains unknown.

References Liem et al., 1971; Orlov, 1997.

Crotalinae

Sister taxon Viperinae.

Content Eighteen genera, *Agkistrodon*, *Atropoides*, *Bothriechis*, *Bothriopsis*, *Bothrops*, *Calloselasma*, *Cerrophidion*, *Crotalus*, *Deinagkistrodon*, *Gloydius*, *Hypnale*, *Lachesis*, *Ophryacus*, *Ovophis*, *Porthidium*, *Sistrurus*, *Trimeresurus,* and *Tropidolaemus*, with ±155 species.

Distribution Southwest and southern Asia and the Americas.

Characteristics Crotalines have a well-developed loreal pit for infrared receptors, have a small choanal process on the palatine, lack a posteromedial process on the prefrontal, and have a tracheal lung, except in *Lachesis.*

Biology Crotalines are small to large snakes, ranging in adult TL from 300 to 660 mm in *Crotalus pricei* to a maximum 3.75 m in *Lachesis muta*. They are predominantly nocturnal snakes, and they use (not exclusively) their heat-sensory apparatus to locate prey. They prey mainly on vertebrates, usually birds and mammals in the larger crotaline species and amphibians and reptiles in the smaller ones; semiaquatic taxa eat fish and frogs. They occur in numerous habitats from deserts to cool mountain forests and wet tropical lowlands. Crotalines are mainly terrestrial, but a few taxa are semiaquatic and 20+ tropical Asian and American species are arboreal. In general, most appear to be long-lived species, maturing slowly and reproducing in 2- to 3-year cycles, except for the species in habitats with high prey density. Most crotalines are viviparous, although a few, such as *Calloselasma*, some *Trimeresurus*, and *Lachesis*, are oviparous and commonly display egg-attendance behavior. Litter or clutch size is generally associated with body size. Smaller species typically produce fewer eggs or young than larger ones; however, even the largest taxon, *L. muta*, produces only about a dozen eggs, and the much smaller *Sistrurus catenatus* averages nearly 12 neonates. Overall, crotalines produce about 10 eggs or neonates per reproductive event, and viviparous species tend to produce more offspring than oviparous ones of equivalent size.

Comment Campbell and Lamar (1989) partitioned the paraphyletic *Bothrops* into five genera, and other divisions have been proposed subsequently. We generally recognize all proposed genera; however, species content and even the recognition of the various genera continue to be actively investigated (e.g., Kraus et al., 1996; Vidal et al., 1997).

References Beaupre and Duvall, 1998; Brown, 1993; Cadle, 1992; Campbell and Brodie, 1992; Campbell and Lamar, 1989; Gloyd and Conant, 1990; Klauber, 1982; Ripa, 1999; Rubio, 1998; Zamudio and Greene, 1997.

Viperinae

Sister taxon Crotalinae.

Content Thirteen genera, *Adenorhinos*, *Atheris*, *Bitis*, *Causus*, *Cerastes*, *Daboia*, *Echis*, *Eristocophis*, *Macrovipera*, *Monatatheris*, *Proatheris*, *Pseudocerastes,* and *Vipera*, with 65+ species.

Distribution Africa, Europe, and Asia.

Characteristics Viperines lack a loreal pit, a choanal process on the palatine, and a posteromedial process on the prefrontal; all have a tracheal lung, except for *Bitis atropos.*

Biology Viperines are modest-sized snakes; none is known to exceed 2 m SVL, and most taxa are less than 1 m adult SVL. *Bitis* contains the largest species (*B. arietans*, *B. gabonica*, and *B. nasicornis*, all with maximum adult SVLs of 1.4 m or larger) and some of the smallest species (*B. peringueyi*, 300 mm maximum adult SVL). Most viperines are terrestrial, although a few forage low in bushes, and *Atheris* is arboreal. They occur in forest to desert habitats and from equatorial to subarctic regions. Although viperines are commonly labeled as diurnal species, many forage nocturnally; the activity patterns of most taxa are associated with climate and seasonal temperature regimes. For example, the European *Vipera* is diurnal and the desert *Cerastes* is nocturnal. Viperines prey mainly on small vertebrates. Viperines include oviparous taxa (e.g., *Causus*, *Echis coloratus*) and viviparous taxa (e.g., *Bitis*, *Echis carinatus*, most *Vipera*). Clutch or litter size is moderate in most taxa, usually not exceeding 10 eggs or neonates, but the large-bodied species of *Bitis* produce 40 to 100 neonates.

Comment Most recent phylogenetic analyses place *Causus* as the basal sister group to all other viperines; however, uncertainty remains in the placement of crotalines relative to *Causus.* Perhaps crotalines diverged before the origin of *Causus*, just after *Causus*, or even from within the viperines (Herrmann and Joger, 1997).

References Ashe and Marx, 1988; Brodmann, 1987; Hermann and Joger, 1997; Saint Girons, 1992; Seigel and Ford, 1987; Sprawl and Branch, 1995.

Atractaspididae

Stiletto vipers or molevipers

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Colubridae or Elapidae.

Content Two subfamilies, Aparallactinae and Atractaspidinae.

Distribution Sub-Saharan Africa and the bordering coast of the Arabian Peninsula including Israel and Jordan (Fig. 21.18).

Characteristics Atractaspidids are slender, cylindrical-bodied snakes with a short, usually blunt-snouted head, small eyes, and a short tail. Occasionally, all taxa are labeled venomous and considered to possess "venom" glands; however, *Atractaspis* is the only taxon capable of a fatal envenomation of humans, although *Macrelaps* is potentially lethal. Cranially, atractaspidids have only a left carotid artery, edentulous premaxillaries, longitudinally oriented maxillaries with enlarged, tubular anterior teeth, and optic foramina that perforate the frontal–parietal–parasphenoid sutures. The mandible lacks a coronoid bone, and the dentary bears teeth. No cranial infrared receptors occur in pits or surface indentations. Girdle and limb elements are absent externally and internally. Intracostal arteries arise from the dorsal aorta at intervals of several trunk segments. The left lung is greatly reduced or absent, and a tracheal lung is also present or absent; left and right oviducts are well developed.

Comment Generic content follows Zaher (1999).

References Cadle, 1994; Underwood, 1967; Underwood and Kochva, 1993; Wallach, 1998; Zaher, 1999.

Aparallactinae

Sister taxon Atractaspidinae.

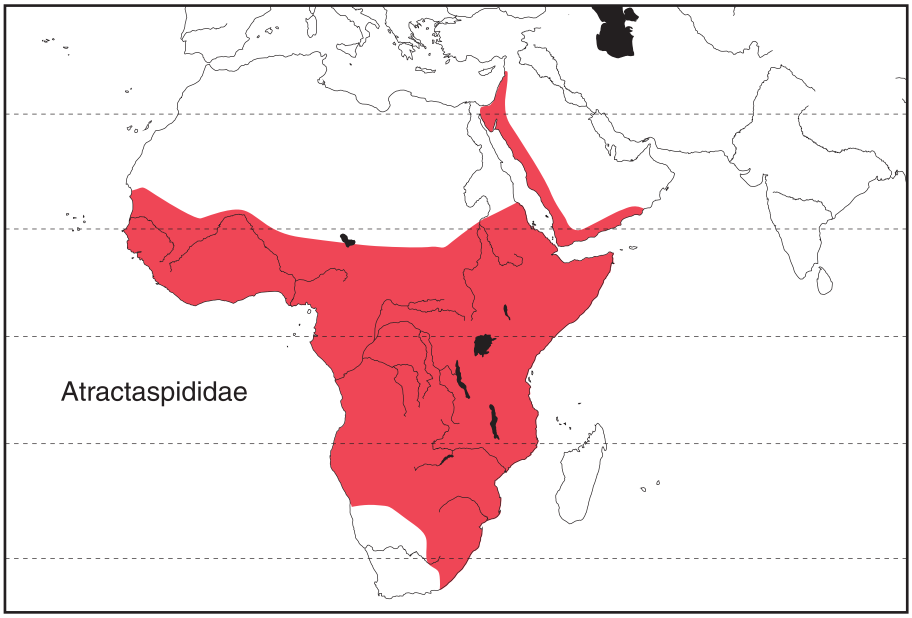


FIGURE 21.18 Geographic distribution of the extant Atractaspididae.

Content Twelve genera, *Amblyodipsas*, *Aparallactus*, *Brachyophis*, *Chilorhinophis*, *Elapocalamus*, *Elapotinus*, *Hypoptophis*, *Macrelaps*, *Micrelaps*, *Poecilopholis*, *Polemon,* and *Xenocalamus*, with 40+ species.

Distribution Sub-Saharan Africa.

Characteristics Enlarged, grooved teeth occur on each maxillary, either posteriorly (opisthoglyphous) or anteriorly (proteroglyphous); a tracheal lung is present; and the left lung is often absent.

Biology Aparallactines are small (200–300 mm adult SVL, *Aparallactus nigriceps*) to large (about 1.1 m maximum TL, *Macrelaps microlepidotus*). All are terrestrial to semifossorial snakes, occurring in a variety of habitats from grassland to moist forest. *Aparallactus* is generally a centipede specialist; the other taxa prey mainly on small vertebrates that live in or on the surface litter. These snakes include oviparous and viviparous species; clutch or litter size is small, usually less than 10 eggs or young.

References Branch, 1988; Villiers, 1975.

Atractaspidinae

Sister taxon Aparallactinae.

Content One genus, *Atractaspis*, with 17 species.

Distribution As for the family (Fig. 21.18).

Characteristics Each maxillary bears a large semi-erect fang anteriorly; a tracheal lung is present or absent; and usually the left lung is present but small.

Biology *Atractaspis* is a venomous, highly fossorial taxon (Fig. 21.19). All species are blunt-headed, apparently capable of using their heads in burrowing, although they are likely dependent upon the burrows of their mammalian prey. Because they live and feed subterraneanly, they cannot use the typical snake strike to achieve envenomation. Instead, they crawl alongside their prey (mainly newborn rodents and burrowing reptiles), depress their lower jaw and shift it toward the opposite side, thereby exposing their exceptionally long fangs, and with a backward stab, envenomate the prey. *Atractaspis* is oviparous and lays small clutches of 2 to 11 eggs. For most species, adults range from 400 to 600 mm TL.

References Branch, 1988; David and Ineich, 1999; Sprawl and Branch, 1995; Underwood and Kochva, 1990; Villiers, 1975.

"Colubridae"

Colubrids

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Paraphyletic.

Content Seven subfamilies, Lamprophiinae, Colubrinae, Homalopsinae, Natricinae, Pareatinae, Xenodermatinae, and Xenodontinae.

Distribution Worldwide, except Antarctica and oceanic islands (Fig. 21.20).

FIGURE 21.19 Representative caenophidian snakes. Clockwise from upper left: Bibron's moleviper *Atractaspis bibronii*, Atractaspidinae (photograph by W. R. Branch); Cape centipede-eater *Aparallactus capensis*, Aparallactinae (R. D. Bartlett); tropical arboreal whipsnake *Chironius carinatus*, Colubrinae (J. P. Caldwell); and yellow belly watersnake *Enhydris plumbea*, Homalopsinae (D. R. Karns).

Characteristics Colubrids represent the most structurally diverse group of snakes and include aglyphous, opisthoglyphous, and proteroglyphous taxa. Cranially, colubrids have only a left carotid artery, edentulous premaxillaries, usually longitudinally oriented maxillaries with solid or grooved teeth, and optic foramina that usually perforate the frontal–parietal–parasphenoid sutures. The mandible lacks a coronoid bone, and the dentary bears teeth. No cranial infrared receptors occur in pits or surface indentations. Girdle and limb elements are absent externally and internally. Intracostal arteries arise from the dorsal aorta at intervals of several trunk segments. The left lung is greatly reduced or more often absent, and a tracheal lung can be present or absent; left and right oviducts are well developed.

Comment The following subfamilies represent only those colubrid groups that are widely recognized by herpetologists. The generic content, especially of the larger groups, also attempts to reflect a general, certainly not unanimous, consensus. We have relied upon Zaher's list of colubrid genera and subfamilial assignments (1999); however, because we recognize fewer subfamilies, we assigned his *incertae sedis* taxa to our different subfamilies. Because some resulting subfamilies are composites, we characterize only those that are likely monophyletic.

References Underwood, 1967; Wallach, 1998; Zaher, 1999.

"Colubrinae"

Sister taxon Uncertain.

Content Over 100 genera, *Aeluroglena*, *Ahaetulla*, *Argyrogena*, *Arizona*, *Blythia*, *Bogertophis*, *Boiga*, *Calamaria*, *Calamorhabdium*, *Cemophora*, *Cercaspis*, *Chilomeniscus*, *Chionactis*, *Chironius*, *Chrysopelea*, *Collorhabdium*, *Coluber*, *Conopsis*, *Coronella*, *Crotaphopeltis*, *Cryptophidion*, *Cyclocorus*, *Dasypeltis*, *Dendrelaphis*, *Den-*

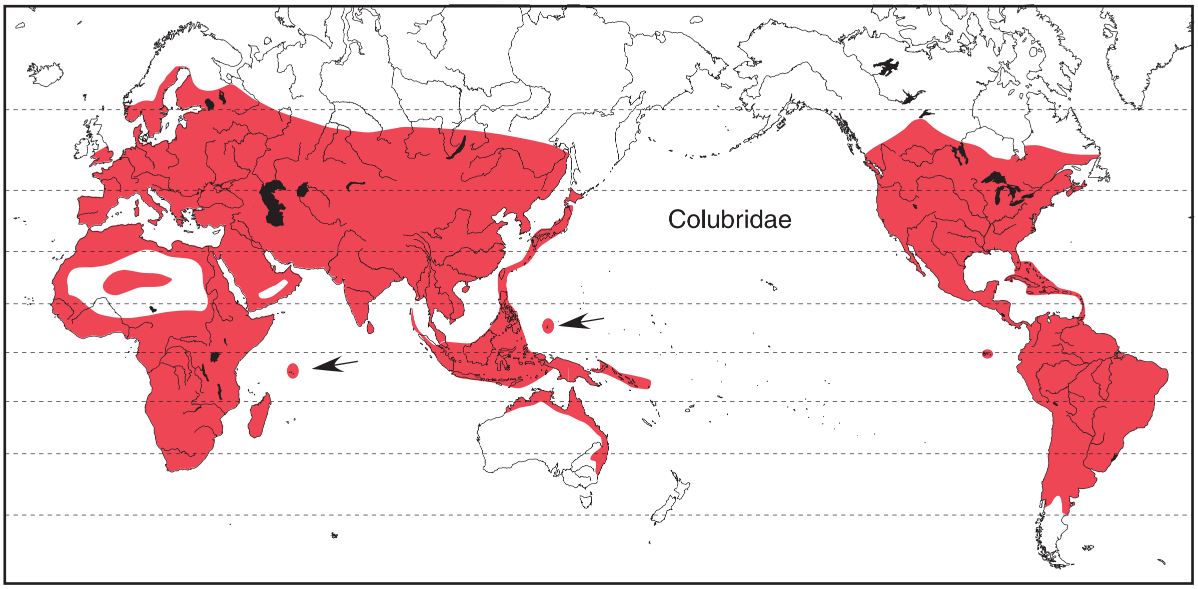


FIGURE 21.20 Geographic distribution of the extant Colubridae.

drophidion, *Dinodon*, *Dipsadoboa*, *Dispholidus*, *Dryadophis*, *Drymarchon*, *Drymobius*, *Drymoluber*, *Dryocalamus*, *Dryophiops*, *Eirenis*, *Elachistodon*, *Elaphe*, *Elapoidis*, *Entechinus*, *Etheridgeum*, *Ficimia*, *Geagras*, *Gongylosoma*, *Gonyophis*, *Gonyosoma*, *Gyalopion*, *Haplocercus*, *Hapsidophrys*, *Helophis*, *Hemirhagerrhis*, *Hierophis*, *Ithycyphus*, *Lampropeltis*, *Leptodrymus*, *Leptophis*, *Lepturophis*, *Liochlorophis*, *Liopeltis*, *Lycodon*, *Lytorhynchus*, *Macrocalamus*, *Macroprotodon*, *Malpolon*, *Masticophis*, *Mastigodryas*, *Meizodon*, *Myersophis*, *Oligodon*, *Opheodrys*, *Oreocalamus*, *Oxybelis*, *Philothamnus*, *Phyllorhynchus*, *Pituophis*, *Poecilopholis*, *Prosyma*, *Psammophis*, *Psammophylax*, *Pseudocyclophis*, *Pseudoficimia*, *Pseudorabdion*, *Pseustes*, *Ptyas*, *Rabdion*, *Rhabdops*, *Rhamphiophis*, *Rhamnophis*, *Rhinobothryum*, *Rhinocheilus*, *Rhynchocalamus*, *Rhynchophis*, *Salvadora*, *Scaphiodontophis*, *Scaphiophis*, *Scolecophis*, *Senticolis*, *Sibynophis*, *Simophis*, *Sonora*, *Spalerosophis*, *Spilotes*, *Stegonotus*, *Stenorrhina*, *Stilosoma*, *Symphimus*, *Sympholis*, *Tantilla*, *Tantillita*, *Telescopus*, *Tetralepis*, *Thelotornis*, *Thermophis*, *Thrasops*, *Toluca*, *Trachischium*, *Trimorphodon*, *Xenelaphis,* and *Zaocys*, with ±650 species.

Distribution Worldwide, as the family.

Biology Colubrines are highly diverse in body form, and in ecology and behavior. They range from small (160–190 mm TL, *Tantilla relicta*) to very large (e.g., 3.7 m TL, *Ptyas carinatus*). Body forms may be slender (*Sibynophis*), elongate viperine (*Boiga*), racerlike (*Masticophis*), or muscular serpentine (*Chironius*), as well as many others. Colubrines occur from brackish water habitats to high montane forest; some are desert inhabitants, whereas others are aquatic. Some are burrowers, many are terrestrial or semiarboreal, and others are arboreal. Species may be diet generalists or specialists. Generalists often prey on small vertebrates and occasionally invertebrates; specialists may eat only orthopteran insects (*Opheodrys*) or birds (*Thelotornis*). Colubrines are predominantly oviparous; the few viviparous species are usually small snakes. Clutch size generally is associated with body size. The small-bodied *Tantilla gracilis* produces clutches of 1 egg, and the much larger *Elaphe obsoleta* has clutches of up to 40 eggs; however, most species produce clutches of 10 or fewer eggs.

Comment Generic content derives from Zaher's (1999) Colubrinae, Calamariinae, Psammophiinae, and Colubridae *incertae sedis.*

References Cox et al., 1998; Ernst and Barbour, 1989b; Seigel and Ford, 1987.

Homalopsinae

Sister taxon Uncertain, possibly Pareatinae.

Content Eleven genera, *Bitia*, *Brachyorrhos*, *Cantoria*, *Cerberus*, *Enhydris*, *Erpeton*, *Fordonia*, *Gerarda*, *Heurnia*, *Homalopsis,* and *Myron*, with 35+ species.

Distribution Southern Asia from India to China and south to northern Australia.

Characteristics Homalopsines are distinguished from other colubrids by valvular, crescentic, dorsal nostrils; small, dorsally oriented eyes (eye diameter less than vertical distance from bottom of orbit to mouth); nasal scales usually larger than internasals; and the last two or three maxillary teeth enlarged and grooved with well-developed venom (Duvernoy) glands.

Biology Homalopsines are aquatic snakes and live in a variety of freshwater, brackish, and marine habitats, typically in shallow water. Envenomation is an important aspect of prey capture for all taxa. Prey is bitten and held; a chewing action introduces the venom into the prey; and once subdued, the prey is swallowed. Most freshwater homalopsines eat fish or fish and frogs. *Fordonia leucobalia* is a crab specialist; it first pins the crab beneath a body loop and then bites and envenomates it. For all taxa, foraging appears to be mainly nocturnal, and most actively search for prey. Homalopsines are small (200–380 mm adult SVL, *Myron richardsonii*) to large (1.4 m maximum TL, *Homalopsis buccata*). All homalopsines are viviparous. Litter size is modest, from 5 to 15 neonates in most species, but larger individuals and larger species can have 20 to 30 young.

References Cox et al., 1998; Greer, 1997; Gyi, 1970; Murphy and Voris, 1994.

"Lamprophiinae"

Sister taxon Uncertain.

Content Forty-four genera, *Alluaudina*, *Boaedon*, *Bothrolycus*, *Bothrophthalmus*, *Brygophis*, *Buhoma*, *Chamaelycus*, *Compsophis*, *Cryptolycus*, *Dendrolycus*, *Dipsina*, *Ditypophis*, *Dromicodryas*, *Dromophis*, *Duberria*, *Exallodontophis*, *Gastropyxis*, *Geodipsas*, *Gonionotophis*, *Grayia*, *Heteroliodon*, *Hormonotus*, *Ithycyphus*, *Lamprophis*, *Langaha*, *Lioheterodon*, *Liophidium*, *Liopholidophis*, *Lycodonomorphus*, *Lycodryas*, *Lycophidion*, *Madagascarophis*, *Mehelya*, *Micropisthodon*, *Mimophis*, *Montaspis*, *Pararhadinaea*, *Polemon*, *Pseudaspis*, *Pseudoboodon*, *Pseudoxyrhopus*, *Pythonodipsas*, *Scaphiophis,* and *Stenophis*, with 205+ species.

Distribution Sub-Saharan Africa and Madagascar.

Biology Lamprophiines are a moderately diverse group. They are mainly terrestrial to semifossorial, but a few (e.g., *Langaha*, *Stenophis*) are arboreal. The majority of species are less than 1 m TL, although some genera (e.g., *Brygophis*, *Dromophis*, *Leioheterodon* [Fig. 21.21], *Mehelya*) have a maximum TL of 1.0 to 1.5 m, and *Grayia smythii* reaches 2.6 m. Body form ranges from typical terrestrial racer habitus to blunt-headed, cylindrical-bodied burrowers, and also includes big-headed, thin-bodied arboreal forms. Most taxa prey upon vertebrates, and none appears to be a dietary specialist. Lamprophiines are nearly exclusively oviparous, although *Stenophis* has both oviparous and viviparous species. Clutch size tends to be small, commonly less than 10 eggs per clutch even in some large-bodied species, but the large *Scaphiophis* has clutches up to 48 eggs.

Comment Generic content is derived from Zaher's (1999) Boodontinae, Boodontinae *incertae sedis*, and Pseudoxyrhophiinae.

References Branch, 1988; Cadle, 1994; Glaw and Vences, 1994; Pitman, 1974; Shine et al., 1996.

"Natricinae"

Sister taxon Uncertain.

Content Thirty-eight genera, *Adelophis*, *Afronatrix*, *Amphiesma*, *Amphiesmoides*, *Amplorhinus*, *Anoplohydrus*, *Aspidura*, *Atretium*, *Balanophis*, *Clonophis*, *Geodipsas*, *Haplocercus*, *Helophis*, *Hologerrhum*, *Hydrablabes*, *Hydraethiops*, *Iguanognathus*, *Limnophis*, *Natriciteres*, *Natrix*, *Nerodia*, *Opisthotropis*, *Pararhabdophis*, *Parahelicops*, *Plagiopholis*, *Psammodynastes*, *Pseudagkistrodon*, *Pseudoxenodon*, *Regina*, *Rhabdophis*, *Seminatrix*, *Sinonatrix*, *Storeria*, *Thamnophis*, *Tropidoclonion*, *Tropidonophis*, *Virginia,* and *Xenochrophis*, with 195+ species.

Distribution North America to northern Central America, Africa, and Eurasia through the East Indies.

Biology Natricines are small (160–250 mm adult SVL, *Virginia striatula*) to large (1.4–2.0 m maximum TL, *Natrix*, *Nerodia*, and *Xenochrophis*). Many species are labeled aquatic, and though these natricines feed and hide in water, they regularly exit the water for basking and reproduction in contrast to the aquatic homalopsines or acrochordids. The aquatic species are with few exceptions freshwater inhabitants, and the exceptions, such as *Nerodia fasciata*, have some populations behaviorally and physiologically adapted to salt water. Most other natricines are terrestrial to semifossorial, the majority of which live in moist habitats from marsh to forest. The aquatic species prey predominantly on fish and amphibians, but a few, like the crayfish-eating *Regina septemvittata*, are dietary specialists. Other species, generally the smaller ones or juveniles of larger species, eat slugs, snails, earthworms, and soft-bodied arthropods. American natricines are exclusively viviparous, whereas the Old World taxa are largely, but not exclusively, oviparous. Clutch size tends to be modest (2–20 eggs) in the oviparous taxa

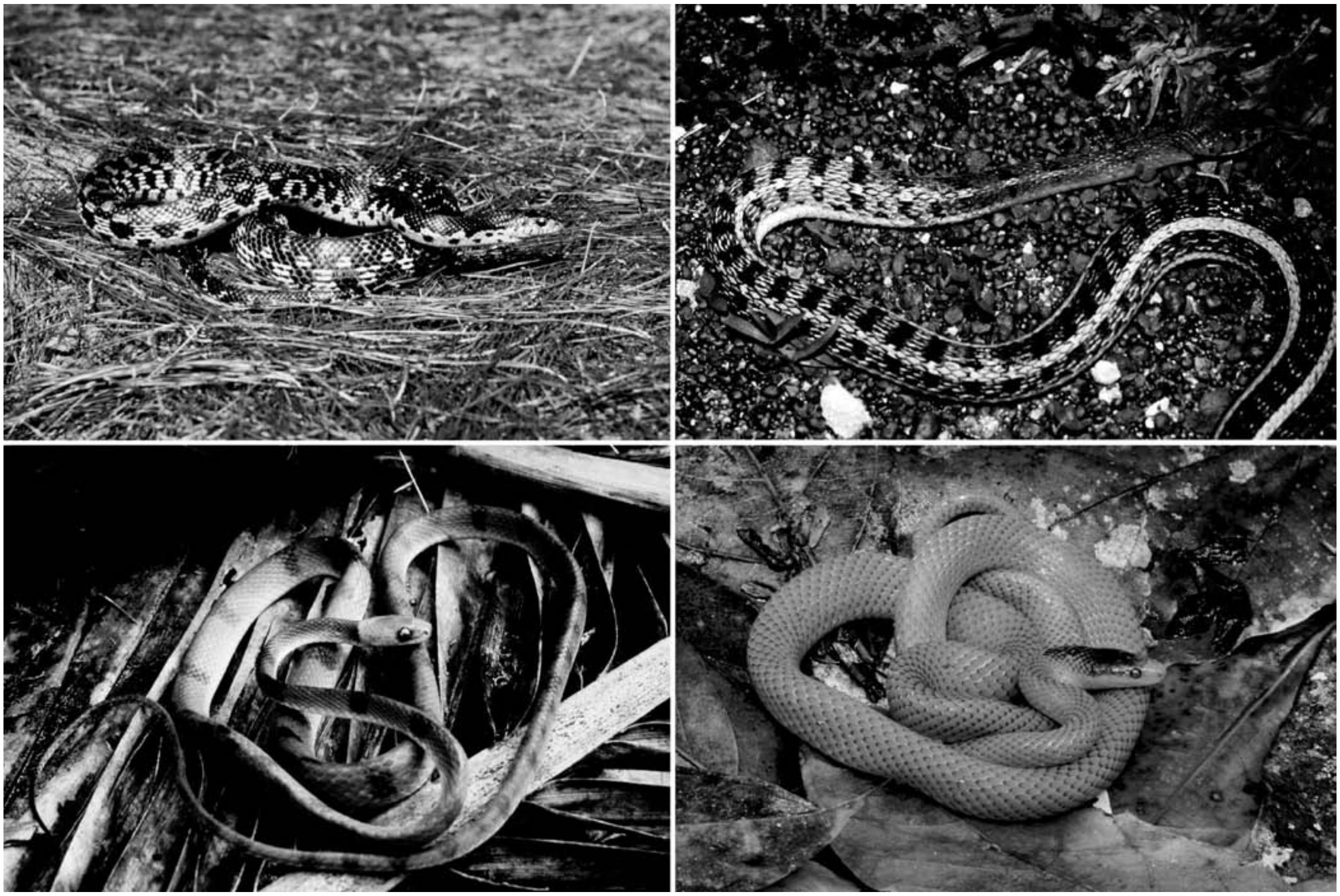


FIGURE 21.21 Representative colubrid snakes. Clockwise from upper left: Madagascan hognose snake *Lioheterodon madagascariensis*, Lamprophiinae (photograph by H. I. Uible); buff-striped keelback *Amphiesma stolata*, Natricinae (G. R. Zug); false coralsnake *Oxyrhopus formosus,* Xenodontinae (L. J. Vitt); and tropical flatsnake *Tripanurgos compressus,* Xenodontinae (L. J. Vitt).

and even in the large-bodied taxa (e.g., 10–40 eggs, *Xenochrophis*). Litter size is somewhat larger in equivalent-sized viviparous species, although the prodigious 80 to 100 fetuses reported for *Nerodia cyclopion* is uncommon.

Comment Kraus and Brown (1998) suggest that natricines are diphyletic; the New World thamnophines are monophyletic, whereas the Old World natricines are paraphyletic. Generic content is derived from Zaher's (1999) Natricinae, Natricinae *incertae sedis*, and Pseudoxenodontinae.

References Cox et al., 1997; Engelmann et al., 1986; Ernst and Barbour, 1989b; Manthey and Grossmann, 1997; Rossman et al., 1996.

Pareatinae

Sister taxon Uncertain, possibly Homalopsinae.

Content Three genera, *Aplopeltura*, *Internatus,* and *Pareas*, with 18+ species.

Distribution Southeast Asia from eastern India to China and southward to Java, Borneo, and Mindanao.

Characteristics Pareatines have a blunt snout, lack a mental groove, and have no teeth on the anterior part of the maxillary.

Biology Pareatines are called slug-eating snakes because of their specialized diet of slugs and snails. Their aforementioned characters are part of their feeding adaptation; the long slender body and oversized head is also seen in other snail specialists. This morphology is an adaptation for slow arboreal searching on the slender twigs and branches at the ends of limbs and for traversing wide gaps. All taxa are moderate-sized and have adults that range between 450 and 900 mm TL, although they appear small because of their slender body form. They forage at night, and upon finding a snail, they slide their lower jaw beneath the snail and the shell and bite the body. They use their teeth and independent jaw bones in a ratchetlike fashion to exert a continuous pulling pressure on the snail's body, which eventually relaxes and is then ripped from its shell attachment. All pareatines are oviparous and have small clutches of two to eight eggs.

References Cox et al., 1998; Manthey and Grossmann, 1997; Rao and Yang, 1992.

Xenodermatinae

Sister taxon Uncertain, possibly all other Colubridae.

Content Six genera, *Achalinus*, *Fimbrios*, *Oxyrhabdium*, *Stoliczkaia*, *Xenodermus,* and *Xylophis*, with 15 species.

Distribution Disjunct, Assam, northern Indochina and adjacent China to Japan, and peninsular Malaysia, Sumatra, Java, and Borneo.

Characteristics Xenodermatines have small orbits from which the optic nerve exits between the parietal and frontal; an ophthalmic nerve that exits through a foramen in the parietal, a unique character; and numerous (>20) small maxillary teeth.

Biology Xenodermatines are a small group of peculiar snakes, generally living in moist forest habitats. They are small to moderate-sized, slender-bodied snakes; the maximum TL is less than 800 mm, but most individuals and species are less than 550 mm TL. All are secretive snakes, probably nocturnal, and either forest-floor or low arboreal foragers. The little dietary data available suggest that they are opportunistic carnivores and that vertebrates are their major prey. Limited reproductive data indicate that all are oviparous and have small clutch sizes, reportedly four or fewer eggs.

References Manthey and Grossmann, 1997; Smith, 1943; Zhao and Adler, 1993.

Xenodontinae

Sister taxon Uncertain, possibly all other Colubridae exclusive of Xenodermatinae.

Content Over 90 genera, *Adelphicos*, *Alsophis*, *Amastridium*, *Antillophis*, *Apostolepis*, *Arrhyton*, *Atractus*, *Boiruna*, *Calamodontophis*, *Carphophis*, *Cercophis*, *Chersodromus*, *Clelia*, *Coniophanes*, *Conophis*, *Contia*, *Crisantophis*, *Cryophis*, *Darlingtonia*, *Diadophis*, *Diaphorolepis*, *Dipsas*, *Ditaxodon*, *Drepanoides*, *Echinanthera*, *Elapomorphus*, *Emmochiliopis*, *Enuliophis*, *Enulius*, *Eridiphas*, *Erythrolamprus*, *Farancia*, *Geophis*, *Gomesophis*, *Helicops*, *Heterodon*, *Hydrodynastes*, *Hydromorphus*, *Hydrops*, *Hypsiglena*, *Hypsirhynchus*, *Ialtris*, *Imantodes*, *Leptodeira*, *Lioheterophis*, *Liophis*, *Lystrophis*, *Manolepis*, *Ninia*, *Nothopsis*, *Opisthoplus*, *Oxyrhopus*, *Parapostolepis*, *Phalotris*, *Philodryas*, *Phimophis*, *Pliocercus*, *Pseudablabes*, *Pseudoboa*, *Pseudoeryx*, *Pseudoleptodeira*, *Pseudotomodon*, *Psomophis*, *Ptycophis*, *Rhachidelus*, *Rhadinaea*, *Rhadinophanes*, *Saphenophis*, *Sibon*, *Sibynomorphus*, *Siphlophis*, *Sordellina*, *Synophis*, *Tachymenis*, *Taeniophallus*, *Tantalophis*, *Thalesius*, *Thamnodynastes*, *Tomodon*, *Tretanorhinus*, *Trimetopon*, *Tripanurgos,* *Tropidodipsas*, *Tropidodryas*, *Umbrivaga*, *Uromacer*, *Uromacerina*, *Urotheca*, *Waglerophis*, *Xenodon*, *Xenopholis,* and *Xenoxybelis*, with 540+ species.

Distribution Americas.

Biology Xenodontines are highly diverse in body form, ecology, and behavior. Most xenodontines are small to moderate-sized snakes (less than 800 mm adult TL); less than a dozen genera have adults greater than 1 m SVL, for example, *Alsophis*, *Clelia*, *Farancia*, *Hydrodynastes,* and *Uromacer.* Body form ranges from small and slender (*Diadophis*) to heavy-bodied (*Xenodon*) and racerlike (*Philodryas*). Arboreal xenodontines display two body forms. Diurnal hunters have long, muscular bodies and elongate, pointed heads (e.g., *Uromacer*), whereas nocturnal searchers are slender-bodied and have blunt oversized heads (e.g., *Dipsas*, *Imantodes*). They occur in all habitats but marine ones, although some taxa are aquatic in freshwater. Some species burrow, while others are terrestrial or arboreal. A majority of the species appear to be generalists or dietary opportunists that eat predominantly small vertebrates. Some species are prey specialists, such as the snail- and slug-eating *Dipsas* and *Sibon.* Xenodontines are predominantly oviparous. Clutch size generally has a direct association with body size and ranges from small clutches of 1 to 3 eggs (*Imantodes cenchoa*) to over 100 eggs (*Farancia abacura*).

Comment Generic content is derived from Zaher's (1999) Dipsadinae, Dipsadinae *incertae sedis*, Xenodontinae, and Xenodontinae *incertae sedis.*

References Cadle, 1984; Ernst and Barbour, 1989b; Lancini and Kornacker, 1989; Pérez-Santos and Moreno, 1991; Starace, 1998; Zaher, 1999.

Elapidae

Cobras, kraits, seasnakes, death adders, and allies

Classification Reptilia; Diapsida; Sauria; Lepidosauria; Squamata.

Sister taxon Uncertain, possibly Colubridae or Atractaspididae.

Content Two subfamilies, Elapinae and Hydrophiinae.

Distribution Southern North America to southern South America, Africa, southern Asia to southern Australia, and the tropical Indian and Pacific oceans (Fig. 21.22).

Characteristics Elapids are venomous snakes that have an erect fang anteriorly on each maxillary bone. Cranially, they have only a left carotid artery, edentulous premaxillaries, longitudinally oriented, shortened maxillaries with anterior teeth that are large and tubular, and optic foramina that usually perforate the frontal–parietal–parasphenoid sutures. The mandible lacks a coronoid bone, and the dentary bears teeth. No cranial infrared receptors occur in pits or surface indentations. The girdle and limb elements are absent externally and internally. Intracostal arteries arise from the dorsal aorta at intervals of several trunk segments. The left lung is greatly reduced or absent; a tracheal lung is commonly present in the marine taxa and absent in terrestrial ones. Left and right oviducts are well developed.

Comments Slowinski and colleagues (1997) show that elapids consist of an African–American–Asian clade (Elapinae) and an Australian seasnake clade (Hydrophiinae). Keogh's data (1998) indicate that the Elapinae are paraphyletic, because *Bungarus* and the hydrophiines are the sister group to all other elapids. Most recent analyses agree that the two marine snake clades (seakraits or *Laticauda*, and *Hydrophis* and other seasnakes) arose independently from within the Australian terrestrial elapids; however, Rasmussen's study (1997) suggests the possibility of three independent origins of marine snakes. The recognized genera of elapids follow the checklist of David and Ineich (1999).

References David and Ineich, 1999; Grandison, 1977; Keogh, 1998; Rasmussen, 1997; Slowinski et al., 1997; Underwood, 1967; Wallach, 1985, 1998.

"Elapinae"

Sister taxon Hydrophiinae or the clade containing hydrophiines and *Bungarus*.

Content Seventeen genera, *Aspidelaps*, *Boulengerina*, *Bungarus*, *Calliophis*, *Dendroaspis*, *Elapsoidea*, *Hemachatus*, *Hemibungarus*, *Homoroselaps*, *Maticora*, *Micruroides*, *Micrurus*, *Naja*, *Ophiophagus*, *Paranaja*, *Pseudohaje*, and *Walterinnesia*, with 130+ species.

Distribution Americas, Africa, and Eurasia through the East Indies to the Philippines.

Characteristics The palatine bones have choanal processes, except in *Dendroaspis*.

Biology Elapines comprise a moderately diverse group of predominantly terrestrial snakes (Fig. 21.23). Of the 17 genera, only two African taxa (mambas, *Dendroaspis*; tree cobras, *Pseudohaje*) are arboreal, and only the African *Boulengerina* is aquatic. The remainder of the taxa are semifossorial (*Aspidelaps*, *Calliophis*, *Micrurus*) and surface foragers (*Bungarus*, *Naja*). The semifossorial or surface-litter foragers are commonly brightly patterned (aposematic), presumably to alert potential

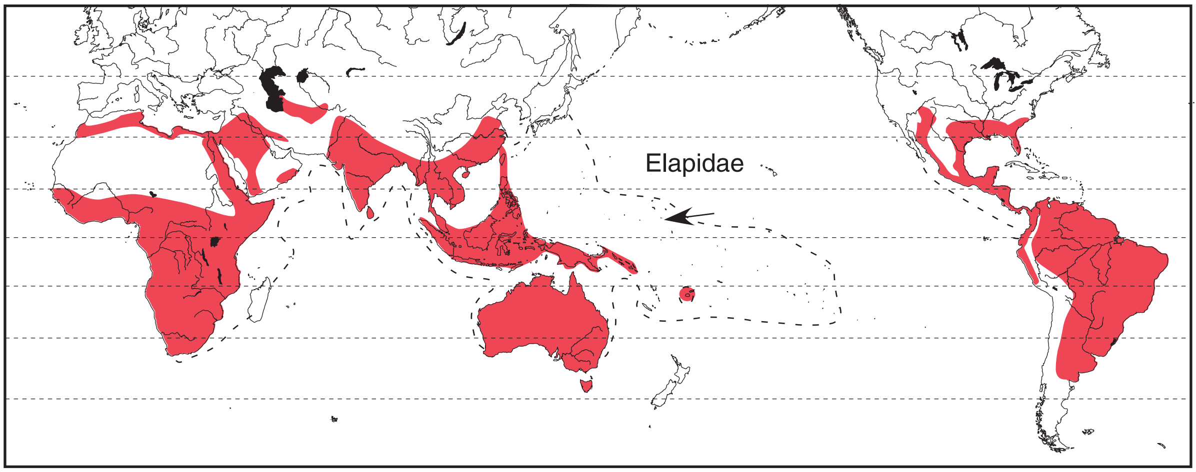


FIGURE 21.22 Geographic distribution of the extant Elapidae.

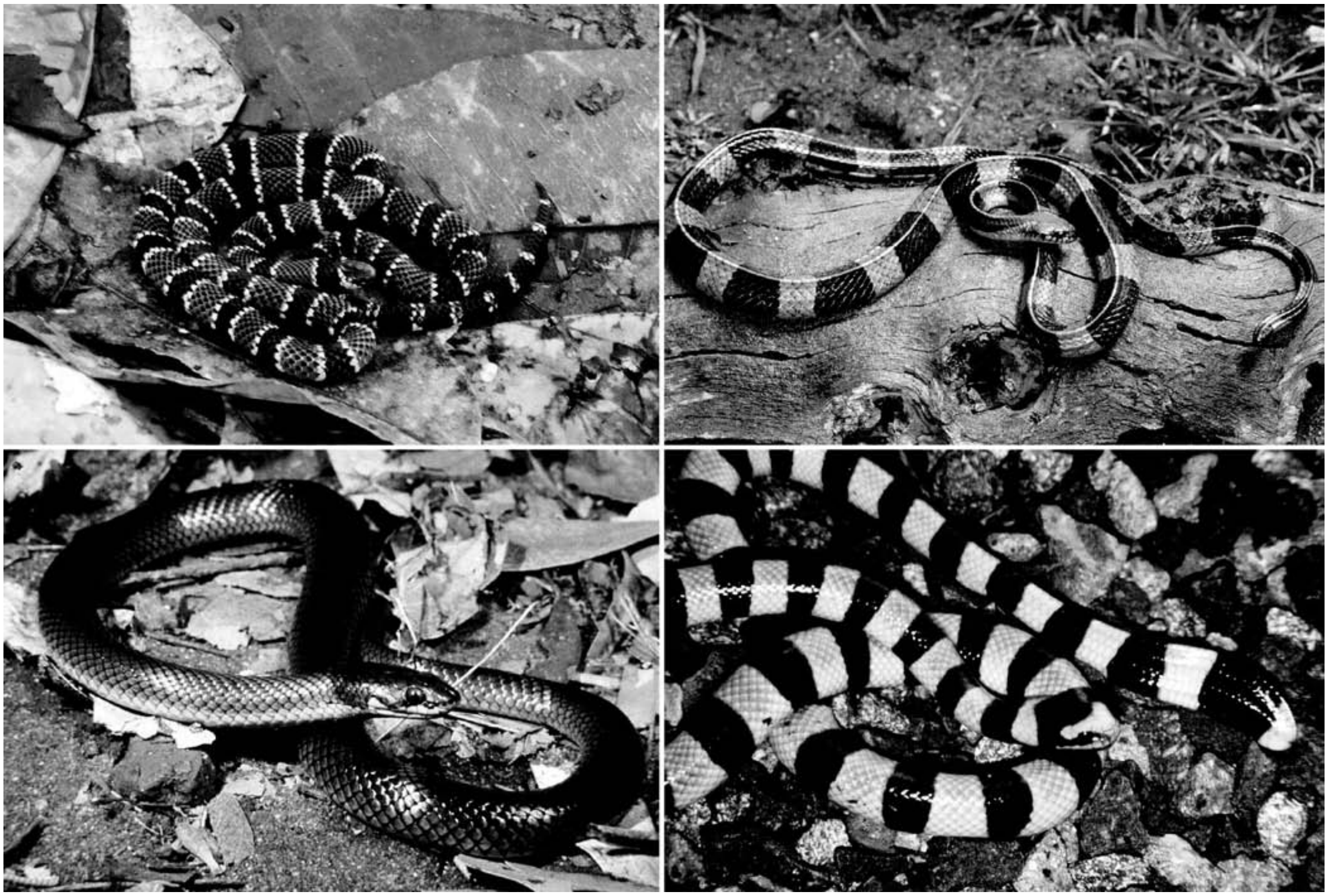


FIGURE 21.23 Representative elapid snakes. Clockwise from upper left: Langsdorff's coralsnake *Micrurus langsdorffi*, Elapinae (photograph by L. J. Vitt); banded krait *Bungarus fasciatus*, Elapinae (R. W. Murphy); yellow-lipped seakrait *Laticauda colubrina*, Hydrophiinae (G. R. Zug); and curl snake *Suta suta*, Hydrophiinae (T. Schwaner).

predators of their venomous bite, and most are called coralsnakes. Adult size in elapines ranges from small (less than 500 mm TL) for some of the semifossorial taxa to the very large king cobra, *Ophiophagus*, which attains lengths to 5.8 m. Adults of most species are less than 4 m TL. The kraits and the various cobras commonly range in adult TL from 1 to 2 m. All elapines are mainly vertebrate predators; for example, *Boulengerina* eats exclusively fish, *Micrurus* mainly snakes and lizards, *Hemachatus* anurans, and *Dendroaspis* birds and mammals. Elapines are mostly oviparous, but a few species are viviparous (e.g., *Hemachatus*). Clutch size is generally associated with body size; smaller species tend to produce 10 or fewer eggs, and the larger species commonly produce more than 20 eggs.

References Branch, 1988; Cox et al., 1998; Manthey and Grossmann, 1997; Pitman, 1974; Roze, 1996.

Hydrophiinae

Sister taxon Elapinae.

Content Forty-three genera, *Acalyptophis*, *Acanthophis*, *Aipysurus*, *Aspidomorphus*, *Astrotia*, *Austrelaps*, *Cacophis*, *Demansia*, *Densonia*, *Drysadalia Echiopsis*, *Elapognathus*, *Emydocephalus*, *Enhydrina*, *Ephalophis*, *Furina*, *Hemiaspis*, *Hoplocephalus*, *Hydrelaps*, *Hydrophis*, *Kerilia*, *Kolphophis*, *Lapemis*, *Laticauda*, *Loveridgelaps*, *Micropechis*, *Notechis*, *Ogmodon*, *Oxyuranus*, *Parahydrophis*, *Parapistocalamus*, *Pelamis*, *Praescutata*, *Pseudechis*, *Pseudonaja*, *Rhinoplocephalus*, *Salomonelaps*, *Simoselaps*, *Suta*, *Thalassophis*, *Toxicocalamus*, *Tropidechis,* and *Vermicella*, with 165+ species.

Distribution Papua-Australia and tropical Indian and Pacific oceans.

Characteristics The palatine bones lack choanal processes.

Biology The hydrophiines contain terrestrial and aquatic taxa (Fig. 21.23). The aquatic group contains two clades, both of which are marine and show distinct adaptations for an aquatic existence. The terrestrial species include semifossorial and surface foragers. A few surface foragers (e.g., *Tropidechis*) occasionally climb low in shrubs or trees, but none is truly arboreal; the same situation exists for the taxa that forage in or near water (e.g., *Notechis ater*), for they are at best semiaquatic. These terrestrial taxa range from small snakes (200–400 mm adult SVL, *Drysadalia*) to large ones (0.8–2.2 m SVL, *Oxyuranus*). Their prey is composed nearly exclusively of vertebrates and lizards. Terrestrial hydrophiines include both oviparous and viviparous species.

The "true" seasnakes include a diverse array of genera (14; e.g., *Aipysurus*, *Hydrophis*, *Thalassophis*). All are totally aquatic; their laterally compressed bodies, paddle-like tail, and loss of enlarged ventral scales and associated muscular links make them incapable of terrestrial locomotion. Most species are 750 mm to 1.5 m SVL (maximum to 2.7 m TL, *Hydrophis spiralis*). Even though they eat mostly fish, they are often specialists, eating only certain types of fish or fish of a limited size range. Surprisingly, they largely avoid invertebrates. All seasnakes are viviparous, and birth occurs in the water. Litter size varies from 1 to 30, but most species produce litters of fewer than 10 neonates.

The seakraits, *Laticauda*, occupy the middle ground between the terrestrial hydrophiines and the seasnakes. Aside from less reduced ventral scales than the seasnakes, they regularly come ashore and have good terrestrial locomotion. As egg layers, they must lay their eggs on land, and *Laticauda colubrina* seemingly always comes ashore to digest its food, mainly eels. In spite of a large adult size (0.8–1.0 m SVL), they produce moderate-sized clutches of 1 to 10 eggs.

References Greer, 1997; Heatwole, 1999; Heatwole and Cogger, 1993; Heatwole and Guinea, 1993; Rasmussen, 1997; Shea et al., 1993; Voris and Voris, 1995.

Glossary

This glossary does not attempt completeness; rather we include potentially unfamiliar words that are not defined when they first appear in the text. Abbreviations: adj, adjective; n, noun; pl, plural; v, verb.

A

abiotic [adj] All nonliving components of the environment, e.g., weather and geology.

alate [adj] State of having wings; also used as a noun in reference to the winged, mating stage of ants and termites.

allele See chromosome.

amniote [n] A tetrapod that arises developmentally from an amniotic egg, e.g., reptiles, birds, and mammals.

amphicoelous See vertebral structure.

amplexus [n], amplex [v], amplectant [adj], amplectic [adj] The "copulatory" behavior of frogs in which the male sits on the female's back and grasps her with his forelimbs; amplexus can be inguinal (forefeet grasping body immediately in front of hindlimbs), axillary (immediately behind forelimbs), cephalic (on head or neck), straddled (male sits on shoulders of female while frogs are vertical and sperm flows down the female's back), or glued (male is attached to females back by adhesive substance). In amplexus, the cloacae of the male and female are adpressed and sperm and eggs are extruded simultaneously. Amplexus is absent in some frogs.

anamniote [n] A tetrapod that lacks an amniotic egg in its development, e.g., amphibians.

anosmic [adj] Unable to smell; absence of the olfactory sense.

anterior [adj] See body location.

arciferal [adj] The anuran pectoral girdle architecture with the epicoracoids of the left and right side fused anteriorly and free and overlapping posteriorly.

auditory meatus [n] The ear canal, either external or internal.

aufwuchs [n] The aquatic community of microorganisms living on the surface of submerged objects. Aufwuchs form a coating, often slimy, on which numerous animals, such as tadpoles, graze.

Australian See biogeographic realms.

autopod See limb segments.

axilla [n], axillary [adj] See body location.

B

Bidder's organ A band or cap of ovarian tissue on the testis of male bufonids.

biogeographic realms The major divisions of the world's terrestrial areas, based on shared endemism of plants and animals.

- **Australian [adj, n]** The biogeographic area of New Guinea and adjacent islands, and Australia and adjacent islands.
- **Ethiopian [adj, n]** The biogeographic area of Saharan and sub-Saharan Africa and the southern half of the Arabian Peninsula.
- **Gondwana** The southern continent arising from the breakup of Pangaea consisting of the future Antarctica, South America, Africa, Australia, and New Zealand.
- **Holarctic [adj, n]** The biogeographic area composed of the Nearctic and Palearctic.

Laurasia The northern continent arising from the breakup of Pangaea consisting of the future North America, Greenland, and Eurasia.

Nearctic [adj, n] The biogeographic area of North America including the Mexican Plateau.

Neotropical [adj, n] The biogeographic area of Central America (excluding the Mexican Plateau), South America, and the Greater and Lesser Antilles.

Oriental [adj, n] Southern Asia, south of the Himalayan mountains and their east and west neighboring mountain ranges from the Indus Valley eastward through southern China and southward to the Seram–Halmahera seas.

Palearctic [adj, n] The biogeographic area of Europe, Africa north of the Sahara, and Asia north of the Himalayan mountains and their east and west neighboring mountain ranges.

Pangaea The megacontinent of the Paleozoic period containing all the continental blocks that would become our present continents. Pangaea began to break up in the early Mesozoic.

biota [n], biotic [adj] All living components of the environment.

bipedal See locomotion.

body location

anterior [adj] The front or head end of an animal.

axilla [n], axillary [adj] At the forelimb insertion.

distal [adj] Toward the tip of an extremity, i.e., most distant from the body.

dorsum [n], dorsal [adj] The top or upper surface of an animal.

inguen [n], inguinal [adj] At the hindlimb insertion.

lateral [adj] The side of an animal.

posterior [adj] The rear or tail end of an animal.

proximal [adj] Toward the origin of an extremity, i.e., closest to the body.

venter [n], ventral [adj] The underside or lower surface of an animal.

C

carnivore See diet.

chromosomes

alleles [n] The different forms of a gene occurring at the same position on different, homologous chromosomes.

diploid [adj] Possessing the typical number of chromosomes following the fusion of the sperm and ovum pronuclei, i.e., a pair each of homologous chromosomes is present. Symbol, 2N.

haploid [adj] Possessing one-half of the homologous chromosomes; the condition obtained by meiotic division to produce sex gametes. Symbol, 1N.

heterozygosity [n], heterozygous [adj] The genetic state in which two different alleles occur at the same position or locus on homologous chromosomes.

homozygosity [n], homozygous [adj] The genetic state in which two identical alleles occur at the same position or locus on homologous chromosomes.

karyotype [n], karyotypic [adj] The chromosome set of an organism and its structural characteristics.

polyploid [adj] Possessing more than two sets of homologous chromosomes.

triploid [adj] Possessing three sets of homologous chromosomes. Symbol, 3N.

clade [n] A group of organisms containing an ancestor and all its descendants.

classification

node name or node-based name This classification category name labels a clade stemming from the immediate common ancestor of two or more designated descendants.

sister group [n] The taxon sharing the most recent common ancestor with another taxon. A pair of taxa sharing the same common ancestor.

stem name or stem-based name This classification category name labels a clade of all taxa that are more closely related to a specified set of descendants than to any other taxa.

congeners [n], congeneric [adj] Individuals, populations, or species of the same genus.

conspecifics [n], conspecific [adj] Individuals or populations of the same species.

crèche [n] Nest chamber.

D

deme See population.

detritovore See diet.

development

direct A developmental pattern in which an egg hatches into a miniature adult body form; no larval stage occurs and development is complete or nearly so prior to hatching.

indirect A developmental pattern in which an egg hatches into a larva; the larva is free-living and grows and develops further prior to metamorphosing into a miniature adult body form.

diet

carnivore [n], carnivorous [adj] A flesh-eating organism.

detritovore [n], detritivorous [adj] A detritus-eating organism.

durophagous [adj] Eating hard-bodied prey; often used in herpetology for snakes and lizards preying on skinks or related lizards armored with osteoderms beneath scales.

folivore [n], folivorous [adj] A foliage-eating organism.

frugivore [n], frugivorous [adj] A fruit-eating organism.

herbivore [n], herbivorous [adj] A plant-eating organism.

insectivore [n], insectivorous [adj] An insect-eating organism, although commonly used for eating any arthropod.

molluscivore [n], molluscivorous [adj] A mollusk-eating organism.

nectivore [n], nectivorous [adj] A nectar-eating organism.

omnivore [n], omnivorous [adj] An organism that consumes a variety of plant and animal matter.

diplasiocoelous See vertebral structure.

diploid See chromosomes.

distal See body location.

diverse [adj] Having numerous, different aspects, such as body forms, courtship behaviors, or temperature or habitat tolerances.

dorsum See body location.

durophagous [adj] See diet.

E

edentate, edentulous [adj] Lacking teeth.

epipodium See limb segments.

Ethiopian See biogeographic realms.

exaptation [n] A structure, behavior, or physiological feature of an organism that serves one function in an ancestor but serves a new and different function in a descendant. A replacement word for the situation previously called preadaptation.

exostosis [n] The condition of a bone having a rugose surface, commonly arising from the fusion of bone and dermis or osteoderms.

extant [adj, n] The state of a population or species of being alive now; not extinct.

F

fertilization [n] The penetration of the ovum's cell membrane by the sperm and the fusion of the sperm and ovum pronuclei to reestablish a diploid state.

external The condition when the sperm and ovum come in contact external to the reproductive tract or cloaca of a female.

internal The condition when the sperm and ovum come in contact within the reproductive tract or cloaca of a female.

firmisternal [adj] The anuran pectoral girdle architecture with the left and right epicoracoids fused anteriorly and posteriorly.

folivore See diet.

fossorial [adj] Living underground; not all fossorial animals are burrowers but instead may use preexisting holes and cavities in the earth.

frugivore See diet.

G

gait See locomotion.

Gondwana See biogeographic realms.

grade [n] A group of organisms that possess a similar adaptative level of organization.

H

habitus [n] The body shape or form of an organism, i.e., its general appearance.

haploid See chromosomes.

hatchling [n] An animal recently hatched from an egg. The duration of the hatchling state is variable, although its end in reptiles might be fixed by the disappearance of the yolk-sac scar.

heliophilic [adj] Sun-loving.

heliothermic [adj] Deriving heat from the sun.

herbivore See diet.

heterozygosity See chromosome.

Holarctic See biogeographic realms.

holochordal See vertebral structure.

homozygosity See chromosome.

hydroperiod [n] A cycle characterized by a period of dryness; often used in amphibian biology in reference to the period when an ephemeral pond has water.

I

inguen [n], inguinal [adj] See body location.

insectivore See diet.

K

karyotype See chromosomes.

L

lateral See body location.

Laurasia See biogeographic realms.

limb segments

autopod [n] The distal part of the limb, including the mesopodium, metapodium, and the phalanges.

epidpodium [n], epipodial [adj] The second segment of the limb, including either the radius and ulna or the tibia and fibula. Zeugopod is a synonym.

mesopodium [n] The third segment of the limb, including either the wrist bones (carpus) or the ankle bones (tarsus).

metapodium [n] A distal segment of the limb, including either the metacarpal or the metatarsal elements.

propodium [n], propodial [adj] The most proximal segment of the limb, including either the humerus or the femur. Stylopod is a synonym.

locomotion

bipedal [adj] Moving on two limbs.

gait [n] The pattern of limb movement.

quadrupedal [adj] Moving on four limbs.

rectilinear locomotion [n] A mode of limbless locomotion dependent upon a wavelike pattern of rib movement to move the animal forward.

saltatory [adj] Moving by jumping, either bipedally or quadrupedally.

serpentine [adj] A mode of limbless, undulatory locomotion in which all portions of the body pass along the same path and use the same frictional surfaces for pushing the body forward.

sidewinding [adj] A specialized mode of serpentine locomotion in which only two parts of the body touch the ground simultaneously.

undulatory [adj] A group of limbless locomotion patterns in which the body moves through a series of curves.

M

manus [n] Hand or forefoot.

meiosis [n], meiotic [adj] Gametic cell division in which the number of chromosomes in a sex cell is halved.

mesic [adj] Habitat with moderate moisture level or water availability; adapted to moist conditions.

Mesoamerica [n] The portion of Central America from central Mexico to Nicaragua.

mesopodium See limb segments.

metapodium See limb segments.

metapopulation See population.

mitosis [n], mitotic [adj] Regular, nongametic cell division in which each homologous chromosome duplicates itself; when the cell and nucleus divide, the sister cells retain their original ploidy or number of chromosomes.

molluscivore See diet.

monoestrous [adj] Having a single gametogenic cycle within a single reproductive season. See also polyestrous.

monophyly [n], monophyletic [adj] A taxonomic group whose members share the same ancestor. See also clade, paraphyly, and polyphyly.

morph [n] A particular body form or colored group of individuals. Morph is used regularly in discussion of polymorphism and variation of individuals within a population or species.

morphology [n], morphological [adj] The study of an organism's form or shape, or the shape of one or more of an organism's parts.

N

Nearctic See biogeographic realms.

nectivore See diet.

neonate [n] An animal recently born, i.e., it has emerged from the female's reproductive tract.

Neotropical See biogeographic realms.

nictitating membrane Same as palpebral membrane.

node-based names See classification.

notochordal See vertebral structure.

O

omnivore See diet.

opisthocoelous See vertebral structure.

Oriental See biogeographic realms.

oviposit [v] To lay eggs.

P

palpebral membrane [n] A transparent "eyelid" that lies beneath the true eyelids and can extend horizontally from its resting position in the inner corner of the eye to the outer corner.

Palearctic See biogeographic realms.

Pangaea See biogeographic realms.

panmixis [n], panmictic [adj] Random and unrestricted mating within a population, thereby allowing the interchange of genes among all parts of a population.

paraphyly [n], paraphyletic [adj] A taxonomic group containing most but not all taxa derived from the same ancestor. See also monophyly and polyphyly.

perennibranchiate [adj] The retention of external (larval) gills as an adult.

periphyton [n] A synonym of aufwuchs; see above.

pes [n] Foot, specifically the hindfoot.

pheromone [n] A chemical signal secreted by one animal that conveys specific information to another animal, usually a conspecific, and often elicits a specific behavioral and/or physiological response.

phylogenesis [n], phylogenetic [adj] The evolutionary history of a taxon.

phytotelma, phytotelmata [pl, n] Small bodies of water within or on plants, e.g., pools in bromeliads.

polyestrous [adj] Having two or more gametogenic cycles within a single reproductive season. See also monoestrous.

polyphyly [n], polyphyletic [adj] A taxonomic group whose members do not share the same ancestor. See also grade, monophyly, and paraphyly.

polyploid See chromosomes.

population

- **deme [n]** A small local population, panmictic in concept if not in actuality.
- **metapopulation [n]** A population of several to many smaller populations or demes in the same geographic area; the smaller populations potentially exchange members by migration.
- **population [n]** All individuals of the same species within a prescribed area.

posterior See body location.

postmetamorph [n] An amphibian that has recently completed metamorphosis, or the entire life stage following metamorphosis, in contrast to the larval or premetamorphic stage.

primitive [adj, n] A character or condition that is the same as an ancestral character or condition.

procoelous See vertebral structure.

propodium See limb segments.

proximal See body location.

Q

quadrupedal See locomotion.

R

rectilinear locomotion See locomotion.

rupicolous [adj] Living on walls or rocks.

S

salps [n, pl] Free-swimming, oceanic tunicates in the genus *Salpa* with transparent, fusiform bodies.

saltatory See locomotion.

saxicolous [adj] Living on or among rocks.

serpentine See locomotion.

sidewinding See locomotion.

sister group See classification.

speciose [adj] A taxon with many species.

spermatheca [n] A chamber for storing spermatozoa, usually multibranched, in the wall of some female salamanders.

spermatophore [n] A mucoid pedestal to support the sperm packets of some male salamanders; it is produced in the cloaca.

stegochordal See vertebral structure.

stem name See classification.

supraciliary [adj] Above the eye; eyebrow area.

SVL [n] Snout-vent length; straight-line distance from the tip of the snout to the anterior edge of the vent.

T

taxon, taxa [pl, n] All members of a taxonomic group of organisms, e.g., *Anolis*, all members of all species classified in this particular genus.

tectorial membrane [n] A membrane in the inner ear covering a patch of sensory hairs.

TL [n] Various; used for Tail Length or Total Length. For tail length, it is distance from posterior edge of the vent to the tip of the tail, and for total length, distance from tip of snout to tip of tail.

trackway [n] A fossilized trail of footprints.

triploid See chromosomes.

tympanum, tympana [pl, n] Eardrum.

U

undulatory See locomotion.

urticating hairs [n] Defensive hairlike structures that break off the surface of an organism and cause irritation to the attacking herbivore or predator.

V

venter, ventral See body location.

vertebral structure

- **amphicoelous [adj]** A vertebra in which the centrum is concave on both the anterior and the posterior surface.
- **diplasiocoelous [adj]** The condition of the vertebral column with seven procoelous presacral vertebrae, the eighth presacral vertebra is biconcave, and the sacral vertebra is biconvex posteriorly.
- **holochordal [adj]** Structurally, a centrum in which the notochord has been totally replaced.
- **notochordal [adj]** Structurally, a centrum in which a small remnant of the notochord remains in the center of the centrum.
- **opisthocoelous [adj]** A vertebra in which the centrum is convex on the anterior surface and concave on the posterior surface.

procoelous [adj] A vertebra in which the centrum is concave on the anterior surface and convex on the posterior surface.

stegochordal [adj] Structurally, a flattened centrum in which only the dorsal portion of the notochordal sheath has ossified.

X

xeric [adj] Habitat with low moisture level or water availability; adapted to dry or arid conditions.

REFERENCES

Lincoln, R. J., et al. (1982). “A Dictionary of Ecology, Evolution and Systematics.” Cambridge Univ. Press, Cambridge.

Lincoln, R. J., and Boxshall, G. A. (1987). “The Cambridge Illustrated Dictionary of Natural History.” Cambridge Univ. Press, Cambridge.

Peters, J. A. (1964). “Dictionary of Herpetology.” Hafner Publ. Co., New York.

Bibliography

Adams, C. S., and Cooper, W. E., Jr. (1988). Oviductal morphology and sperm storage in the keeled earless lizard, *Holbrookia propinqua*. *Herpetologica* **44:** 190–197.

Adler, K. (1970). The role of extraoptic photoreceptors in amphibian rhythms and orientation: A review. *J. Herpetol.* **4:** 99–112.

Adler, K. (1976). Extraocular photoreception in amphibians. *Photochem. Photobiol.* **23:** 275–298.

Adler, K., and Phillips, J. B. (1991). Orientation in a desert lizard (*Uma notata*): Time compensated compass movement and polarotaxis. *J. Comp. Physiol.* **156:** 547–552.

Adler, K., and Taylor, D. H. (1973). Extraocular perception of polarized light by orienting salamanders. *J. Comp. Physiol.* **87:** 203–212.

Adler, K., and Zhao, E. (1990). Studies on hynobiid salamanders, with description of a new genus. *Asiatic Herpetol. Res.* **3:** 37–45.

Adler, K., Zhao, E., and Darevsky, I. S. (1992). First records of the pipe snake (*Cylindrophis*) in China. *Asiatic Herpetol. Res.* **4:** 37–41.

Adolf, E. F. (1932). The vapor tension relations of frogs. *Biol. Bull.* **62:** 112–125.

Affenberg, W. (1982). Feeding strategy of the Caicos ground iguana, Cyclura carinata. *In* "Iguanas of the World. Their Behavior, Ecology, and Conservation." (G. M. Burghardt and A. S. Rand, Eds.), pp. 84–116. Park Ridge, New Jersey, Noyes Publ.

Agassiz, L. (1857). "Contributions to the Natural History of the United States of America. Vol. I. Part I. Essay on Classification. Part II. North American Testudinata. Vol. II., Part III. Embryology of the Turtle." Little, Brown and Co., Boston.

Aguirre, A. A., Spraker, T. R., Balazs, G. H., and Zimmerman, B. (1998). Spirorchidiasis and fibropapillomatosis in green turtles from the Hawaiian Islands. *J. Wildl. Disease* **34:** 91–98.

Ahlberg, P. E. (1995). *Elginerpeton pancheni* and the earliest tetrapod clade. *Nature* **373:** 420–425.

Ahlberg, P. E., and Milner, A. R. (1994). The origin and the early diversification of tetrapods. *Nature* **368:** 507–514.

Alberts, A. C. (1992). Pheromonal self-recognition in the desert iguana. *Copeia* **1992:** 229–232.

Albino, A. M. (1996). The South American fossil Squamata (Reptilia: Lepidosauria). *In* "Contributions of Southern South America to Vertebrate Paleontology" (G. Arratia, Ed.), pp. 185–202. *Müncher Geowiss. Abh. A* **30.**

Alcala, A. C., and Brown, W. C. (1987). Notes on the microhabitat of the Philippine discoglossid frog *Barbourula*. *Silliman J.* **34:** 12–17.

Alcala, A. C., Ross, C. A., and Alcala, E. L. (1987/1988). Observations on reproduction and behavior of captive Philippine crocodiles (*Crocodylus mindorensis* Schmidt). *Silliman J.* **34:** 18–28.

Alcock, J. (1998). "Animal Behavior." Sinauer Associates, Inc., Sunderland, MA.

Aleksiuk, M., and Gregory, P. T. (1974). Regulation of seasonal mating behavior in *Thamnophis sirtalis parietalis*. *Copeia* **1974:** 681–689.

Alifanov, V. R. (1993). New lizards of Maerocephalosauridae from the Upper Cretaceous of Mongolia, with some critical comments to the classification of Teiidae (sensu Estes, 1983). *Zool. Zhur.* **1993:** 57–74. [In Russian]

Altig, R., and Johnston, G. F. (1986). Major characteristics of free-living anuran tadpoles. *Smith. Herpetol. Info. Serv.* **67:** 1–75.

Altig, R., and Johnston, G. F. (1989). Guilds of anuran larvae: Relationships among developmental modes, morphologies, and habitats. *Herpetol. Monog.* **3:** 81–109.

Amato, G., and Gatesy, J. (1994). PCR assays of variable nucleotide sites for identification of conservation units. *In* "Ecology and Evolution: Approaches and Applications" (B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle, Eds.), pp. 215–226. Birkhauser Verlag, Basel.

Ananjeva, N. B., Borkin, L. Y., Darevsky, I. S., and Orlov, N. L. (1988). "Dictionary of Animal Names in Five Languages. Amphibians and Reptiles." Russky Yazyk Publ., Moscow.

Anderson, J. D. (1967). A comparison of the life histories of coastal and montane populations of *Ambystoma macrodactylum* in California. *Am. Midl. Nat.* **77:** 323–355.

Anderson, R. A. (1993). An analysis of foraging in the lizard, *Cnemidophorus tigris. In* "Biology of Whiptail Lizards (Genus *Cnemidophorus*)" (J. W. Wright and L. J. Vitt, Eds.), pp. 83–116. Oklahoma Mus. Nat. Hist., Norman, OK.

Anderson, R. A., and Karasov, W. H. (1981). Contrasts in energy intake and expenditure in sit- and-wait and widely foraging lizards. *Oecologia* **49:** 67–72.

Anderson, R. A., and Vitt, L. J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* **84:** 145–157.

Andrews, R. M. (1976). Growth rate in island and mainland anoline lizards. *Copeia* **1976:** 477–482.

Andrews, R. M. (1979). Reproductive effort of female *Anolis limifrons* (Sauria: Iguanidae). *Copeia* **1979:** 620–626.

Andrews, R. M. (1982a). Patterns of growth in reptiles. *In* "Biology of the Reptilia, Volume 13. Physiology D" (C. Gans and F. H. Pough, Eds.), pp. 273–320. Academic Press, London.

Andrews, R. M. (1982b). Spatial variation in egg mortality of the lizard *Anolis limifrons. Herpetologica* **38:** 165–171.

Andrews, R. M., and Rand, A. S. (1974). Reproductive effort in anoline lizards. *Ecology* **55:** 1317–1327.

Andrews, R. M., and Wright, S. J. (1994). Long-term population fluctuations of a tropical lizard: A test of causality. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 267–285. Princeton Univ. Press, Princeton, NJ.

Arnold, E. N. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *J. Nat. Hist.* **18:** 127–169.

Arnold, E. N. (1986). Mite pockets of lizards, a possible means of reducing damage by ectoparasites. *Biol. J. Linn. Soc.* **29:** 1–21.

Arnold, E. N. (1988). Caudal autotomy as a defense. *In* "Biology of the Reptilia. Volume 16, Ecology B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 235–273. Alan R. Liss, Inc., New York.

Arnold, E. N. (1989). Towards a phylogeny and biogeography of the Lacertidae: Relationships within an Old-World family of lizards derived from morphology. *Bull. Brit. Mus. Nat. Hist. (Zool.)* **55:** 209–257.

Arnold, E. N. (1993). Phylogeny and the Lacertidae. *In* "Lacertids of the Mediterranean Region: A Biological Approach" (E. D. Valakos, W. Böhme, V. Pérez-Mellado, and P. Maragou, Eds.), pp. 1–16. Hellenic Zoological Society, Athens.

Arnold, E. N. (1998). Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey. *Bull. Brit. Mus. Nat. Hist. (Zool.)* **64:** 63–89.

Arnold, S. J. (1982). A quantitative approach to antipredator performance: Salamander defenses against snake attack. *Copeia* **1982:** 247–253.

Arnold, S. J., and Duvall, D. (1994). Animal mating systems: A synthesis based on selection theory. *Am. Nat.* **143:** 317–348.

Arntzen, J. W., and García-París, N. (1995). Morphological and allozyme studies of midwife toads (genus *Alytes*), including the description of two new taxa from Spain. *Contrib. Zool.* **65:** 5–34.

Asana, J. J. (1931). The natural life history of *Calotes versicolor* (Boulenger), the common blood sucker. *J. Bombay Nat. Hist. Soc.* **34:** 1041–1047.

Ash, A. N. (1997). Disappearance and return of salamanders to clearcut plots in the southern Blue Ridge mountains. *Conserv. Biol.* **11:** 983–989.

Ash, A. N., and Bruce, R. C. (1994). Impact of timber harvesting on salamanders. *Conserv. Biol.* **8:** 300–301.

Ashe, J. S., and Marx, H. (1988). Phylogeny of the viperine snakes (Viperinae): Part II. Cladistic analysis and major lineages. *Fieldiana, Zool.* **52:** 1–23.

Ashton, R. E. (1975). A study of movement, home range, and winter behavior of *Desmognathus fuscus. J. Herpetol.* **9:** 85–91.

Ashton, R. E., Jr. (1990). *Necturus lewisi* Brimley. *Catalog. Am. Amphib. Rept.* **456:** 1–2.

Atsatt, S. R. (1939). Color changes as controlled by temperature and light in the lizards of the desert regions of southern California. *Univ. Calif., Los Angeles Publ. Biol. Sci.* **1:** 237–276.

Auffenberg, W. (1965). Sex and species discrimination in two sympatric South American tortoises. *Copeia* **1965:** 335–342.

Auffenberg, W. (1978). Social and feeding behavior in *Varanus komodoensis. In* "Behavior and Neurology of Lizards" (N. Greenberg and P. D. MacLean, Eds.), pp. 301–331. Natl. Inst. Mental Health, Poolesville, MD.

Auffenberg, W. (1981). "The Behavioral Ecology of the Komodo Dragon." Univ. Press of Florida, Gainesville, FL.

Auffenberg, W. (1988). "Gray's Monitor Lizard." Univ. Press of Florida, Gainesville, FL.

Auffenberg, W. (1994). "The Bengal Monitor." Univ. Press of Florida, Gainesville, FL.

Auffenberg, W., and Weaver, W. G. (1969). *Gopherus berlandieri* in southeastern Texas. *Bull. Florida State Mus.* **13:** 141–203.

Autumn, K., and Han, B. (1989). Mimicry of scorpions by juvenile lizards, *Teratoscincus roborowskii* (Gekkonidae). *Chin. Herpetol. Res.* **2:** 60–64.

Autumn, K., Weinstein, R. B., and Full, R. J. (1994). Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol. Zool.* **67:** 238–262.

Averianov, A., and Danilov, I. (1996). Agamid lizards (Reptilia, Sauria, Agamidae) from the Early Eocene of Kyrgyzstan. *N. Jb. Geol. Paläont. Mh.* **1996:** 739–750.

Avila, L. J., Acosta, J. C., and Marotri, R. A. (1992). Composición, variación, anual y estacional de la dieta de *Teius suquiensis* (Sauria: Teiidae) en la provincia de Córdoba (Argentina). *Caud. Herpetol.* **7:** 5–13.

Avila-Pires, T. C. S. (1995). Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zool. Verh., Leiden* **299:** 1–706.

Ayala, S. C. (1977). Plasmodia of reptiles. *In* "Parasitic Protozoa. Volume 3: Gregarines, Haemogregarines, Coccidia, Plasmodia, and Haemoprotids" (J. P. Kreier, Ed.). Academic Press, New York.

Bachman, M. D. (1984). Defensive behavior of brooding female red-backed salamanders, *Plethodon cinereus. Herpetologica* **40:** 436–443.

Backwell, P. R. Y., and Passmore, N. (1990). Polyandry in the leaf-folding frog, *Afrixalus delicatus. Herpetologica* **46:** 7–10.

Badenhorst, A. (1978). The development and the phylogeny of the organ of Jacobson and the tentacular apparatus of *Ichthuphis glutinosus* (Linné). *Ann. Univ. van Stellenbosch* **1:** 1–26.

Báez, A. M. (1996). The fossil record of the Pipidae. *In* "The Biology of *Xenopus*" (R. C. Tinsley and H. R. Kobel, Eds.), pp. 329–347. Zool. Soc. London, London.

Báez, A. M., and Basso, N. G. (1996). The earliest known frogs of the Jurassic of South America: Review and cladistic appraisal of their relationships. *In* "Contributions of Southern South America to Vertebrate Paleontology" (G. Arratia, Ed.), pp. 131–158. *Müncher Geowiss. Abh. A* **30.**

Báez, A. M., and Pugener, L. A. (1998). A new Paleogene pipid frog from northwestern Patagonia. *J. Vert. Paleontol.* **18:** 511–524.

Báez, A. M., and Trueb, L. (1997). Redescription of the Paleogene *Shelania pascuali* from Patagonia and its bearing on the relationships of fossil and Recent pipoid frogs. *Sci. Pap., Nat. Hist. Mus. Univ. Kansas* **4:** 1–41.

Bagnara, J. T. (1986). Pigment cells. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 136–149. Springer Verlag, Berlin.

Bagnara, J. T., and Rastogi, R. K. (1992). Reproduction in the Mexican leaf frog, *Pachymedusa dacnicolor.* In "Reproductive Biology of South American Vertebrates" (W. C. Hamlett, Ed.), pp. 98–111. Springer-Verlag, New York.

Baird, I. L. (1970). The anatomy of the reptilian ear. *In* "Biology of the Reptilia. Volume 2. Morphology B" (C. Gans and T. S. Parsons, Eds.), pp. 193–275. Academic Press, London.

Balinsky, J. B. (1981). Adaptations of nitrogen metabolism to hyperosmotic environments in Amphibia. *J. Exp. Zool.* **215:** 335–350.

Ballinger, R. E. (1977). Reproductive strategies: Food availability as a source of proximal variation in a lizard. *Ecology* **58:** 628–635.

Ballinger, R. E., Lemos-Espinal, J., Sanoja-Sarabia, S., and Coady, N. R. (1995). Ecological observations of the lizard, *Xenosaurus grandis* in Cuautlapán, Veracruz, México. *Biotropica* **27:** 128–132.

Barandun, J. (1995). "Reproductive Ecology of *Bombina variegata* (Amphibia)." Inaugural-Dissertation der Universität Zürich, Zürich.

Barbault, R. (1972). Les peuplements d'amphibiens des savanes de Lamto (Cote-d'Ivoire). *Ann. Univ. Abidjan, Ser. E* **5:** 59–142.

Barbault, R. (1975a). Les peuplements de lézards des savanes de Lamto (Cote-d'Ivoire). *Ann. Univ. Abidjan, Ser. E* **8:** 147–221.

Barbault, R. (1975b). Observations écologiques sur la reproduction des lézards tropicaux: Les stratégies de ponte en forêt en an savane. *Bull. Soc. Zool. France* **100:** 153–168.

Barbault, R. (1976a). Population dynamics and reproductive patterns of three African skinks. *Copeia* **1976:** 483–490.

Barbault, R. (1976b). Notes sur la composition et la diversité spécifiques d'une herpétocénose tropicale (Bouaké, Côte d'Ivoire). *Bull. I. F. A. N.* **38A:** 445–456.

Barbault, R., and Mou, Y. -P. (1988). Population dynamics of the common wall lizard, *Podarcis muralis,* in southwestern France. *Herpetologica* **44:** 38–47.

Barbault, R., and Rodrigues, M. T. (1978). Observations sur la reproduction et la dynamique des populations de quelques anoures tropicaux. II. *Phrynobatrachus plicatus. Geo.-Eco.-Trop.* **2:** 455–466.

Barbault, R., and Rodrigues, M. T. (1979). Observations sur la reproduction et la dynamique des populations de quelques anoures tropicaux. III. *Arthroleptis poecilonotus. Trop. Ecol.* **20:** 64–77.

Barbour, R. W., Harvey, M. J., and Hardin, J. W. (1969). Home range, movements, and activity of the eastern worm snake, *Carphophis amoenus amoenus. Ecology* **50:** 470–476.

Barker, D. G., and Barker, T. M. (1994). "Pythons of the World. Volume 1, Australia." The Herpetocultural Library, Lakeside, CA.

Barker, J., Grigg, G., and Tyler, M. (1995). "A Field Guide to Australian Frogs." Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Barthalmus, G. T., and Bellis, E. D. (1972). Home range, homing and the homing mechanism of the salamander, *Desmognathus fuscus. Copeia* **1974:** 632–642.

Bartholomew, G. A. (1982). Physiological control of body temperature. *In* "Biology of the Reptilia. Volume 12. Physiology C. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 167–211. Academic Press, New York.

Bauchot, R., Ed. (1994). "Les Serpents." Bordas, Paris.

Bauer, A. M. (1990). Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn. Zool. Monog.* **30:** 1–218.

Bauer, A. M. (1994). Gekkonidae (Reptilia, Sauria). Part I. Australia and Oceania. *Tierreich* **109:** 1–306.

Bauer, A. M. (1997). Peritoneal pigmentation and generic allocation in the Chamaeleonidae. *Afr. J. Herpetol.* **46:** 117–123.

Bauer, A. M. (1999). Twentieth century amphibian and reptile discoveries. *Cryptozoology* [1997–1998] **13:** 1–17.

Bauer, A. M., Russell, A. P., and Shadwick, R. E. (1989). Mechanical properties and morphological correlates of fragile skin in gekkonid lizards. *J. Exp. Biol.* **145:** 79–102.

Bauer, A. M., Russell, A. P., and Dollahon, N. R. (1990). Skin folds in the gekkonid genus *Rhacodactylus:* A natural test of the damage limitation hypothesis of mite pocket function. *Can. J. Zool.* **68:** 1196–1201.

Bauer, A. M., Russell, A. P., and Dollahon, N. R. (1993). Function of the mite pockets of lizards: A reply to E. N. Arnold. *Can. J. Zool.* **71:** 865–868.

Bauwens, D., Garland, T. J., Castilla, A. M., and Damme, R. V. (1995). Evolution of sprint speed in lacertid lizards: Morphological, physiological, and behavioral covariation. *Evolution* **49:** 848–863.

Baverstock, P. R., King, D., King, M., Birrell, J., and Krieg, M. (1993). The evolution of species of the Varanidae: Microcomplement fixation analysis of serum albumins. *Aust. J. Zool.* **41:** 621–638.

Beaupre, S. J., and Duvall, D. J. (1998). Integrative biology of rattlesnake. Contributions to biology and evolution. *BioScience* **48:** 531–538.

Bechtel, H. B., and Bechtel, E. (1991). Scaleless snakes and a breeding report of scaleless *Elaphe obsoleta linheimeri. Herpetol. Rev.* **22:** 12–14.

Beck, D. D, and Lowe, C. H. (1991). Ecology of the beaded lizard, *Heloderma horridum,* in a tropical dry forest in Jalisco, México. *J. Herpetol.* **25:** 395–406.

Beebee, T. J. C. (1996). "Ecology and Conservation of Amphibians." Chapman & Hall, London.

Bell, B. D. (1978). Observations on the ecology and reproduction of the New Zealand leiopelmid frogs. *Herpetologica* **34:** 340–354.

Bell, B. D. (1985). Development and parental-care in the endemic New Zealand frogs. *In* "Biology of Australasian Frogs and Reptiles" (G. Grigg, R. Shine, and H. Ehmann, Eds.), pp. 269–278. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Bell, B. D. (1994). A review of the status of New Zealand *Leiopelma* species (Anura: Leiopelmatidae), including a summary of demographic studies in Coromandel and Maud Island. *NZ J. Zool.* **21:** 341–349.

Bell, C. J., Mead, J. I., and Fay, L. P. (1995). Neogene history of *Anniella* Gray, 1852 (Squamata, Anniellidae), with comments on postcranial osteology. *Copeia* **1995:** 719–726.

Bell, E. L. (1955). An aggregation of salamanders. *Proc. Penn. Acad. Sci.* **24:** 265–66.

Bell, G. (1980). The costs of reproduction and their consequences. *Am. Nat.* **116:** 45–76.

Bell, G. L., Jr. (1997). A phylogenetic revision of North American and Adriatic Mosasauroidea. *In* "Ancient Marine Reptiles" (J. M. Callaway and E. L. Nicholls, Eds.), pp. 281–332. Academic Press, San Diego.

Bellairs, A. d'A. (1969). "The Life of Reptiles. Volumes I & II." Weidenfeld & Nicolson, London.

Bellairs, A. d'A., and Kamal, A. M. (1981). The chondrocranium and the development of the skull in Recent reptiles. *In* "Biology of the Reptilia. Volume 11. Morphology F" (C. Gans and T. S. Parsons, Eds.), pp. 1–263. Academic Press, London.

Benabib, M. (1994). Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis. Herpetol. Monog.* **8:** 160–180.

Benabib, M., and Congdon, J. D. (1992). Metabolic and water-flux rates of free-ranging tropical lizards *Sceloporus variabilis. Physiol. Zool.* **65:** 788–802.

Bennett, A. F. (1980). The metabolic foundations of vertebrate behavior. *BioScience* **30:** 452–456.

Bennett, A. F. (1982). The energetics of reptilian activity. *In* "Biology of the Reptilia. Volume 13. Physiology D. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 155–199. Academic Press, New York.

Bennett, A. F., and Gleeson, T. T. (1979). Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus. Copeia* **1979:** 573–577.

Bennett, D. (1998). "Monitor Lizards. Natural History, Biology & Husbandry." Edition Chimaira, Frankfurt a. M.

Bentley, P. J. (1966). The physiology of the urinary bladder of Amphibia. *Biol. Rev.* **41:** 275–316.

Bentley, P. J., and Blumer, W. F. C. (1962). Uptake of water by the lizard, *Moloch horridus. Nature* **194:** 699–700.

Benton, M. J. (1991). Amniote phylogeny. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 317–330. Comstock Publ. Assoc., Ithaca, NY.

Benton, M. J. (1994). Late Triassic to Middle Jurassic extinctions among continental tetrapods: Testing the pattern. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 366–397. Cambridge Univ. Press, New York.

Benton, M. J. (1997a). "Vertebrate Paleontology," 2nd ed. Chapman & Hall, London.

Benton, M. J. (1997b). Origin and early evolution in dinosaurs. *In* "The Complete Dinosaur" (J. O. Farlow and M. K. Brett-Surman, Eds.), pp. 204–215. Indiana Univ. Press, Bloomington.

Benton, M. J., and Clark, J. M. (1988). Archosaur phylogeny and the relationships of Crocodylidae. *In* "The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds" (M. J. Benton, Ed.), pp. 295–338. Clarendon Press, Oxford.

Berger, L. (1977). Systematics and hybridization in the *Rana esculenta* complex. *In* "The Reproductive Biology of Amphibians" (D. H. Taylor and S. I. Guttman, Eds.), pp. 367–410. Plenum Press, New York.

Berger, L., and Michalowski, J. (1973). "Keys for the Identification of Vertebrates of Poland. Part 2. Amphibia." Inst. Systematic Zool., Krakow.

Berry, J. F., and Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (order Testudines). *Oecologia* **44:** 185–191.

Berry, P. Y. (1975). "The Amphibian Fauna of Peninsular Malaysia." Tropical Press, Kuala Lumpur.

Bezy, R. L. (1988). The natural history of the night lizards, family Xantusiidae. *In* "Proceedings of the Conference on

California Herpetology" (H. F. De Lisle et al., Eds.), pp. 1–12. Southwest. Herpetol. Soc., Van Nuys, CA.

Bezy, R. L. (1989). Morphological differentiation in unisexual and bisexual xantusiid lizards of the genus *Lepidophyma* in Central America. *Herpetol. Monog.* **3:** 6–80.

Bhatta, G. (1998). A field guide to the caecilians of the Western Ghats, India. *J. Biosci.* **23:** 73–85.

Bickham, J. W., and Carr, J. L. (1983). Taxonomy and phylogeny of the higher categories of cryptodiran turtles based on a cladistic analysis of chromosomal data. *Copeia* **1983:** 918–932.

Billo, R., and Wake, M. H. (1987). Tentacle development in *Dermophis mexicanus* (Amphibia, Gymnophiona) with an hypothesis of tentacle origin. *J. Morphol.* **192:** 101–111.

Billo, R. R., Straub, J. O., and Senn, D. G. (1985). Vivipare Apode (Amphibia: Gymnophiona), *Typhlonectes compressicaudus* (Duméril & Bibron, 1841): Kopulation, Tragziet und Geburt. *Amphibia-Reptilia* **6:** 1–9.

Birkhead, T. R., and Moller, A. P. (1995). Extra-pair copulation and extra-pair paternity in birds. *Anim. Behav.* **49:** 843–848.

Bishop, C. A., and Pettit, K. E., Eds. (1992). Declines in Canadian amphibian populations: Designing a national monitoring strategy. *Can. Wildl. Serv. Occas. Pap.* **76.**

Bishop, S. C. (1941). The salamanders of New York. *N. Y. State Mus. Bull.* 324:1–365.

Bjorndal, K. A. (1980). Nutritional and grazing behavior of the green turtle, *Chelonia mydas. Mar. Biol.* **56**: 147–154.

Bjorndal, K. A. (1987). Digestive efficiency in a temperate herbivorous reptile, *Gopherus polyphemus. Copeia* **1987:** 714–720.

Bjorndal, K. A. (1989). Flexibility of digestive responses in two generalist herbivores, the tortoises *Geochelone carbonaria* and *Geochelone denticulata. Oecologia* **78:** 317–321.

Bjorndal, K. A. (1996). Foraging ecology and nutrition of sea turtles. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 199–231. CRC Press, Boca Raton, FL.

Blackburn, D. (1982). Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia* **3:** 185–205.

Blackburn, D. (1985). Evolutionary origins of viviparity in the Reptilia. II. Serpentes, amphisbaenia, and ichthyosauria. *Amphibia-Reptilia* **6:** 259–291.

Blackburn, D. G. (1993a). Standardized criteria for the recognition of reproductive modes in squamate reptiles. *Herpetologica* **49:** 118–132.

Blackburn, D. G. (1993b). Chorioallantoic placentation in squamate reptiles: Structure, function, development, and evolution. *J. Exp. Zool.* **266:** 414–430.

Blackburn, D. G., and Vitt, L. J. (1992). Reproduction in viviparous South American lizards of the genus *Mabuya. In* "Reproductive Biology of South American Vertebrates" (W. C. Hamlett, Ed.), pp. 150–164. Springer-Verlag, New York.

Blackburn, D. G., Vitt, L. J., and Beuchat, C. A. (1984). Eutherian-like reproductive specializations in a viviparous reptile. *Proc. Natl. Acad. Sci. USA* **81:** 4860–4863.

Blackburn, D. G., Evans, H. E., and Vitt, L. J. (1985). The evolution of fetal nutritional adaptations. *Fortschr. Zool.* **30:** 437–439.

Blair, W. F. (1960). "The Rusty Lizard: A Population Study." Univ. Texas Press, Austin.

Blair, W. F., Ed. (1972). "Evolution in the Genus *Bufo*." Univ. Texas Press, Austin.

Blanc, C. P. (1977). Reptiles, Sauriens Iguanidae. *Faune Madagascar* **45:** 1–195.

Blaylock, L. A., Ruibal, R., and Platt-Aloia, K. (1976). Skin structure and wiping behavior of phyllomedusine frogs. *Copeia* **1976:** 283–295.

Blommers-Schlösser, R. M. A. (1993). Systematic relationships of Mantellinae Laurent 1946 (Anura Ranoidea). *Ethol. Ecol. Evol.* **5:**199–218.

Blommers-Schlösser, R. M. A., and Blanc, Ch. P. (1991). Amphibiens (première partie). *Faune Madagascar* **75:** 1–379.

Blouin, M. S. (1990). Evolution of palatability differences between closely-related treefrogs. *J. Herpetol.* **24:** 309–311.

Boersma, P. D. (1982). The benefits of sleeping aggregations in marine iguanas, *Amblyrhynchus cristatus. In* "Iguanas of the World" (G. M. Burghardt and A. S. Rand, Eds.), pp. 292–299. Noyes Publ., Park Ridge, NJ.

Bogert, C. M. (1993). Preface. *In* "The Gila Monster and Its Allies," Reprint ed., pp. v-xv. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Böhme, W., Ed. (1981). "Handbuch der Reptilien und Amphibien Europas. Band 1. Echsen (Sauria) I." Akad. Verlagsges., Wiesbaden.

Böhme, W., Hutterer, R., and Bings, W. (1985). Die Stimme der Lacertidae, speziell der Canareneidechsen. *Bonn. Zool. Beitr.* **36:** 337–354.

Boiko, V. P. (1984). The participation of chemoreception in the organization of reproductive behavior in *Emys orbicularis* (Testudines, Emydidae). *Zool. Zh.* **63:** 584–589. [English abstract]

Bolt, J. R. (1991). Lissamphibian origins. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 194–222. Comstock Publ. Assoc., Ithaca, NY.

Borkin, L. J., and Anissimova, E. V. (1987). The vertebral structure and vocal sacs in the Caucasian parsley frog (*Pelodytes caucasicus*) and its taxonomic position. *Proc. Zool. Inst., Leningrad* **158:** 59–76. [In Russian]

Boulenger, G. A. (1882). "Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. Second Edition." Trustees of British Museum, London.

Boulenger, G. A. (1893). "Catalogue of the Snakes in the British Museum (Natural History). Vols. I-III." British Museum (Nat. Hist.), London.

Bour, R. (1984). Les tortues terrestres géantes des iles de océan indien occidental: Données géographiques, taxinomiques et phylogénétiques. *Stvd. Geol. Salmanticensia Espec.* **1:** 17–76.

Bourn, D., and Coe, M. (1978). The size, structure and distribution of the giant tortoise population of Aldabra. *Philos. Trans. R. Soc. London, Ser. B* **282:** 139–175.

Bourquin, O., and Sowler, S. G. (1980). The vertebrates of Vernon Crookes Nature Reserve: 1. *Lammergeyer* **28:** 20–32.

Bowen, B. W., and Avise, J. C. (1996). Conservation genetics of marine turtles. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 190–237. CRC Press, Boca Raton, FL.

Bowen, B. W., and Karl, S. W. (1996). Population genetics, phylogeography, and molecular evolution. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 29–50. CRC Press, Boca Raton, FL.

Boycott, R. C. (1988). Evidence of tactile communication during courtship in *Heleophryne* (Anura: Heleophrynidae). *J. Herpetol. Assoc. Afr.* **35:** 12–13.

Boycott, R. C., and de Villiers, A. L. (1986). The status of *Heleophyrne rosei* Hewitt (Anura: Leptodactylidae) on Table Mountain and recommendations for its conservation. *S. Afr. J. Wildl. Res.* **16:** 129–134.

Bragg, A. N. (1965). "Gnomes of the Night." Univ. Pennsylvania Press, Philadelphia.

Braña, F., and Bea, A. (1987). Bimodalite de la reproduction chez *Lacerta vivipara* (Reptilia, Lacertidae). *Bull. Soc. Herp. France* **44:** 1–5.

Branch, B (1988). "Field Guide to the Snakes and Other Reptiles of Southern Africa." Ralph Curtis Books, Sanibel, FL.

Branch, B. (1991). "Everyone's Guide to Snakes of Southern Africa." CNA, Johannesburg.

Branch, L. C. (1983). Social behavior of the tadpoles of *Phyllomedusa vaillanti*. *Copeia* **1983:** 420–428.

Brandão, C. R. F., and Vanzolini, P. E. (1985). Notes on the incubatory inquilinism between Squamata (Reptilia) and the Neotropical fungus-growing ant genus *Acromyrmex* (Hymenoptera: Formicidae). *Pap. Av. Zool. (S. Paulo)* **36:** 31–36.

Brattstrom, B. H. (1963). A preliminary review of the thermal requirements of amphibians. *Ecology* **44:** 238–255.

Brattstrom, B. H. (1965). Body temperature of reptiles. *Am. Midl. Nat.* **73:** 376–422.

Brattstrom, B. H. (1979). Amphibian temperature regulation studies in the field and laboratory. *Am. Zool.* **19:** 345–356.

Brazaitis, P., Watanabe, M. E., and Amato, G. (1998). The caiman trade. *Sci. Am.* **278:** 52–58.

Breckenridge, W. R., Nathanael, S., and Pereira, L. (1987). Some aspects of the biology and development of *Ichthyophis glutinosus* (Amphibia: Gymnophiona). *J. Zool., London* **211:** 437–449.

Breitenbach, G. L. (1982). The frequency of communal nesting and solitary brooding in the salamander, *Hemidactylium scutatum*. *J. Herpetol.* **16:** 341–346.

Breitenbach, G. L., Congdon, J. D., and Van Loben Sels, R. C. (1984). Winter temperatures of *Chrysemys picta* nest in Michigan: Effects on hatchling survival. *Herpetologica* **40:** 76–81.

Brenowitz, E. A., and Rose, G. J. (1999). Female choice and plasticity of male calling behaviour in the Pacific treefrog. *Anim. Behav.* **57:** 1337–1342.

Briggs, J. L., and Storm, R. M. (1970). Growth and population structure of the cascade frog, *Rana cascadae* Slater. *Herpetologica* **26:** 283–300.

Britson, C. A. (1998). Predatory responses of largemouth bass (*Micropterus salmoides*) to conspicuous and cryptic hatchling turtles: A comparative experiment. *Copeia* **1998:** 383–390.

Britson, C. A., and Gutzke, W. (1993). Antipredator mechanisms of hatchling freshwater turtles. *Copeia* **1993:** 435–440.

Broadley, D. G. (1974). Reproduction in the genus *Platysaurus* (Sauria: Cordylidae). *Herpetologica* **30:** 379–380.

Broadley, D. G. (1978). A revision of the genus *Platysaurus* A. Smith (Sauria: Cordylidae). *Occas. Pap. Nat. Mus. Monum. Rhodesia* **6:** 129–185.

Broadley, D. G. (1983). "Fitzsimons' Snakes of Southern Africa." Delta Books, Johannesburg.

Broadley, D. G. (1997a). Family Scincidae. *In* "Proceedings of the Fitzsimons Commemorative Symposium" (J. H. van Dyke, Ed.), pp. 66–75. Herpetol. Assoc. Africa, Matieland, South Africa.

Broadley, D. G. (1997b). Sub-order Amphisbaenia. *In* "Proceedings of the Fitzsimons Commemorative Symposium" (J. H. van Dyke, Ed.), pp. 83–86. Herpetol. Assoc. Africa, Matieland, South Africa.

Brochu, C. A. (1997a). Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Syst. Biol.* **46:** 479–522.

Brochu, C. A. (1997b). A review of "*Leidyosuchus*" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *J. Vert. Paleontol.* **17:** 679–697.

Brochu, C. A. (1999). Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Soc. Vert. Paleontol. Mem.* **6:** 9–100.

Brockelman, W. Y. (1969). An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* **50:** 632–644.

Brockmann, H. J. (1993). Parasitizing conspecifics: Comparisons between Hymenoptera and birds. *Trends Evol. Ecol.* **8:** 2–4.

Brodie, E. D., III. (1993). Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47:** 227–235.

Brodie, E. D., III, and Janzen, F. J. (1995). Experimental studies of coral snake mimicry: Generalized avoidance of ringed snake patterns by free-ranging avian predators. *Funct. Ecol.* **9:** 186–190.

Brodie, E. D., Jr. (1968). Investigation on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. *Am. Midl. Nat.* **80:** 276–280.

Brodie, E. D., Jr., and Brodie, E. D., III. (1980). Differential avoidance of mimetic salamanders by free-ranging birds. *Science* **208:** 181–183.

Brodie, E. D., Jr., and Smatresk, N. J. (1990). The antipredator arsenal of fire salamanders: Spraying of secretions from highly pressurized dorsal skin glands. *Herpetologica* **46:** 1–7.

Brodie, E. D., Jr., Nussbaum, R. A., and Storm, R. M. (1969). An egg-laying aggregation of five species of Oregon reptiles. *Herpetologica* **25:** 223–227.

Brodie, E. D., Jr., Johnson, J. A., and Dodd, C. K., Jr. (1974). Immobility as a defensive behavior in salamanders. *Herpetologica* **30:** 79–85.

Brodmann, P. (1987). "Die Giftschlangen Europas und die Gattung *Vipera* in Afrika und Asien." Kümmerly-Frey, Bern.

Brown, H. A. (1975). Temperature and development of the tailed frog, *Ascaphus truei. Comp. Biochem. Physiol.* **50A:** 397–405.

Brown, H. A. (1989). Developmental anatomy of the tailed frog (*Ascaphus truei*): A primitive frog with large eggs and slow development. *J. Zool., London* **217:** 525–537.

Brown, J. L., and Orians, G. H. (1970). Spacing patterns in mobile animals. *Ann Rev. Ecol. Syst.* **1:** 239–262.

Brown, W. M, and Krauss, F. (1998). Phylogenetic relationships of colubroid snakes based on mitochondrial DNA sequences. *Zool. J. Linn. Soc.* **122:** 455–487.

Brown, W. S. (1993). Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): A guide for conservation. *Herpetol. Circ.* **22:** 1–78.

Brown, W. S., and Parker, W. S. (1984). Growth, reproduction and demography of the racer, *Coluber constrictor mormon,* in northern Utah. *Mus. Nat. Hist., Univ. Kansas Spec. Publ.* **10:** 13–40.

Bruce, R. C. (1988a). An ecological life table for the salamander *Eurycea wilderae. Copeia* **1988:** 15–26.

Bruce, R. C. (1988b). Life history variation in the salamander *Desmognathus quadramaculatus. Herpetologica* **44:** 218–227.

Brust, D. G. (1993). Maternal brood care by *Dendrobates pumilio:* A frog that feeds its young. *J. Herpetol.* **27,** 96–98.

Brygoo, É. R., and Roux-Estève, R. (1983). *Feylinia,* genre de lézards africains de la famille des Scincidae, sous-famille des Feyliniinae. *Bull Mus. Natn. Hist. Nat., Paris, 4e Sér.* **5:** 307–341.

Buffetaut, E. (1989). Evolution. *In* "Crocodiles and Alligators" (C. A. Ross, Ed.), pp. 26–41. Golden Press, Silverwater, N.S.W.

Bull, C. M. (1988). Mate fidelity in an Australian lizard *Trachydosaurus rugosus. Behav. Ecol. Sociobiol.* **23:** 45–49.

Bull, C. M. (1994). Population dynamics and pair fidelity in sleepy lizards. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 159–174. Princeton Univ. Press, Princeton, NJ.

Bull, C. M., and Bagurst, B. C. (1998). Home range overlap of mothers and their offspring in the sleepy lizard, *Tiliqua rugosa. Behav. Ecol. Sociobiol.* **42:** 357–362.

Bull, C. M., and Burzacott, D. (1993). The impact of tick load on the fitness of their lizard hosts. *Oecologia* **96:** 415–419.

Bull, C. M., and Pamula, Y. (1998). Enhanced vigilance in monogamous pairs of the lizard, *Tiliqua rugosa. Behav. Ecol.* **9:** 452–455.

Bull, C. M., Cooper, S. J. B., and Baghurst, B. C. (1998). Social monogamy and extra-pair fertilization in an Australian lizard, *Tiliqua rugosa. Behav. Ecol. Sociobiol.* **44:** 63–72.

Bull, J. J. (1980). Sex determination in reptiles. *Quart. Rev. Biol.* **55:** 3–21.

Bull, J. J. (1987). Evolution of phenotypic variance. *Evolution* **41:** 303–315.

Bunnell, P. (1973). Vocalizations in the territorial behavior of the frog, *Dendrobates pumilio. Copeia* **1973:** 277–284.

Burbrink, F. T., Phillips, C. A., and Heske, E. J. (1998). A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. *Biol. Conserv.* **86:** 107–115.

Burger, J., and Zappalorti, R. T. (1986). Nest site selection by pine snakes, *Pituophis melanoleucus,* in the New Jersey Pine Barrens. *Copeia* **1986:** 116–121.

Burggren, W. W. (1987). Form and function in reptilian circulations. *Am. Zool.* **27:** 5–19.

Burghardt, G. M., and Rand, A. S. (1982). "Iguanas of the World: Their Behavior, Ecology, and Conservation." Noyes Publ., Park Ridge, NJ.

Burke, A. C. (1989). Development of the turtle carapace: Implications for the evolution of a novel bauplan. *J. Morphol.* **199:** 363–378.

Burke, R. L. (1991). Relocations, repatriations, and translocations of amphibians and reptiles: Taking a broader view. *Herpetologica* **47:** 350–357.

Burke, R. L., Ewert, M. A., McLemore, J. B., and Jackson, D. R. (1996). Temperature-dependent sex determination and hatching success in the gopher tortoise (*Gopherus polyphemus*). *Chelonian Conserv. Biol.* **2:** 86–88.

Burke, V. J., and Gibbons, J. W. (1995). Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina bay. *Conserv. Biol.* **9:** 1365–1369.

Burke, V. J., Nagle, R. D., Osentoski, M., and Congdon, J. D. (1993). Common snapping turtles association with ant mounds. *J. Herpetol.* **27:** 114–115.

Burke, V. J., Greene, J. L., and Gibbons, J. W. (1995). The effect of sample size and study duration on metapopulation estimates for slider turtles (*Trachemys scripta*). *Herpetologica* **51:** 451–456.

Burns, G., Ramos, A., and Muchlinski, A. (1996). Fever response in North American snakes. *J. Herpetol.* **30:** 133–139.

Burrage, B. R. (1973). Comparative ecology and behavior of *Chamaeleo pumilus pumilus* (Gmelin) & *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). *Ann. S. Afr. Mus.* **61:** 1–158.

Burton, T. C. (1986). A reassessment of the Papuan subfamily Asterophryinae (Anura: Microhylidae). *Rec. S. Aust. Mus.* **19:** 405–450.

Burton, T. C., and Zweifel, R. G. (1995). A new genus of genyophrynine microhylid frog from New Guinea. *Am. Mus. Novitates* **3129:** 1–7.

Burton, T. M., and Likens, G. E. (1975). Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest. *Ecology* **56:** 1068–1080.

Bury, R. B., and Corn, P. S. (1988). Douglas-fir forests in the Oregon and Washington Cascades: Abundance of terrestrial herpetofauna. *USDA Forest Serv. Tech. Rep.* **RM166:** 11–22.

Bury, R. B., and Whelan, J. A. (1984). Ecology and management of the bullfrog. *U.S. Fish Wildl. Serv. Resour. Publ.* **155:** 1–23.

Busack, S. D. (1977). Zoogeography of amphibians and reptiles in Cádiz Province, Spain. *Ann. Carnegie Mus.* **46:** 285–316.

Busse, K. (1970). Care of the young by male *Rhinoderma darwini. Copeia* **1970:** 395.

Bustard, H. R. (1967). Gekkonid lizards adapt fat storage to desert environments. *Science* **158:** 1197–1198.

Buth, D. G. (1984). The application of electrophoretic data in systematic studies. *Ann. Rev. Ecol. Syst.* **15:** 501–522.

Cadle, J. E. (1984). Molecular systematics of Neotropical xenodontine snakes. III. Overview of xenodontine phylogeny and the history of New World snakes. *Copeia* **1984:** 641–652.

Cadle, J. E. (1987). Geographic distribution: Problems in phylogeny and zoogeography. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Siegel, J. T. Collins, and S. S. Novak, Eds.), pp. 77–105. Macmillan Publ. Co., New York.

Cadle, J. E. (1992). Phylogenetic relationships among vipers: Immunological evidence. *In* "Biology of the Pitvipers" (J. A. Campbell and E. D. Brodie, Jr., Eds.), pp. 41–48. Selva, Tyler, TX.

Cadle, J. E. (1994). The colubrid radiation in Africa (Serpentes: Colubridae): Phylogenetic relationships and evolutionary patterns based on immunological data. *Biol. J. Linn. Soc.* **110:** 103–140.

Cadle, J. E., and Greene, H. W. (1993). Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblages. *In* "Species Diversity in Ecological Communities: Historical and Geographical Perspectives" (R. E. Ricklefs and D. Schluter, Eds.), pp. 281–293. Chicago Univ. Press, Chicago.

Cadle, J. E., Dessauer, H. C., Gans, C., and Gartside, D. F. (1990). Phylogenetic relationships and molecular evolution in uropeltid snakes (Serpentes: Uropeltidae): Allozymes and albumin immunology. *Biol. J. Linn. Soc.* **40:** 293–320.

Caldwell, J. P. (1982). Disruptive selection: A tail color polymorphism in *Acris* tadpoles in response to differential predation. *Can. J. Zool.* **60:** 2818–2827.

Caldwell, J. P. (1987). Demography and life history of two species of chorus frogs (Anura: Hylidae) in South Carolina. *Copeia* **1987:** 114–127.

Caldwell, J. P. (1989). Structure and behavior of *Hyla geographica* tadpole schools, with comments on classification of group behavior in tadpoles. *Copeia* **1989:** 938–950.

Caldwell, J. P. (1992). Diversity of reproductive modes in anurans: Facultative nest construction in gladiator frogs. *In* "Reproductive Biology of South American Vertebrates" (W. C. Hamlett, Ed.), pp. 85–97. Springer-Verlag, New York.

Caldwell, J. P. (1993). Brazil nut fruit capsules as phytotelmata: Interactions among anuran and insect larvae. *Can. J. Zool.* **71:** 1193–1201.

Caldwell, J. P. (1994). Natural history and survival of eggs and early larval stages of *Agalychnis calcarifer* (Anura: Hylidae). *Herpetol. Nat. Hist.* **2:** 57–66.

Caldwell, J. P. (1996a). The evolution of myrmecophagy and its correlates in poison frogs (family Dendrobatidae). *J. Zool., London* **240:** 75–101.

Caldwell, J. P. (1996b). Diversity of Amazonian anurans: The role of systematics and phylogeny in identifying macroecological and evolutionary patterns. *In* "Neotropical Biodiversity and Conservation" (A. Gibson, Ed.), pp. 73–88. *Occas. Pap. Mildred E. Mathias Bot. Garden* **1.**

Caldwell, J. P. (1997). Pair bonding in spotted poison frogs. *Nature* **385:** 211.

Caldwell, J. P., and Hoogmoed, M. S. (1998). Allophrynidae, *Allophryne, A. ruthveni. Catalog. Am. Amphib. Rept.* **661:** 1–3.

Caldwell, J. P., and Lopez, P. T. (1989). Foam-generating behavior in tadpoles of *Leptodactylus mystaceus. Copeia* **1989:** 498–502.

Caldwell, J. P., and Oliveira,V. R. L. (1999). Determinants of biparental care in the spotted poison frog, *Dendrobates vanzolinii* (Anura: Dendrobatidae). *Copeia* **1999:** 565–575.

Caldwell, J. P., and Vitt, L. J. (1999). Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. *Oikos* **84:** 383–397.

Caldwell, J. P., Thorpe, J. H., and Jervey, T. O. (1980). Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia* **46:** 285–289.

Caldwell, M. W. (1996). Ichthyosauria: A preliminary phylogenetic analysis of diapsid affinities. *N. Jb. Geol. Paläont. Abh.* **200:** 361–386.

Caldwell, M. W., and Lee, M. S. Y. (1997). A snake with legs from the marine Cretaceous of the Middle East. *Nature* **386:** 705–709.

Callaway, J. M. (1997). Introduction. *In* "Ancient Marine Reptiles" (J. M. Callaway and E. L. Nicholls, Eds.), pp. 3–16. Academic Press, San Diego.

Cambar, R., and Gipouloux, J.-D. (1956). Table chronologique du développement embryonnaiore et larvaire du crapaud commun: *Bufo bufo* L. *Bull. Biol. France Belgique* **90:** 198–217.

Camp, C. L. (1923). Classification of the lizards. *Bull. Am. Nat. Hist.* **48:** 289–481.

Campbell, J. A., and Brodie, E. D., Jr., Eds. (1992). "Biology of the Pitvipers." Selva, Tyler, TX.

Campbell, J. A., and Camarillo R. J. A. (1992). The Oaxacan dwarf boa, *Exiliboa placata* (Serpentes: Tropidophiidae): Descriptive notes and life history. *Carib. J. Sci.* **28:** 17–20.

Campbell, J. A., and Frost, D. R. (1993). Anguid lizards of the genus *Abronia*: Revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. *Bull. Am. Nat. Hist.* **216:** 1–121.

Campbell, J. A., and Lamar, W. W. (1989). "The Venomous Reptiles of Latin America." Comstock Publ. Assoc., Ithaca, NY.

Campbell, J. A., and Quinn, H. R. (1975). Reproduction in a pair of Asiatic cobras, *Naja naja* (Serpentes, Elapidae). *J. Herpetol.* **9:** 229–233.

Cann, J. (1998). "Australian Freshwater Turtles." Beaumont Publ. Pte Ltd., Singapore.

Cann, J., and Legler, J. M. (1994). The Mary River tortoise: A new genus and species of short-necked chelid from Queensland, Australia (Testudines; Pleurodira). *Chelonian Conserv. Biol.* **1:** 81–96.

Cannatella, D. C., and de Sá, R. O. (1993). *Xenopus laevis* as a model organism. *Syst. Biol.* **42:** 476–507.

Cannatella, D. C., and Trueb, L. (1988a). Evolution of pipoid frogs: Intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zool. J. Linn. Soc.* **94:** 1–38.

Cannatella, D. C., and Trueb, L. (1988b). Evolution of pipoid frogs: Morphology and phylogenetic relationships of *Pseudhymenochirus. J. Herpetol.* **22:** 439–456.

Capranica, R. R. (1986). Morphology and physiology of the auditory system. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 551–575. Springer Verlag, Berlin.

Carpenter, C. C. (1953). A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. *Ecology* **34:** 74–80.

Carpenter, C. C. (1957). Hibernation, hibernacula and associated behavior of three toed box turtle (*Terrapene carolina triunguis*). *Copeia* **1957:** 278–282.

Carpenter, C. C. (1961). Patterns of social behavior in the desert iguana, *Dipsosaurus dorsalis. Copeia* **1961:** 396–405.

Carpenter, C. C. (1977). Communication and displays of snakes. *Am. Zool.* **17:** 217–223.

Carr, A. F., Jr. (1940). A contribution to the herpetology of Florida. *Univ. Florida Publ., Biol. Sci. Ser.* **3:** 1–118.

Carr, A. F., Jr., and Ogren, L. (1960). The ecology and migrations of sea turtles, 4: The green turtle in the Caribbean Sea. *Bull. Am. Mus. Nat. Hist.* **121:** 1–48.

Carroll, R. L. (1988). "Vertebrate Paleontology and Evolution." W. H. Freeman & Co., New York.

Carroll, R. L. (1991). The origin of reptiles. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 331–353. Comstock Publ. Assoc., Ithaca, NY.

Carroll, R. L. (1995). Problems of the phylogenetic analysis of Paleozoic choanates. *Bull. Mus. Natl. Hist. Nat., Paris* **7:** 389–445.

Carroll, R. L., and Wild, R. (1994). Marine members of the Sphenodontia. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 70–83. Cambridge Univ. Press, New York.

Case, T. J. (1976a). Body size differences between populations of the chuckwalla, *Sauromalus obesus. Ecology* **57:** 313–323.

Case, T. J. (1976b). Seasonal aspects of thermoregulatory behavior in the chuckwall, *Sauromalus obesus* (Reptilia, Lacertilia,: Iguanidae). *J. Herpetol.* **10:** 85–95.

Case, T. J., Bolger, D. T., and Richman, A. D. (1992). Reptilian extinctions: The last ten thousand years. *In* "Conservation Biology" (P. L. Fledler and S. K. Jain, Eds.), pp. 91–125. Chapman and Hall, New York.

Castanet, J., and Baez, M. (1991). Adaptation and evolution in *Gallotia* lizards from the Canary Islands: Age, growth, maturity and longevity. *Amphibia-Reptilia* **12:** 81–102.

Castanet, J., Newman, D. G., and Saint Girons, H. (1988). Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus,* on Stephens and Lady Alice islands, New Zealand. *Herpetologica* **44:** 25–37.

Catton, W. T. (1976). Cutaneous mechanoreceptor. *In* "Frog Neurobiology. A Handbook." (R. Llinás and W. Precht , Eds.), pp. 629–642. Springer-Verlag, Berlin.

Caughley, G., and Gunn, A. (1996). "Conservation Biology in Theory and Practice." Blackwell Science, Cambridge, MA.

Cayot, L. J., and Morillo, G. E. (1998). Rearing and repatriation of Galápagos tortoises: *Geochelone nigra hoodensis,* a case study. *In* "Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference" [1997] (J. V. Abbema, Ed.), pp. 178–183. New York Turtle and Tortoise Society, New York.

Cecil, S. G., and Just, J. J. (1979). Survival rate, population density and development of a naturally occurring anuran larvae (*Rana catesbeiana*). *Copeia* **1979:** 447–453.

Cei, J. M. (1980). Amphibians of Argentina. *Monit. Zool. Italiano, N. S. Monog.* **2:** 1–609.

Cei, J. M. (1993). Reptiles del nord, nordeste y este de la Argentina. Herpetofauna de las selvas subtropicales, puna y pampas. *Mus. Reg. Sci. Nat.-Torino Monog.* **14:** 1–949.

Censky, E. J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva plei. Behaviour* **132:** 529–557.

Censky, E. J. (1996). The evolution of sexual size dimorphism in the teiid lizard *Ameiva plei:* A test of alternative hypotheses. *In* "Contributions to West Indian Herpetology: A tribute to Albert Schwartz" (R. Powell and R. W. Henderson, Eds.), pp. 277–289. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Censky, E. J. (1997). Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). *Behav. Ecol. Sociobiol.* **40:** 221–225.

Channing, A. (1989). A re-evaluation of the phylogeny of Old World treefrogs. *S. Afr. Tydskr. Dierk.* **24:** 116–131.

Channing, A. (1995). The relationship between *Breviceps* (Anura: Microhylidae) and *Hemisus* (Hemisotidae) remains equivocal. *J. Herpetol. Assoc. Afr.* **44:** 55–57.

Channing, A., du Preez, L., and Passmore, N. (1994). Status, vocalization and breeding biology of two species of African bullfrogs (Ranidae: *Pyxicephalus*). *J. Zool., London* **234:** 141–148.

Choudhury, B. C., and Choudhury, S. (1986). Lessons from the crocodile reintroduction projects in India. *Indian Forest.* **112:** 881–890.

Christian, K. A. (1996). Solar absorptance of some Australian lizards and its relationship to temperature. *Aust. J. Zool.* **44:** 59–67.

Christian, K., and Bedford, G. (1993). High reproductive expenditure per progeny in geckos relative to other lizards. *J. Herpetol.* **27:** 351–354.

Christian, K., and Bedford, G. S. (1995). Physiological consequences of filarial parasites in the frillneck lizard, *Chlamydosaurus kingii,* in northern Australia. *Can. J. Zool.* **73:** 2302–2306.

Christian, K., and Parry, D. (1997). Reduced rates of water loss and chemical properties of skin secretions of the frogs *Litoria caerulea* and *Cyclorana australis. Aust. J. Zool.* **45:** 13–20.

Christian, K. A., Tracy, C. R., and Porter, W. P. (1983). Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* **64:** 463–468.

Christian, K., Green, B., and Kennett, R. (1996). Some physiological consequences of estivation by freshwater crocodiles, *Crocodylus johnstoni*. *J. Herpetol.* **30:** 1–9.

Christiansen, J. L., and Dunham, A. E. (1972). Reproduction of the yellow mud turtle (*Kinosternon flavescens flavenscens*) in New Mexico. *Herpetologica* **28:** 130–137.

Cifelli, R. L., and Nydam, R. L. (1995). Primitive, helodermatid-like platynotan from the Early Cretaceous of Utah. *Herpetologica* **51:** 286–291.

Ciofi, C., and Chelazzi, G. (1994). Analysis of homing pattern in the colubrid snake *Coluber viridiflavus*. *J. Herpetol.* **28:** 477–484.

Clack, J. A. (1998). A new Early Carboniferous tetrapod with a mélange of crown-group characters. *Nature* **394:** 66–69.

Clark, D. R. Jr. (1971). The strategy of tail-autotomy in the ground skink, *Lygosoma laterale*. *J. Exp. Zool.* **176:** 295–302.

Clark, J. M. (1994). Patterns of evolution in Mesozoic Crocodyliformes. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 84–97. Cambridge Univ. Press, New York.

Clark, N. B. (1970). The parathyroid. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 235–262. Academic Press, London.

Clarke, B. T. (1981). Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). *Monit. Zool. Italiano, N. S. Suppl.* **15:** 285–331.

Clarke, B. T. (1997). The natural history of amphibian skin secretions, their normal functioning and potential medical applications. *Biol. Rev.* **72:** 365–379.

Clobert, J., Massot, M., Lecomte, J., Sorci, G., Fraipont, M., and Barbault, R. (1994). Determinants of dispersal behavior: The common lizard as a case study. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 183–206. Princeton Univ. Press, Princeton, NJ.

Clos, L. M. (1995). A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *J. Vert. Paleontol.* **15:** 254–267.

Coates, M. I., and Clack, J. A. (1995). Romer's gap: Tetrapod origins and terrestriality. *Bull. Mus. Natl. Hist. Nat., Paris* **7:** 373–388.

Cock Buning, T. (1985). Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Am. Zool.* **23:** 363–75.

Cocroft, R. B. (1994). A cladistic analysis of chorus frog phylogeny (Hylidae: *Pseudacris*). *Herpetologica* **50:** 420–437.

Cody, M. L. (1996). Introduction to long-term community ecological studies. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 1–15. Academic Press, San Diego.

Cogger, H. G., and Zweifel, R. G., Eds. (1998). "Encyclopedia of Reptiles & Amphibians." Academic Press, San Diego.

Colbert, E. H. (1967). Adaptations for gliding in the lizard *Draco*. *Am. Mus. Novitates* **2283:** 1–20.

Cole, C. J. (1984). Unisexual lizards. *Sci. Am.* **250:** 94–100.

Cole, C. J., and Townsend, C. R. (1983). Sexual behavior in unisexual lizards. *Anim. Behav.* **31:** 724–728.

Cole, C. J., and Townsend, C. R. (1990). Parthenogenetic lizards as vertebrate systems. *J. Exp. Zool.* **4:** 174–176.

Cole, C. J., Dessauer, H. C., Townsend, C. R., and Arnold, M. G. (1990). Unisexual lizards of the genus *Gymnophthalmus* (Reptilia: Teiidae) in the Neotropics: Genetics, origin, and systematics. *Am. Mus. Novitates* **2994:** 1–29.

Cole, C. J., Dessauer, H. C., Townsend, C. R., and Arnold, M. G. (1995). *Kentropyx borckiana* (Squamata: Teiidae) a unisexual lizards of hybrid origin in the Guiana region, South America. *Am. Mus. Novitates* **3145:** 1–23.

Colli, G. R., Péres, A. K., and Cunha, H. J. (1998). A new species of *Tupinambis* (Squamata: Teiidae) from central Brazil, with an analysis of morphological and genetic variation in the genus. *Herpetologica* **54:** 477–492.

Conant, R., and Collins, J. T. (1991). "A Field Guide to Reptiles and Amphibians. Eastern and Central North America," 3rd ed. Houghton Mifflin Co., Boston.

Congdon, J. D., and Gibbons, J. W. (1987). Morphological constraint on egg size: A challenge to optimal egg size theory? *Proc. Natl. Acad. Sci. USA* **84:** 4145–4147.

Congdon, J. D., and Gibbons, J. W. (1996). Structure and dynamics of a turtle community over two decades. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 137–159. Academic Press, San Diego.

Congdon, J. D., Vitt, L. J., and King, W. W. (1974). Geckos: Adaptive significance and energetics of tail autotomy. *Science* **184:** 1379–1380.

Congdon, J. D., Ballinger, R. E., and Nagy, K. A. (1979). Energetics, temperature and water relations in winter aggregated *Sceloporus jarrovi* (Sauria: Iguanidae). *Ecology* **60:** 30–35.

Congdon, J. D., Dunham, A. E., and Tinkle, D. W. (1982a). Energy budgets and life histories of reptiles. *In* "Biology of the Reptilia. Volume 13. Physiology D. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 233–271. Academic Press, New York.

Congdon, J. D., Vitt, L. J., van Loben Sels, R. C., and Ohmart, R. D. (1982b). The ecological significance of water flux rates in arboreal desert lizards of the genus *Urosaurus*. *Physiol. Zool.* **55:** 317–322.

Congdon, J. D., Tinkle, D. W., Breitenbach, G. L., and van Loben Sels, R. C. (1983). Nesting ecology and hatchling success in the turtle *Emydoidea blandingi*. *Herpetologica* **39:** 417–429.

Congdon, J. D., Breitenbach, G. L., van Loben Sels, R. C., and Tinkle, D. W. (1987). Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. *Herpetologica* **43:** 39–54.

Congdon, J. D., Dunham, A. E., and van Loben Sels, R. C. (1993). Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. *Conserv. Biol.* **7:** 826–833.

Congdon, J. D., Dunham, A. E., and van Loben Sels, R. C. (1994). Demographics of common snapping turtles (*Chely-*

dra serpentina): Implications for conservation and management of long-lived organisms. *Am. Zool.* **34:** 397–408.

Cooper, W. E., Jr. (1984). Female secondary sexual coloration and sex recognition in the keeled earless lizard, *Holbrookia propinqua. Anim. Behav.* **32:** 1142–1150.

Cooper, W. E., Jr. (1985). Female residency and courtship intensity in a territorial lizard, *Holbrookia propinqua. Amphibia-Reptilia* **6:** 63–69.

Cooper, W. E., Jr. (1994a). Prey chemical discrimination, foraging mode, and phylogeny. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 95–116. Princeton Univ. Press, Princeton, NJ.

Cooper, W. E., Jr. (1994b). Chemical discrimination by tongue-flicking in lizards: A review with hypotheses on its origin and its ecological and phylogenetic relationships. *J. Chem. Ecol.* **20:** 439–487.

Cooper, W. E., Jr. (1995). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* **50:** 973–985.

Cooper, W. E., Jr. (1996). Chemosensory recognition of familiar and unfamiliar conspecifics by the scincid lizard *Eumeces laticeps. Ethology* **102:** 1–11.

Cooper, W. E., Jr., and Alberts, A. C. (1990). Responses to chemical food stimuli by an herbivorous actively foraging lizard, *Dipsosaurus dorsalis. Herpetologica* **46:** 259–266.

Cooper, W. E., Jr., and Crews, D. (1988). Sexual coloration, plasma concentrations of sex steroid hormones, and responses to courtship in the female keeled earless lizard (*Holbrookia propinqua*). *Horm. Behav.* **22:** 12–25.

Cooper, W. E., Jr., and Greenberg, N. (1992). Reptilian coloration and behavior. *In* "Biology of the Reptilia. Volume 18, Physiology. Hormones, Brain, and Behavior" (C. Gans and D. Crews, Eds.), pp. 298–422. Univ. Chicago Press, Chicago.

Cooper, W. E., Jr., and Vitt, L. J. (1985). Blue tails and autotomy: Enhancement of predation avoidance in juvenile skinks. *Zeitsch. Tierpsych.* **70:** 265–276.

Cooper, W. E., Jr., and Vitt, L. J. (1987a). Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces:* Chemical detection of conspecific sexual competitors. *Herpetologica* **43:** 7–14.

Cooper, W. E., Jr., and Vitt, L. J. (1987b). Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps. Oecologia* **72:** 321–326.

Cooper, W. E., Jr., and Vitt, L. J. (1991). Influence of detectability and ability to escape on natural selection of conspicuous autotomous defenses. *Can. J. Zool.* **69:** 757–764.

Cooper, W. E., Jr., Vitt, L. J., Hedges, R., and Huey, R. B. (1990). Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): Behavioral shift in activity may offset costs of reproduction in an active forager. *Behav. Ecol. Sociobiol.* **27:** 153–157.

Cope, E. D. (1889). The Batrachia of North America. *Bull. U.S. Natl. Mus.* **34:** 1–525.

Cope, E. D. (1900). The crocodilians, lizards, and snakes of North America. *Ann. Rep. Smith. Inst. 1898*, 153–1270.

Corbett, K. F. (1988). Conservation strategy for the sand lizard (*Lacerta agilis agilis*) in Britain. *Mertensiella* **1:** 101–109.

Corbett, K. (1989). "Conservation of European Reptiles & Amphibians." Christopher Helm, London.

Corn, P. S., and Bury, R. B. (1988). Logging in western Oregon: Responses of headwater habitats and stream amphibians. *Forest Ecol. Manag.* **29:** 39–57.

Cott, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and northern Rhodesia. *Trans. Zool. Soc. London* **29:** 211–356.

Coulson, K. L. (1974). The polarization of light in the environment. *In* "Planets, Stars, and Nebula: Studied with Photopolarimetry" (T. Grebels, Ed.), pp. 444–471. Univ. Arizona Press, Tucson.

Coulson, R. A., and Hernandez, T. (1983). Alligator metabolism. Studies on chemical reactions in vivo. *Comp. Biochem. Physiol.* **74B:** 1–182.

Covacevich, J., Couper, P., Molnar, R. E., Witten, G., and Young, W. (1990). Miocene dragons from Riversleigh: New data on the history of the family Agamidae (Reptilia: Squamata) in Australia. *Mem. Queensl. Mus.* **29:** 339–360.

Cowles, R. B., and Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Nat. Hist.* **83:** 261–296.

Cox, M. J., van Dijk, P. P., Nabhitabhata, J., and Thirakhupt, K. (1998). "A Photographic Guide to Snakes and Other Reptiles of Peninsular Malaysia, Singapore and Thailand." Ralph Curtis Books, Sanibel, FL.

Crawshaw, G. J. (1997). Disease in Canadian amphibian populations. *In* "Amphibians in Decline. Canadian Studies of a Global Problem" (D. M. Green, Ed.), pp. 258–270. *Herpetol. Conserv.* **1.**

Cree, A., Thompson, M. B., and Daugherty, C. H. (1995). Tuatara sex determination. *Nature* **375:** 543.

Crews, D., and Moore, M. C. (1993). Psychobiology of reproduction of unisexual whiptail lizards. *In* "Biology of Whiptail Lizards (genus *Cnemidophorus*)" (J. W. Wright and L. J. Vitt, Eds.), pp. 257–282. Oklahoma Mus. Nat. Hist., Norman.

Crews, D., Bergeron, J. M., Bull, J. J., Flores, D., Tousignant, A., Skipper, J. K., and Wibbles T. (1994). Temperature dependent sex determination in reptiles: Proximate mechanisms, untimate outcomes, and practical applications. *Develop. Genetics* **15:** 297–312.

Crossland, M. R. (1998). A comparison of cane toad and native tadpoles as predators of native anuran eggs, hatchlings and larvae. *Wildl. Res.* **25:** 373–381.

Crother, B. I., and Presch, W. F. (1994). Xantusiid lizards, concern for analysis, and the search for a best estimate of phylogeny: Further comments. *Mol. Phylog. Evol.* **3:** 272–274.

Crouse, D. T., Crowder, L. B., and Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68:** 1412–1423.

Crowder, W. C., Nie, M., and Ultsch, G. R. (1998). Oxygen uptake in bullfrog tadpoles (*Rana catesbeiana*). *J. Exp. Zool.* **280:** 121–134.

Crumly, C. R. (1982). A cladistic analysis of *Geochelone* using cranial osteology. *J. Herpetol.* **16:** 215–234.

Crumly, C. R. (1984). A hypothesis for the relationships of land tortoise genera (family Testudinidae). *Stvd. Geol. Salmanticensia Espec.* **1:** 115–124.

Crump, M. L. (1986). Homing and site fidelity in a Neotropical frog, *Atelopus varius* (Bufonidae). *Copeia* **1986:** 438–444.

Crump, M. L. (1995). Parental care. *In* "Amphibian Biology. Volume 2, Social Behaviour" (H. Heatwole and B. K. Sullivan, Eds.), pp. 518–567. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Cruz, C. A. G. da (1990). Sobre as relaçoes intergenénericas de Phyllomedusinae da foresta atlântica (Amphibia, Anura, Hylidae). *Rev. Brasil. Biol.* **50:** 709–726.

Cuéllar, O. (1976). Intraclonal histocompatibility in a parthenogenetic lizard: Evidence of genetic homogeneity. *Science* **193:** 150–153.

Cundall, D. (1995). Feeding behaviour in *Cylindrophis* and its bearing on the evolution of alethinophidian snakes. *J. Zool., London* **237:** 353–376.

Cundall, D., and Irish, F. J. (1986). Aspects of locomotor and feeding behaviour in the Round Island boa *Casarea dussumieri. Dodo, J. Jersey Wildl. Trust* **23:** 108–111.

Cundall, D., and Irish, F. J. (1989). The function of the intramaxillary joint in the Round Island boa, *Casarea dussumieri. J. Zool., London* **217:** 569–598.

Cundall, D., and Rossman, D. A. (1993). Cephalic anatomy of the rare Indonesian snake *Anomochilus weberi. Zool. J. Linn. Soc.* **109:** 253–273.

Cundall, D., Lorenz-Elwood, J., and J. D. Groves. (1987). Asymmetric suction feeding in primitive salamanders. *Experientia* **43:** 1229–1231.

Cundall, D., Wallach, V., and Rossman, D. A. (1993). The systematic relationships of the snake genus *Anomochilus. Zool. J. Linn. Soc.* **109:** 275–299.

Cunningham, J. D. (1960). Aspects of the ecology of the Pacific slender salamander, *Batrachoseps pacificus,* in southern California. *Ecology* **41:** 88–99.

Czopek, J. (1961). Vascularization of respiratory surfaces in *Ambystoma mexicanum* (Cope) in ontogeny. *Zool. Poloniae* **8:** 131–149.

Czopek, J. (1965). Quantitative studies on the morphology of respiratory surfaces in amphibians. *Acta Anat.* **62:** 296–323.

Daltry, J. C., and Martin, G. N. (1997). Rediscovery of the black narrow-mouth frog, *Melanobatrachus indicus* Beddome, 1978. *Hamadryad* **22:** 57–58, Plate 2.

Daly, J. W. (1998). Thirty years of discovering arthropod alkaloids in amphibian skin. *J. Nat. Prod.* **61:** 162–172.

Daly, J. W., Myers, C. W., and Whittaker, N. (1987). Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. *Toxicon* **25:** 1023–1095.

Daly, J. W., Andriamaharavo, N. R., Andriantsiferana, M., and Myers, C. W. (1996). Madagascan poison frogs (*Mantella*) and their skin alkaloids. *Am. Mus. Novitates* **3177:** 1–34.

Daniel, J. C. (1983). "The Book of Indian Reptiles." Bombay Nat. Hist. Soc., Bombay.

Daniels, C. B. (1983). Running: An escape strategy enhanced by autotomy. *Herpetologica* **3:** 162–165.

Dansfeltd, R. T. (1975). Local geographical variation in the demographic parameters and body size of *Desmognathus fuscus. Ecology* **56:** 1054–1067.

Darevskii, I. S. (1978). "Rock Lizards of the Caucasus." Indian Natl. Sci. Docum. Centre, New Delhi.

Darevsky, I. S. (1958). Natural parthenogenesis in certain subspecies of rock lizard, *Lacerta saxicola* Eversmann. *Doklady Akad. Nauk SSSR, Biol. Sci.* **122:** 877–879.

Darevsky, I. S. (1992). Evolution and ecology of parthenogenesis in reptiles. *In* "Herpetology: Current Research on the Biology of Amphibians and Reptiles" (K. Adler, Ed.), pp. 21–39. Soc. Study Amphibians and Reptiles, Oxford, OH.

Das, I. (1995). "Turtles and Tortoises of India." Oxford Univ. Press, Bombay.

Das, I. (1996). Folivory and seasonal changes in diet in *Rana hexadactyla* (Anura: Ranidae). *J. Zool., London* **238:** 785–794.

Daugherty, C. H., Cree, A., Hay, J. M., and Thompson, M. B. (1990). Neglected taxonomy and continuing existence of tuatara (*Sphenodon*). *Nature* **347:** 177–179.

David, P. (1994). Liste des reptiles actuels du monde I. Chelonii. *Dumerilia* **1:** 7–127.

David, P., and Ineich, I. (1999). Les serpents venimeux du monde: Systématique et répartition. *Dumerilia* **3:** 3–499.

David, P., and Vogel, G. (1996). "The Snakes of Sumatra." Edition Chimaira, Frankfurt am Main.

David, R. S., and Jaeger, R. G. (1981). Prey location through chemical cues by a terrestrial salamander. *Copeia* **1981:** 435–440.

Dawson, W. R. (1975). On the physiological significance of the preferred body temperatures of reptiles. *In* "Perspectives in Biophysical Ecology" (D. M. Gates and R. B. Schmerl, Eds.), pp. 443–473. Springer-Verlag, New York.

Day, D. (1981). "The Doomsday Book of Animals. A Natural History of Vanished Species." Viking Press, New York.

DeBraga, M., and Rieppel, O. (1997). Reptile phylogeny and the interrelationships of turtles. *Zool. J. Linn. Soc.* **120:** 281–354.

Del Pino, E. M. (1989). Marsupial frogs. *Sci. Am.* **160:** 76–84.

Delsol, M., Flatin, J., Extrayat, J.-M., and Bons, M. (1981). Développement de *Typhlonectes compressicaudus. C. R. Acad. Sci. (Paris)* **293:** 281–285.

Delsol, M., Flatin, J., Extrayat, J.-M., and Bons, M. (1983). Développement embronnaire de *Typhlonectes compressicaudus* (Duméril et Bibron, 1841). Constitution d'un ectotrophoblaste. *Bull. Soc. Zool., France* **108:** 680–681.

Delsol, M., Extrayat, J.-M., Flatin, M. J., and Gueydan-Baconnier, M. (1986). Nutrition embronnaire chez *Typhlonectes* *compressicaudus* (Duméril et Bibron, 1841), Amphibien Apode vivipare. *Mem. Soc. Zool., France* **43:** 39–54.

Demaynadier, P. G., and Hunter, M. L., Jr. (1998). Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conserv. Biol.* **8:** 300–301.

Densmore, L. D. (1983). Biochemical and immunological systematics of the order Crocodilia. *Evol. Biol.* **16:** 397–465.

Densmore, L. D., and White, P. S. (1991). The systematics and evolution of the Crocodilia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. *Copeia* **1991:** 602–615.

Denton, R. K., Jr., and O'Neill, R. C. (1995). *Prototeius stageri* gen. et sp. nov., a new teiid lizard from the Upper Cretaceous Marshalltown Formation of New Jersey, with a preliminary phylogenetic revision of the Teiidae. *J. Vert. Paleontol.* **15:** 235–253.

Denver, R. J. (1997). Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *Am. Zool.* **37:** 172–184.

De Queiroz, K. (1997). The Linnean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* **15:** 125–144.

De Queiroz, K., and Gauthier, J. (1992). Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* **23:** 449–480.

De Queiroz, K., and Gauthier, J. (1994). Toward a phylogenetic system of biological taxonomy. *Trends Ecol. Evol.* **9:** 27–31.

Derickson, W. K. (1976). Ecological and physiological aspects of reproductive strategies in two lizards. *Ecology* **57:** 445–458.

De Silva, P. H. D. H. (1980). "Snake Fauna of Sri Lanka with Special Reference to Skull, Dentition and Venom in Snakes." Natl. Mus. Sri Lanka, Colombo.

Dial, B. E. (1981). Function and energetics of autotomized tail thrashing in *Lygosoma laterale* (Sauria: Scincidae). *Am. Zool.* **21:** 1001.

Dial, B. E., and Fitzpatrick, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* **51:** 310–317.

Dial, B. E., and Fitzpatrick, L. C. (1983). Lizard tail autotomy: Function and energetics of post autotomy tail movement in *Scincella lateralis. Science* **219:** 391–393.

Dial, B. E., and Grismer, L. L. (1992). A phylogenetic analysis of physiological-ecological character evolution in the lizard genus *Coleonyx* and its implications for historical biogeographic reconstruction. *Syst. Biol.* **4:** 178–195.

Dial, B. E., and Grismer, L. L. (1994). Phylogeny and physiology: Evolution of lizards in the genus *Coleonyx. In* "Herpetology of the North American Deserts: Proceedings of a Symposium" (P. R. Brown and J. W. Wright, Eds.), pp. 239–254. Southwest. Herpetol. Soc. Spec. Publ. no. 5, Van Nuys, CA.

Dial, B. E., and Schwenk, K. (1996). Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. *J. Exp. Zool.* **276:** 415–424.

Diller, L. V., and Wallace, R. L. (1999). Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in north coastal California. *J. Herpetol.* **33:** 71–79.

Dixon, J. R., and Kofron, C. P. (1983). The Central and South American anomalepid snakes of the genus *Liotyphlops. Amphibia-Reptilia* **4:** 241–264.

Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.* **38:** 209–221.

Dodd, C. K. (1994). The effects of drought on population structure, activity, and orientation of toads (*Bufo quercicus* and *B. terrestris*) at a temporary pond. *Ethol. Ecol. Evol.* **6:** 331–349.

Dodd, C. K., Jr. (1982). Immobilility in *Sooglossus gardineri* (Anura: Sooglossidae). *Herpetol. Rev.* **13:** 33–34.

Dodd, C. K., Jr. (1989). Status of the Red Hills salamander is reassessed. *Endangered Species Tech. Bull.* **14:** 10–11.

Dodd, C. K., Jr. (1997). Imperiled amphibians. A historical perspective. *In* "Aquatic Fauna in Peril: The Southeastern Perspective" (G. W. Benz and D. E. Collins, Eds.), pp. 165–200. Lenz Design & Comm., Decatur, GA.

Dodd, C. K., Jr., and Cade, R. S. (1998). Movement patterns and the conservation of amphibians breeding in small temporary wetlands. *Conserv. Biol.* **12:** 331–339.

Dodd, C. K., Jr., and Seigel, R. A. (1991). Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? *Herpetologica* **47:** 336–350.

Dole, D. W., Rose, B. B., and Tachiki, K. H. (1981). Western toads (*Bufo boreas*) learn odor of prey insects. *Herpetologica* **37:** 63–68.

Donnellan, S. C., Hutchinson, M. N., and Saint, K. M. (1999). Molecular evidence for the phylogeny of Australian gekkonoid lizards. *Biol. J. Linn. Soc.* **67:** 97–118.

Donnelly, M. A., and Guyer, C. (1994). Patterns of reproduction and habitat use in an assemblage of neotropical hylid frogs. *Oecologia* **98:** 291–302.

Donnelly, M. A., de Sá, R., and Guyer, C. (1990). Description of the tadpoles of *Gastrophyrne pictiventris* and *Nelsonophryne aterrima* (Anura: Microhylidae) with a review of morphological variation in free-swimming microhylid larvae. *Am. Mus. Novitates* **2976:** 1–19.

Donoso-Barros, R. (1966). "Reptiles de Chile." Edic. Univ. Chile, Santiago de Chile.

Doody, J. S., and Young, J. E. (1995). Temporal variation in reproduction and clutch mortality of leopard frogs (*Rana utricularia*) in south Mississippi. *J. Herpetol.* **29,** 614–616.

Doughty, P., Sinervo, B., and Burghardt, G. M. (1994). Sex-biased dispersal in a polygynous lizard, *Uta stansburiana. Anim. Behav.* **47:** 227–229.

Dowling, H. G., and Duellman, W. E. (1974–1978). "Systematic Herpetology. A Synopsis of Families and Higher Categories." HISS Publ., New York.

Dowling, H. G., Hass, C. A., Hedges, S. B., and Highton, R. (1996). Snake relationships revealed by slow-evolving proteins: A preliminary survey. *J. Zool., London* **240:** 1–28.

Downie, J. R. (1984). How *Leptodactylus fuscus* tadpoles make foam, and why. *Copeia* **1984:** 778–780.

Drewes, R. C. (1984). A phylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands. *Occas. Pap. Calif. Acad. Sci.* **139:** 1–70

Drury, W. H., Jr. (1998). "Chance and Change. Ecology for Conservationists." Univ. California Press, Los Angeles.

Dubois, A. (1981). Liste de genres et sous-genres nominaux de Ranoidea (amphibien anoures) du monde, avec identification de leurs espèces-types: Conséquences nomenclaturales. *Monit. Zool. Italiano, N. S. Suppl.* **15:** 225–284.

Dubois, A. (1984). La nomenclature supragénérique des amphibiens anoures. *Mém. Mus. Natl. Hist. Nat., Ser. A, Zool.* **131:** 1–64.

Dubois, A. (1985). Diagnose préliminaire d'un nouveau genre de Ranoidea (Amphibiens, Anoures) du sud de l'Inde. *Alytes* **4:** 113–118.

Dubois, A. (1986). Miscellanea taxinomica batrachologica (I). *Alytes* **5:** 7–95.

Dubois, A. (1992). Notes sur la classification des Ranidae (amphibiens anoures). *Bull. Mens. Soc. Linn. Lyon* **61:** 305–352.

Duellman, W. E. (1970). The frogs of Middle America. Volume 1. *Monog. Mus. Nat. Hist., Univ. Kansas* **1:** 1–427.

Duellman, W. E. (1975). On the classification of frogs. *Occas. Pap. Mus. Nat. Hist., Univ. Kansas* **42:** 1–14.

Duellman, W. E. (1978). The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Publ. Mus. Nat. Hist., Univ. Kansas* **65:** 1–352.

Duellman, W. E. (1993). Amphibian species of the world: Additions and corrections. *Univ. Kansas Mus. Nat. Hist. Spec. Publ.* **21:** 1–372.

Duellman, W. E., and Trueb, L. (1986). "Biology of Amphibians." McGraw-Hill Book Co., New York.

Duellman, W. E., and Wiens, J. J. (1992). The status of the hylid frog genus *Ololygon* and the recognition of *Scinax* Wagler, 1830. *Occas. Pap. Mus. Nat. Hist., Univ. Kansas* **151:** 1–23.

Duellman, W. E., Maxson, L. R., and Jesiolowski, C. A. (1988). Evolution of marsupial frogs (Hylidae: Hemiphractinae): Immunological evidence. *Copeia* **1988:** 527–543.

Duméril, A. C. G. (1853). "Prodrome de la classification des reptiles ophidiens." Didot Frère, Paris.

Dundee, H. A., and Miller, M. C. (1968). Aggregative behavior and habitat conditioning by the prairie ringneck snake, *Diadophis punctatus arnyi. Tulane Stud. Zool. Bot.* **15:** 41–58.

Dunham, A. E. (1978). Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami. Ecology* 59, 770–778.

Dunham, A. E. (1980). An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus. Ecol. Monog.* **50:** 309–330.

Dunham. A. E. (1993). Realized niche overlap, resource abundance, and the intensity of interspecific competition. *In* "Lizard Ecology: Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 261–280. Harvard Univ. Press, Cambridge, MA.

Dunham, A. E., and Miles, D. B. (1985). Patterns of covariation in life history traits of squamate reptiles: The effects of size and phylogeny reconsidered. *Am. Nat.* **126:** 231–257.

Dunham, A. E., Miles, D. B., and Reznick, D. N. (1988). Life history patterns in squamate reptiles. *In* "Biology of the Reptilia. Volume 16. Ecology B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 441–552. A. R. Liss, New York.

Dunham, A. E., Grant, B. W., and Overall, K. L. (1989). Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol. Zool.* **62:** 335–355.

Dunson, W. A. (1970). Some aspects of electrolyte and water balance in three estuarine reptiles, the diamondback terrapin, American alligator, and "salt water" crocodile. *Comp. Biochem. Physiol.* **32:** 161–174.

Dunson, W. A. (1978). Role of the skin in sodium and water exchange of aquatic snakes placed in seawater. *Am. J. Physiol.* **235:** R151–R159.

Dunson, W. A. (1979). Control mechanisms in reptiles. *In* "Mechanisms of Osmoregulation in Animals: Regulation of Cell Volume" (R. Gilles, Ed.), pp. 273–322. Wiley Interscience, New York.

Dunson, W. A. (1980). The relation of sodium and water balance to survival in sea water of estuarine and freshwater races of the snakes *Nerodia fasciata, N. sipedon,* and *N. valida. Copeia* **1980:** 268–280.

Dunson, W. A., Wyman, R. L., and Corbett, E. S., covenors (1992). A symposium on amphibian declines and habitat acidification. *J. Herpetol.* **26:** 349–442.

Durand, J. P. (1983). Données et hypothéses sur l'évolution des Proteidae. *Bull. Soc. Zool. France* **108:** 617–630.

During, M. von, and Miller, M. R. (1979). Sensory nerve endings of the skin and deeper structures. *In* "Biology of the Reptilia. Volume 9" (C. Gans, A. R. G. Northcutt, and P. Ulinski, Eds.), pp. 407–441. Academic Press, London.

Dutta, S. K., and Manamendra-Archchi, K. (1996). "The Amphibian Fauna of Sri Lanka." Wildlife Heritage Trust Sri Lanka, Colombo.

Dutton, P. H., Davis, S. K., Guerra, T., and Owens, D. (1996). Molecular phylogeny for marine turtles based on sequences of the ND4–Leucine tRNA and control regions of mitochondrial DNA. *Mol. Phylog. Evol.* **5:** 511–521.

Duvall, D., King, M. B., and Gutzwiller, K. J. (1985). Behavioral ecology of the prairie rattlesnake. *Natl. Geog. Res.* **1:** 80–111.

Duvall, D., Arnold, S. J., and Schuett, G. W. (1992). Pitviper mating systems: Ecological potential, sexual selection and microevolution. *In* "Biology of Pitvipers" (J. A. Campbell and E. D. Brodie, Jr., Eds.), pp. 321–336. Selva, Tyler, TX.

Duvall, D., Schuett, G. W., and Arnold, S. J. (1993). Ecology and evolution of snake mating systems. *In* "Snakes-Ecology and Behavior" (R. A. Seigel and J. T. Collins, Eds.), pp. 165–200. McGraw-Hill, Inc., New York.

Echelle, A. A., Echelle, A. F., and Fitch, H. S. (1971). A comparative analysis of aggressive display in nine species of Costa Rican *Anolis. Herpetologica* **27:** 271–288.

Edmund, A. G. (1969). Dentition. *In* "Biology of the Reptilia. Volume 1. Morphology A" (C. Gans, A. d'A. Bellairs, and T. S. Parsons, Eds.), pp. 117–200. Academic Press, London.

Edwards, J. L. (1976). Spinal nerves and their bearing on salamander phylogeny. *J. Morphol.* **148:** 305–328.

Edwards, J. L. (1989). Two perspectives on the evolution of the tetrapod limb. *Am. Zool.* **29:** 235–254.

Eernisse, D. J., and Kluge, A. G. (1993). Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. *Mol. Biol. Evol.* **10:** 1170–1195.

Ehmann, H. (1993). Family Boidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 284–289. Aust. Govern. Publ. Serv., Canberra.

Ehmann, H., and Bamford, M. J. (1993). Family Typhlopidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 280–283. Aust. Govern. Publ. Serv., Canberra.

Ehmann, H., and Swan, G. (1985). Reproduction and development in the marsupial frog, *Assa darlingtoni* (Leptodactylidae, Anura). *In* "Biology of Australian Frogs and Reptiles" (G. Grigg, R. Shine, and H. Ehmann, Eds.), pp. 279–285. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Elias, H., and Shapiro, J. (1957). Histology of the skin of some toads and frogs. *Am. Mus. Novitates* **1819:** 1–27.

Elinson, R. P. (1987). Changes in developmental patterns: Embryos of amphibians with large eggs. *In* "Development as an Evolutionary Process" (R. A. Faff and E. C. Raff, Eds.), pp. 1–21. Alan R. Liss, Inc., New York.

Elphick, M. J., and Shine, R. (1998). Longterm effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi,* Scincidae). *Biol. J. Linn. Soc.* **63:** 429–447.

Emerson, S. B. (1975). Burrowing in frogs. *J. Morphol.* **149:** 437–458.

Emerson, S. B. (1988). The giant tadpole of *Pseudis paradoxa*. *Biol. J. Linn. Soc.* **34:** 93–104.

Emerson, S. B., and Berrigan, D. (1993). Systematics of Southeast Asian ranids: Multiple origins of voicelessness in the subgenus *Limnonectes* (Fitzinger). *Herpetologica* **49:** 22–31.

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197:** 215–223.

Endler, J. A. (1978). A predator's view of animal color patterns. *In* "Evolutionary Biology. Volume 11" (M. K. Hecht, W. C. Steere, and B. Wallace, Eds.), pp. 319–364. Plenum Press, New York.

Engbretson, G. A. (1992). Neurobiology of the lacertilian parietal eye system. *Ethol. Ecol. Evol.* **4:** 89–107.

Engelmann, W.-E., Fritsche, J., Günther, R., and Obst, F. J. (1986). "Lurche und Kriechtiere Europas." F. Enke Verlag, Stuttgart.

Epple, A., and Brinn, J. E. (1986). Pancreatic islets. *In* "Vertebrate Endocrinology: Fundamentals and Biomedical Implications. Vol. 1. Morphological Considerations" (P. K. T. Pang and M. P. Schreibman, Eds.), pp. 279–317. Academic Press, Orlando.

Ernst, C. H. (1971). Population dynamics and activity cycles of *Chrysemys picta* in southeastern Pennsylvania. *J. Herpetol.* **5:** 151–160.

Ernst, C. H., and Barbour, R. W. (1989a). "Turtles of the World." Smithsonian Inst. Press, Washington, DC.

Ernst, C. H., and Barbour, R. W. (1989b). "Snakes of Eastern North America." George Mason Univ. Press, Fairfax, VA.

Ernst, C. H., and Zug, G. R. (1996). "Snakes In Question." Smithsonian Inst. Press, Washington, DC.

Ernst, C. H., Lovich, J. E., and Barbour, R. W. (1994). "Turtles of the United States and Canada." Smithsonian Inst. Press, Washington, DC.

Erspamer, V. (1994). Bioactive secretions of the amphibian integument. *In* "Amphibian Biology. Volume 1, The Integument" (H. Heatwole and G. T. Barthalmus, Eds.), pp. 178–350. Surrey Beatty & Sons, Chipping Norton, N.S.W.

Estes, R. (1981). "Gymnophiona, Caudata. Handbuch der Paläoherpetologie, 2/2." Gustav Fischer Verlag, Stuttgart.

Estes, R. (1983a). "Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, 10A." Gustav Fischer Verlag, Stuttgart.

Estes, R. (1983b). The fossil record and early distribution of lizards. *In* "Advances in Herpetology and Evolutionary Biology"(A. G. J. Rhodin and K. Miyata, Eds.), pp. 365–398. Harvard Univ. Press, Cambridge.

Estes, R., and Reig, O. A. (1973). The early fossil record of frogs. A review of the evidence. *In* "Evolutionary Biology of the Anurans" (J. L. Vial, Ed.), pp. 11–63. Univ. Missouri Press, Columbia.

Estes, R., and Reig, O. A. (1976). Les urodèles du Miocène de la Grive-Saint-Alban (Isères, France). *Bull. Mus. Natl. Hist. Nat., Sci. Terre* **57:** 297–343.

Estes, R., de Queiroz, K., and Gauthier, J. (1988). Phylogenetic relationships within Squamata. *In* "Phylogenetic Relationships of the Lizard Families" (R. Estes and G. Pregill, Eds.), pp. 119–281. Stanford Univ. Press, Stanford, CA.

Etheridge, K. (1990). Water balance in estivating sirenid salamanders (*Siren lacertina*). *Herpetologica* **46:** 400–406.

Etheridge, R. (1995). Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). *Am. Mus. Novitates* **3142:** 1–34.

Etheridge, R., and Williams, E. E. (1991) A review of the South American lizard genera *Urostrophus* and *Anisolepis* (Squamata: Iguania: Polychridae). *Bull. Mus. Comp. Zool.* **152:** 317–361.

Evans, C. M., and Brodie, E. D., Jr. (1994). Adhesive strength of amphibian skin secretions. *J. Herpetol.* **28:** 499–502.

Evans, S. E. (1993). Jurassic lizard assemblages. *Rev. Paléobiologie,* Vol. spéc.: 55–65.

Evans, S. E. (1994). A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology* **37:** 33–49.

Evans, S. E., and Barbadillo, L. J. (1998). An unusual lizard (Reptilia: Squamata) from the Early Cretaceous of Las Hoyas, Spain. *Zool. J. Linn. Soc.* **124:** 235–265.

Evans, S. E., and Chure, D. C. (1998). Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *J. Vert. Paleontol.* **18:** 99–114.

Evans, S. E., and Milner, A. R. (1993). Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. *J. Vert. Paleontol.* **13:** 24–30.

Evans, S. E., and Milner, A. R. (1994). Middle Jurassic microvertebrate assemblages from the British Isles. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 23–37. Cambridge Univ. Press, New York.

Evans, S. E., and Milner, A. R. (1996). A metamorphosed salamander from the early Cretaceous of Las Hoyas, Spain. *Philos. Trans. Roy. Soc. London* **351:** 627–646.

Evans, S. E., Milner, A. R., and Mussett, F. (1988). The earliest known salamander (Amphibia, Caudata): A record from the Middle Jurassic of England. *Geobios* **21:** 539–552.

Evans, S. E., Milner, A. R., and Mussett, F. (1990). A discoglossid frog from the Middle Jurassic of England. *Palaeontology* **33:** 299–311.

Evans, S. E., Milner, A. R., and Werner, C. (1996). Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. *Palaeontology* **39:** 77–95.

Ewert, M. A. (1985). Embryology of turtles. *In* "Biology of the Reptilia. Volume 14, Development A" (C. Gans, F. Billett, and P. F. A. Maderson, Eds.), pp. 75–267. John Wiley & Sons, New York.

Exbrayat, J.-M. (1984). Cycle sexuel et reproduction chez un amphibien apode: *Typhlonectes compressicaudus* (Duméril et Bibron, 1841). *Bull. Soc. Herpetol. France* **32:** 31–35.

Exbrayat, J.-M. (1985). Le cycle de reproduction chez un amphibien apodes influence des variations saisonnieres. *Bull. Soc. Zool. France* **110:** 301–305.

Exbrayat, J.-M., and Hraoui-Bloquet, S. (1992). La nutrition embryonnaire et les relations foeto-maternelles chez *Typhlonectes compressicaudus* amphibien gymnophione vivipare. *Bull. Soc. Herpetol. France* **61:** 53–61.

Farlow, J. O., and Brett-Surman, M. K., Eds. (1997). "The Complete Dinosaur." Indiana Univ. Press, Bloomington.

Farrell, A. P., Gamperl, A. K., and Francis, E. T. B. (1998). Comparative aspects of heart morphology. *In* "Biology of the Reptilia. Volume 19, Morphology G" (C. Gans and A. S. Gaunt, Eds.), pp. 375–424. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Farrell, T. M., May, P. G., and Pilgrim, M. A. (1995). Reproduction in the rattlesnake, *Sistrurus miliarius barbouri,* in central Florida. *J. Herpetol.* **29:** 21–27.

Feder, M. E., and Lynch, J. F. (1982). Effects of latitude, season, elevation, and microhabitat on field body temperatures of neotropical and temperate zone salamanders. *Ecology* **63:** 1657–1664.

Feder, M. E., Lynch, J. F., Shaffer, H. B., and Wake, D. B. (1982). Field body temperatures of tropical and temperate zone salamanders. *Smiths. Herpetol. Inf. Serv.* **52:** 1–23.

Feduccia, A., and Wild, R. (1993). Birdlike characters in the Triassic archosaur *Megalancosaurus. Naturwissenschaften* **80:** 564–566.

Fellers, G. M., and Drost, C. A. (1991a). Ecology of the island night lizard, *Xantusia riversiana,* on Santa Barbara Island, California. *Herpetol. Monog.* **5:** 28–78.

Fellers, G. M., and Drost, C. A. (1991b). *Xantusia riversianna. Catalog. Am. Amphib. Rept.* **518:** 1–4.

Ferguson, D. E. (1967). Sun-compass orientation in anurans. *In* "Animal Orientation and Navigation" (R. E. Storm, Ed.), pp. 21–34. Oregon State Univ. Press, Corvallis.

Ferguson, D. E. (1971). The sensory basis of orientation in amphibians. *Ann N. Y. Acad. Sci.* **188:** 30–36.

Ferguson, G. W., Bohlen, C. H., and Woolley, P. (1980). *Sceloporus undulatus:* Comparative life history and regulation of a Kansas population. *Ecology* **61:** 313–322.

Ferguson, G. W., Hughes, J. L., and Brown, K. L. (1983). Food availability and territorial establishment of juvenile *Sceloporus undulatus. In* "Lizard Ecology: Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 134–148. Harvard Univ. Press, Cambridge, MA.

Ferguson, M. W. J., and Joanen, T. (1982). Temperature of egg incubation determines sex in *Alligator mississippiensis. Nature* **297:** 850–853.

Fisher, R. A. (1930). "The Genetical Theory of Natural Selection." Oxford Univ. Press, Oxford.

Fisher, R. N., and Shaffer, H. B. (1996). The decline of amphibians in the California's Great Central Valley. *Conserv. Biol.* **10:** 1387–1397.

Fitch, H. S. (1954). Life history and ecology of the five-lined skink, *Eumeces fasciatus. Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **8:** 1–156.

Fitch, H. S. (1955). Habits and adaptations of the great plains skink (*Eumeces obsoletus*). *Ecol. Monog.* **25:** 59–83.

Fitch, H. S. (1960). Autecology of the copperhead. *Mus. Nat. Hist., Univ. Kansas Publ.* **13:** 85–288.

Fitch, H. S. (1965). The University of Kansas Natural History Reserve in 1965. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **42:** 1–60.

Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **52:** 1–247.

Fitch, H. S. (1975). A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **62:** 1–53.

Fitch, H. S. (1982). Reproductive cycles in tropical reptiles. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* **96:** 1–53.

Fitch, H. S. (1985). Variation in clutch and litter size in New World reptiles. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **76:** 1–76.

Fittkau, E.-J. (1970). Role of caimans in the nutrient regime of mouth-lakes of Amazon affluents (an hypothesis). *Biotropica* **2:** 138–142.

Fitzgerald, L. A. (1994a). *Tupinambis* lizards and people: A sustainable use approach to conservation and development. *Conserv. Biol.* **8:** 12–16.

Fitzgerald, L. A. (1994b). The interplay between life history and environmental stochasticity: Implications for the management of exploited lizard populations. *Am. Zool.* **34:** 371–381.

Fitzgerald, L. A., Cruz, F. B., and Perotti, G. (1993). The reproductive cycle and the size at maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the dry Chaco of Argentina. *J. Herpetol.* **27:** 70–78.

Fleishman, L. J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* **139:** S36–S61.

Fleming, A. F. (1994). Male and female reproductive cycles of the viviparous lizard, *Mabuya capensis* (Sauria: Scincidae) from South Africa. *J. Herpetol.* **28:** 334–341.

Fleming, A. F., and van Wyk, J. H. (1992). The female reproductive cycle of the lizard *Cordylus p. polyzonus* (Sauria: Cordylidae) in the southwestern Cape Province, South Africa. *J. Herpetol.* **26:** 121–127.

Flores-Villela, O. A., and Zug, G. R. (1995). Reproductive biology of the chopontil, *Claudius angustatus* (Testudines: Kinosternidae), in southern Veracruz, México. *Chelonian Conserv. Biol.* **1:** 181–186.

Follett, B. K., and Redshaw, M. R. (1974). The physiology of vitellogenesis. *In* "Physiology of the Amphibia" (B. Lofts, Ed.), pp. 219–308. Academic Press, New York.

Fontenot, C. L., Jr. (1999). Reproductive biology of the aquatic salamander *Amphiuma tridactylum* in Louisiana. *J. Herpetol.* **33:** 100–105.

Ford, L. S. (1993). The phylogenetic position of the dart-poison frogs (Dendrobatidae) among anurans: An examination of the competing hypotheses and their characters. *Ethol. Ecol. Evol.* **5:** 219–231.

Ford, L. S., and Cannatella, D. C. (1993). The major clades of frogs. *Herpetol. Monog.* **7:** 94–117.

Ford, N. B., and O'Bleness, M. L. (1986). Species and sexual specificity of pheromone trails of the checkered garter snake, *Thamnophis marcianus. J. Herpetol.* **20:** 259–262.

Ford, N. B., and Schofield, C. W. (1984). Species specificity of sex pheromone trails in the plains garter snake, *Thamnophis radix. Herpetologica* **40:** 51–55.

Ford, N. B., and Seigel, R. A. (1989). Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake. *Ecology* **70:** 1768–1774.

Forester, D. C., and Czarnowsky, R. (1985). Sexual selection in the spring peeper, *Hyla crucifer* (Amphibia, Anura): The role of the advertisement call. *Behavior* **92:** 112–128.

Formanowicz, D. R., Jr., Brodie, E. D., Jr., and Wise, S. C. (1989). Foraging behavior of matamata turtles: The effects of prey density and the presence of a conspecific. *Herpetologica* **45:** 61–67.

Forsman, A., and Shine, R. (1995). Sexual size dimorphism in relation to frequency of reproduction in turtles (Testudines: Emydidae). *Copeia* **1995:** 727–729.

Foster, M. S., and McDiarmid, R. W. (1983). *Rhinophrynus dorsalis* (alma de vaca, sapo borracho, Mexican burrowing toad). *In* "Costa Rican Natural History" (D. H. Janzen, Ed.), pp. 419–421. Univ. Chicago Press, Chicago.

Fouquette, M. J., Jr. (1969). Rhinophrynidae, *Rhinophrynus, R. dorsalis. Catalog. Am. Amphib. Rept.* **78:** 1–2.

Fouquette, M. J. J., and Delahoussaye, A. J. (1977). Sperm morphology in the *Hyla rubra* group (Amphibia, Anura, Hylidae), and its bearing on generic status. *J. Herpetol.* **11:** 387–396.

Fox, H. (1977). The urogenital system of reptiles. *In* "Biology of the Reptilia. Volume 6. Morphology E" (C. Gans and T. S. Parsons, Eds.), pp.1–157, 463–464. Academic Press, London.

Fox, H. (1983). "Amphibian Morphogenesis." Humana Press, Clifton, NJ.

Fox, H. (1985). Changes in amphibian skin during larval development and metamorphosis. *In* "Metamorphosis" (M. Balls and M. Bownes, Eds.), pp. 59–87. Clarendon Press, Oxford.

Fox, H. (1986). Epidermis. Dermis. Dermal glands. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 78–110, 111–115, 116–135, respectively. Springer Verlag, Berlin.

Fox, S. F., and Rostker, M. A. (1982). Social cost of tail loss in *Uta stansburiana*. *Science* **218:** 692–693.

Fox, S. F., Heger, N. A., and Delay, L. S. (1990). Social cost of tail loss in *Uta stansburiana:* Lizard tails as status-signalling badges. *Anim. Behav.* **39:** 549–554.

Foxon, G. E. H. (1964). Blood and respiration. *In* "Physiology of the Amphibia" (J. A. Moore, Ed.), pp. 151–209. Academic Press, New York.

Frair, W., Ackman, R. G., and Mrosovsky, N. (1972). Body temperature of *Dermochelys coriacea:* Warm turtle from cold water. *Science* **177:** 191.

Francis, E. T. B. (1934). "The Anatomy of the Salamander." Clarendon Press, Oxford.

Frazer, D. (1989). "Reptiles and Amphibians in Britain." Bloomsbury Books, London.

Frazer, N. B. (1992). Sea turtle conservation and halfway technology. *Conserv. Biol.* **6:** 179–184.

Frazer, N. B., Gibbons, J. W., and Greene, J. L. (1990). Life tables of a slider turtle population. *In* "Life History and Ecology of the Slider Turtle" (J. W. Gibbons, Ed.), pp. 183–200. Smithsonian Inst. Press, Washington, DC.

Frazer, N. B., Gibbons, J, W., and Greene, J. L. (1991). Life history and demography of the common mud turtle *Kinosternon subrubrum* in South Carolina, USA. *Ecology* **72:** 2218–2231.

Frazier, J., and Peters, G. (1981). The call of the Aldabra tortoise (*Geochelone gigantea*). *Amphibia-Reptilia* **2:** 165–179.

Frazzetta, T. H. (1986). The origin of amphikinesis in lizards. A problem in functional morphology and the evolution of adaptive systems. *Evol. Biol.* **20:** 419–461.

Frey, E., Sues, H.-D., and Munk, W. (1997). Gliding mechanism in the Late Permian reptile *Coelurosauravus. Science* **275:** 1450–1452.

Friedl, T. W., and Klump, G. M. (1997). Some aspects of population biology in the European treefrog, *Hyla arborea. Herpetologica* **53:** 321–330.

Fritts, T. H. (1988). The brown tree snake, *Boiga irregularis,* a threat to Pacific islands. *U.S. Fish Wildl. Serv., Biol. Rep.* **88:** i–vi, 1–36.

Fritzsch, B. (1990). Evolution of tetrapod hearing. *Nature* **344:** 116.

Fritzsch, B., and Wake, M. H. (1988). The inner ear of gymnophione amphibians and its nerve supply: A comparative study of regressive events in a complex sensory system. *Zoomorphology* **108:** 201–217.

Frolich, L. M. (1997). The role of the skin in the origin of amniotes: Permeability barrier, protective covering and mechanical support. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 327–352. Academic Press, San Diego.

Frost, D. R., Ed. (1985). "Amphibian Species of the World." Allen Press & Assoc. System. Collns., Lawrence, KS.

Frost, D. R. (1992). Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). *Am. Mus. Novitates* **3033:** 1–68.

Frost, D. R., and Etheridge, R. (1989). A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ., Univ. Kansas, Mus. Nat. Hist.* **81:** 1–65.

Full, R. J. (1986). Locomotion without lungs: Energetics and performance of a lungless salamander. *Am. J. Physiol.* **251:** 775–780.

Fusari, M. H. (1985). Drinking of soil water by the California legless lizard, *Anniella pulchra. Copeia* **1985:** 981–986.

Gabe, M. (1970). The adrenal. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 263–318. Academic Press, London.

Gaffney, E. S. (1975). A phylogeny and classification of the higher categories of turtles. *Bull. Am. Mus. Nat. Hist.* **155:** 387–436.

Gaffney, E. S. (1977). The side-necked turtle family Chelidae: A theory of relationships using shared derived characters. *Am. Mus. Novitates* **2620:** 1–28.

Gaffney, E. S. (1979). Comparative cranial morphology of Recent and fossil turtles. *Bull. Am. Mus. Nat. Hist.* **164:** 65–376.

Gaffney, E. S. (1980). Phylogenetic relationships of the major groups of amniotes. *In* "The Terrestrial Environment and the Origin of Land Vertebrates" (L. Panchen, Ed.), pp. 593–610. Academic Press, London.

Gaffney, E. S. (1984). Historical analysis of theories of chelonian relationship. *Syst. Zool.* **33:** 283–301.

Gaffney, E. S. (1986). Triassic and Early Jurassic turtles. *In* "The Beginnings of the Age of Dinosaurs" (K. Padian, Ed.), pp. 183–187. Cambridge Univ. Press, Cambridge.

Gaffney, E. S. (1990). The comparative osteology of the Triassic turtle *Proganochelys. Bull. Am. Mus. Nat. Hist.* **194:** 1–263.

Gaffney, E. S. (1991). The fossil turtles of Australia. *In* "Vertebrate Palaeontology of Australasia" (P. Vickers-Rich, J. M. Monaghan, R. F. Baird, and T. H. Rich, Eds.), pp. 704–719. Pioneer Design Studio, Lilydale, Australia.

Gaffney, E. S., and Kitching, J. W. (1994). The most ancient African turtle. *Nature* **369:** 55–58.

Gaffney, E. S., and Meylan, P. (1988). A phylogeny of turtles. *In* "The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds" (M. J. Benton, Ed.), pp. 157–219. Clarendon Press, Oxford.

Gaffney, E., and Schleich, H. H. (1994). New reptile material from the German Tertiary. 16. On *Chelydropsis murchisoni* (Bell, 1892) from the Middle Miocene locality of Unterwohlbach/south Germany. *Courier Forsch.-Inst. Senckenberg* **173:** 197–213.

Gaffney, E. S., Hutchinson, J. H., Jenkins, F. A., Jr., and Meeker, L. J. (1987). Modern turtle origins: The oldest known cryptodire. *Science.* **237:** 289–291.

Gaffney, E. S., Meylan, P. A., and Wyss, A. R. (1991). A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics* **7:** 313–335.

Gallardo, J. M. (1987). "Anfibios Argentinos." Bibliotecha Mosaico, Buenos Aires.

Gans, C., and coeditors (1969 et seq.). "Biology of the Reptilia," Vols. 1–4, 6, 11, 19. Several publishers.

Gans, C. (1974). "Biomechanics: An Approach to Vertebrate Biology." J. B. Lippincott Co., Philadelphia.

Gans, C. (1976). Aspects of the biology of uropeltid snakes. *In* "Morphology and Biology of Reptiles" (A. d'A. Bellairs and C. B. Cox, Eds.), pp. 191–205. Linnean Society of London, London.

Gans, C. (1978). The characteristics and affinities of the Amphisbaenia. *Trans. Zool. Soc. London* **34:** 347–416.

Gans, C. (1979). A subterranean snake with a funny tail. *Nat. Hist.* **88:** 70–75.

Gans, C. (1986). Automimicry and Batesian mimicry in uropeltid snakes: Pigment pattern, proportions, and behavior. *J. Bombay Nat. Hist. Soc.* **83:** 152–158.

Gans, C., and Gorniak, G. C. (1982). Functional morphology of lingual protrusion in marine toad (*Bufo marinus*). *J. Morphol.* **163:** 195–222.

Gans, C., and Kraklau, D. M. (1989). Studies on amphisbaenians (Reptilia) 8. Two genera of small species from East Africa (*Geocalamus* and *Loveridgea*). *Am. Mus. Novitates* **2944:** 1–28.

Gans, C., and Maderson, P. F. A. (1973). Sound producing mechanisms in recent reptiles: A review and comment. *Am. Zool.* **13:** 1195–1203.

Gans, C., Gillingham, J. C., and Clark, D. L. (1984). Courtship, combat and male combat in tuatara. *J. Herpetol.* **18:** 194–197.

Gans, C., Darevski, I., and Tatarinov, L. P. (1987). *Sharovipteryx,* a reptilian glider? *Paleobiology* **13:** 415–426.

Gao, K. (1997). *Sineoamphisbaena* phylogenetic relationships discussed: Reply. *Can. J. Earth Sci.* **34:** 886–889.

Gao, K., and Fox, R. C. (1996). Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bull. Carnegie Mus. Nat. Hist.* **33:** 1–107.

Gao, K., and Hou, L. (1995). Late Cretaceous fossil record and paleobiogeography of iguanian squamates. *In* "Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers" (A. Sun and Y. Wang, Eds.), pp. 47–50. China Ocean Press, Beijing.

Gao, K., and Nessov, L. A. (1998). Early Cretaceous squamates from the Kyzylkum Desert, Uzbekistan. *N. Jb. Geol. Paläont. Abh.* **207:** 289–309.

Gao, K., and Norell, M. A. (1998). Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguimorphan lizards. *Am. Mus. Novitates* **3230:** 1–51.

Gardner, J. D., Russell, A. P., and Brinkman, D. B. (1995). Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. *Can. J. Earth Sci.* **32:** 631–643.

Garland, T., Jr. (1994). Phylogenetic analysis of lizard endurance capacity in relation to body size and body temperature. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 237–259. Princeton Univ. Press, Princeton, NJ.

Garland, T., Jr., and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. *In* "Ecological Morphology: Integrative Organismal Biology" (P. C. Wainwright and S. M. Reilly, Eds.), pp. 204–302. Univ. Chicago Press, Chicago.

Garrick, L. D., and Lang, J. W. (1977). Social signals and behaviors of adult alligators and crocodiles. *Am. Zool.* **17:** 225–239.

Garrick, L. D., Lang, J. W., and Herzog, J. H. A. (1978). Social signals of adult American alligators. *Bull. Am. Mus. Nat. Hist.* **160:** 153–192.

Garstka, J. W., and Crews, D. (1981). Female sex pheromones in the skin and circulation of a garter snake. *Science* **214:** 681–683.

Garstka, J. W., and Crews, D. (1986). Pheromones and reproduction in garter snakes. *In* "Chemical Signals in Vertebrates, IV. Ecology, Evolution, and Comparative Biology" (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, Eds.), pp. 243–260. Plenum Press, New York.

Gasc, J.-P. (1981). Axial musculature. *In* "Biology of the Reptilia. Volume 11. Morphology F" (C. Gans and T. S. Parsons, Eds.), pp. 355–435. Academic Press, London.

Gasparini, Z. (1996). Biogeographic evolution of the South American crocodilians. *In* "Contributions of Southern South America to Vertebrate Paleontology" (G. Arratia, Ed.), pp. 159–184. *Müncher Geowiss. Abh. A* **30.**

Gauthier, J. A. (1982). Fossil xenosaurid and anguid lizards from the Early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contrib. Geol., Univ. Wyoming* **21:** 7–54.

Gauthier, J. (1986). Saurischian monophyly and the origin of birds. *In* "The Origin of Birds and the Evolution of Flight" (K. Padian, Ed.), pp. 1–55. Mem. Calif. Acad. Sci., San Francisco.

Gauthier, J., Estes, R., and de Queiroz, K. (1988a). A phylogenetic analysis of Lepidosauromorpha. *In* "Phylogenetic Relationships of the Lizard Families. Essay Commemorating Charles L. Camp" (R. Estes and G. Pregill, Eds.), pp.15–98. Stanford Univ. Press, Stanford, CA.

Gauthier, J., Kluge, A. G., and Rowe, T. (1988b). Amniote phylogeny and the importance of fossils. *Cladistics* **4:** 105–209.

Gauthier, J. A., Kluge, A. G., and Rowe, T. (1988c). The early evolution of the Amniota. *In* "The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds" (M. J. Benton, Ed.), pp. 103–155. Clarendon Press, Oxford.

Gauthier, J., Cannatella, D., de Queiroz, K., Kluge, A. G., and Rowe, T. (1989). Tetrapod phylogeny. *In* "The Hierarchy of Life" (B. Fernholm, K. Bremer, and H. Jörnwall, Eds.), pp. 337–353. Elsevier Science Publisher B. V., Amsterdam.

Gehlbach, F. R., and Walker, B. (1970). Acoustic behavior of the aquatic salamander, *Siren intermedia*. *BioScience* **20:** 1107–1108.

Gehlbach, F. R., Kimmel, J. R., and Weems, W. A. (1969). Aggregations and body water relations in tiger salamanders (*Ambystoma tigrinum*) from the Grand Canyon rims, Arizona. *Physiol. Zool.* **42:** 173–182.

Geiger, A. (1995). Der Laubfrosch (*Hyla arborea*) Ökologie und Artenschutz. *Mertensiella* **6:** 1–196.

Geise, W., and Linsenmair, K. E. (1986). Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment: 2. Some aspects of the water economy of *Hyperolius viridiflavus nitidulus* under wet and dry season conditions. *Oecologia* **68:** 542–548.

Gensel, P. G., and Andrews, H. N. (1987). The evolution of early land plants. *Am. Sci.* **75:** 478–489.

George, R. H. (1996). Health problems and diseases of sea turtles. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 363–385. CRC Press, Boca Raton, FL.

Georges, A. G., and Wombey, J. C. (1993). Family Carettochelyidae. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 153–156. Aust. Govern. Publ. Serv., Canberra.

Georges, A. G., Limpus, C. J., and Parmenter, C. J. (1993). Natural history of the Chelonia. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 120–128. Aust. Govern. Publ. Serv., Canberra.

Georges, A., Birrell, J., Saint, K. M., McCord, W., and Donnellan, S. C. (1998). A phylogeny for side-necked turtles (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequence variation. *Biol. J. Linn. Soc.* **67:** 213–246.

Gerritsen, J., and Strickler, J. R. (1977). Encounter probabilities and community structure in zooplankton: A mathematical model. *J. Fish. Res. Bd. Can.* **34:** 73–82.

Gibbons, J. W. (1968). Carapacial algae in a population of the painted turtle, *Chrysemys picta*. *Am. Midl. Nat.* **79:** 517–519.

Gibbons, J. W. (1970). Terrestrial activity and the population dynamics of aquatic turtles. *Am. Midl. Nat.* **83:** 404–414.

Gibbons, J. W. (1972). Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia* **1972:** 222–226.

Gibbons, J. W., Ed. (1990). "Life History and Ecology of the Slider Turtle." Smithsonian Inst. Press, Washington. DC.

Gibbons, J. W. (1994). Reproductive patterns of reptiles and amphibians: Considerations for captive breeding and conservation. *In* "Captive Management and Conservation of Amphibians and Reptiles" (J. B. Murphy, K. Adler, and J. T. Collins, Eds.), pp. 119–123. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Gibbons, J. W., and Bennett, D. H. (1974). Determination of anuran terrestrial activity patterns by a drift fence method. *Copeia* **1974:** 236–243.

Gibbons, J. W., and Lovich, J. E. (1990). Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monog.* **4:** 1–29.

Gibbons, J. W., and Nelson, D. H. (1978). The evolutionary significance of delayed emergence from the nest by hatchling turtles. *Evolution* **32:** 297–303.

Gibbons, J. W., and Semlitsch, R. D. (1991). "Guide to the Reptiles and Amphibians of the Savannah River Site." Univ. Georgia Press, Athens, GA.

Gibbons, J. W., and Smith, M. H. (1968). Evidence of orientation by turtles. *Herpetologica* **24:** 331–333.

Gibbons, J. W., Greene, J. L., and Congdon, J. D. (1990). Temporal and spatial movement patterns of sliders and other turtles. *In* "Life History and Ecology of the Slider Turtle" (J. W. Gibbons, Ed.), pp. 201–215. Smithsonian Inst. Press, Washington, DC.

Gibbs, J. P. (1998). Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecol.* **13:** 263–268.

Gill, B., and Whitaker, T. (1996). "New Zealand Frogs & Reptiles." David Bateman, Auckland.

Gill, D. E. (1978). The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens. Ecol. Monog.* **48:** 145–166.

Gill, D. E. (1979). Density dependence and homing behavior in adult red-spotted newts *Notophthalmus viridescens* (Rafinesque). *Ecology* **60:** 800–813.

Gillingham, J. C. (1987). Social behavior. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 184–209. Macmillan, New York.

Gillingham, J. C., Carmichael, C., and Miller, T. (1995). Social behavior of the tuatara, *Sphenodon punctatus. Herpetol. Monog.* **9:** 5–16.

Gillis, R., and Ballinger, R. E. (1992). Reproductive ecology of red-chinned lizards (*Sceloporus undulatus erythrocheilus*) in southcentral Colorado: Comparisons with other populations of a wide-ranging species. *Oecologia* **89:** 236–243.

Given, M. F. (1988). Territoriality and aggressive interactions of male carpenter frogs, *Rana virgatipes. Copeia* **1988:** 411–421.

Glaw, F., and Köhler, J. (1998). Amphibian species diversity exceeds that of mammals. *Herpetol. Rev.* **29:** 11–12.

Glaw, F., and Vences, M. (1994). "A Fieldguide to the Amphibians and Reptiles of Madagascar" (M. Vences and F. Glaw, Eds.) Verlag GbR, Cologne.

Glaw, F., Vences, M., and Böhme, W. (1998). Systematic revision of the genus *Aglyptodactylus* Boulenger, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna, Boophis, Mantidactylus,* and *Mantella*). *J. Zool. Syst. Evol. Res.* **36:** 17–37.

Glodek, G. S., and Voris, H. K. (1982). Marine snake diets: Prey composition, diversity and overlap. *Copeia* **1982:** 661–666.

Gloyd, H. K., and Conant, R. (1990). "Snakes of the *Agkistrodon* Complex: A Monographic Review." Soc. Study Amphibians and Reptiles, Ithaca, NY.

Godley, J. S. (1980). Foraging ecology of the stripped swamp snake, *Regina alleni,* in southern Florida. *Ecol. Monog.* **50:** 411–436.

Godley, J. S. (1983). Observations on the courtship, nests and young of *Siren intermedia* in southern Florida. *Am. Midl. Nat.* **110:** 215–219.

Goicoechea, O., Carrido, O, and Jorquera, B. (1986). Evidence for a trophic paternal-larval relationship in the frog *Rhinoderma darwinii. J. Herpetol.* **20:** 168–178.

Goin, C. J. (1960). Amphibians, pioneers of terrestrial breeding habits. *Smith. Rep.* **1959:** 427–455.

Goldberg, S. R. (1971). Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. *Herpetologica* **27:** 123–131.

Goldberg, S. R., and Miller, C. M. (1985). Reproduction of the silvery legless lizard, *Anniella puchra pulchra* (Anniellidae), in southern California. *Southw. Nat.* **30:** 617–619.

Good, D. A. (1989). Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). *Evolution* **43:** 728–744.

Good, D. A. (1994). Species limits in the genus *Gerrhonotus* (Squamata: Anguidae). *Herpetol. Monog.* **8:** 180–202.

Good, D. A., and Wake, D. B. (1992). Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). *Univ. Calif. Publ., Zool.* **126:** i–xii, 1–91.

Goodman, M., Miyamoto, M., and Czelusniak, J. (1987). Patterns and process in vertebrate phylogeny revealed by coevolution of molecules and morphologies. *In* "Molecules and Morphology in Evolution: Conflict or Compromise" (C. Patterson, Ed.), pp. 141–176. Cambridge Univ. Press, Cambridge.

Goodrich, E. S. (1930/1958). "Studies on the Structure and Development of Vertebrates. Volume I," reprint. Dover Publ., Inc., New York.

Goodwin, T. M., and Marion, W. R. (1978). Aspects of the nesting ecology of American alligators (*Alligator mississippiensis*) in north-central Florida. *Herpetologica* **34:** 43–47.

Goodyear, C. P. (1971). Y-axis orientation of the oak toad, *Bufo quercicus. Herpetologica* **27:** 320–323.

Goodyear, C. P., and Altig, R. (1971). Orientation of bullfrogs (*Rana catesbeiana*) during metamorphosis. *Copeia* **1971:** 362–364.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16:** 183–190.

Gower, D. J., and Wilkinson, M. (1996). Is there any consensus on basal archosaur phylogeny? *Proc. Roy. Soc. London B* **263:** 1399–1406.

Gradstein, S. R., and Equihua, C. (1995). An epizoic bryophyte and algae growing on the lizard *Corytophanes cristatus* in Mexican rain forest. *Biotropica* **27:** 265–268.

Graf, J.-D. (1996). Molecular approaches to the phylogeny of *Xenopus. In* ''The Biology of *Xenopus*'' (R. C. Tinsley and H. R. Kobel, Eds.), pp. 379–401. Zool. Soc. London, London.

Graf, J.-D., and Polls Pelaz, M. (1989). Evolutionary genetics of the *Rana esculenta* complex. *In* ''Evolution and Ecology of Unisexual Vertebrates'' (R. M. Dawley and J. P. Bogart, Eds.), pp. 289–302. State Univ. New York, Albany.

Graham, A., and Beard, P. (1973). ''Eyelids of Morning. The Mingled Destinies of Crocodiles and Men.'' New York Graphic Soc., Ltd., Greenwich, CT.

Graham, J. B. (1997). ''Air-Breathing Fishes. Evolution, Diversity, and Adaptation.'' Academic Press, San Diego.

Grandison, A. G. C. (1977). ''H. W. Parker Snakes. A Natural History. Second Edition.'' British Mus. (Nat. Hist.), London.

Grandison, A. G. C., and Ashe, S. (1983). The distribution, behavioural ecology and breeding strategy of the pygmy toad, *Mertensophryne micranotis* (Lov.). *Bull. Br. Mus. Nat. Hist. (Zool.)* **45:** 85–93.

Grant, B. W. (1990). Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami. Ecology* **71:** 2323–2333.

Grant, D., Anderson, O., and Twitty, V. C. (1973). Homing orientation by olfaction in newts (*Taricha rivularis*). *Science* **160:** 1354–1355.

Grant, T., Humphrey, E. C., and Myers, C. W. (1997). The median lingual process of frogs: A bizarre character of Old World ranoids discovered in South American dendrobatids. *Am. Mus. Novitates* **3212:** 1–40.

Grassman, M. A., Owens, D. W., McVey, J. P., and Marquez, M. R. (1984). Olfactory-based orientation in artificially imprinted sea turtles. *Science* **224:** 83–84.

Gray, E. M. (1995). DNA fingerprinting reveals a lack of genetic variation in northern populations of the western pond turtle (*Clemmys marmorata*). *Conserv. Biol.* **9:** 1244–1255.

Gray, R. D. (1987). Faith and foraging: a critique of the 'paradigm argument from design.' *In* ''Foraging Behavior'' (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, Eds.), pp. 69–140. Plenum Press, New York.

Graybeal, A. (1997). Phylogenetic relationships of bufonid frogs and tests of alternate macroevolutionary hypotheses characterizing their radiation. *Zool. J. Linn. Soc.* **119:** 297–338.

Graybeal, A., and Cannatella, D. C. (1995). A new taxon of Bufonidae from Peru, with descriptions of two new species and a review of the phylogenetic status of supraspecific bufonid taxa. *Herpetologica* **51:** 105–131.

Green, D. M. (1994). Genetic and cytogenetic diversity in Hochstetter's frog, *Leiopelma hochstetteri,* and its importance for conservation management. *NZ J. Zool.* **21:** 417–424.

Green, D. M., and Campbell, R. W. (1984). ''The Amphibians of British Columbia.'' Royal British Columbia Museum Handbook, Victoria.

Green,. D. M., and Cannatella, D. C. (1993). Phylogenetic significance of the amphicoelous frogs, Ascaphidae and Leiopelmatidae. *Ethol. Ecol. Evol.* **5:** 233–245.

Green, D. M., and Sessions, S. K., Eds. (1991). ''Amphibian Cytogenetics and Evolution.'' Academic Press, New York.

Green, D. M., Sharbel, T. F., Hitchmough, R. A., and Daugherty, G. H. (1989). Genetic variation in the genus *Leiopelma* and relationships to other primitive frogs. *Z. Zool. Syst. Evol.-Forsch.* **27:** 65–79.

Greenberg, G., and Noble, G. K. (1944). Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Physiol. Zool.* **17:** 392–439.

Greene, H. W. (1982). Dietary and phenotypic diversity in lizards: Why are some organisms specialized? *In* ''Environmental Adaptation and Evolution'' (D. Mossakowski and G. Roth, Eds.), pp. 107–128. Gustav Fischer, Stuttgart.

Greene, H. W. (1986). Natural history and evolutionary biology. *In* ''Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates'' (M. E. Feder and G. V. Lauder, Eds.), pp. 99–108. Univ. Chicago Press, Chicago.

Greene, H. W. (1988). Antipredator mechanisms in reptiles. *In* ''Biology of the Reptilia. Volume 16: Ecology B. Defense and Life History'' (C. Gans and R. B. Huey, Eds.), pp. 1–152. Alan R. Liss, Inc., New York.

Greene, H. W. (1997). ''Snakes. The Evolution of Mystery in Nature.'' Univ. California Press, Berkeley.

Greene, H. W., and McDiarmid, R. W. (1981). Coral snake mimicry: Does it occur? *Science* **213:** 1207–1212.

Greer, A. E. (1970a). Evolutionary and systematic significance of crocodilian nesting habits. *Nature* **227:** 523–524.

Greer, A. E. (1970b). A subfamilial classification of scincid lizards. *Bull. Mus. Comp. Zool.* **139:** 151–183.

Greer, A. E. (1974). The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Aust. J. Zool., Suppl. Ser.* **31:** 1–67.

Greer, A. E. (1975). Clutch size in crocodilians. *J. Herpetol.* **9:** 319–322.

Greer, A. E. (1976). On the evolution of the giant Cape Verde scincid lizard *Macroscincus coctei. J. Nat. Hist.* **10**: 691–712.

Greer, A. E. (1985). The relationships of the lizard genera *Anelytropsis* and *Dibamus. J. Herpetol.* **19:** 116–156.

Greer, A. E. (1989). ''The Biology and Evolution of Australian Lizards.'' Surrey Beatty & Son, Pty Ltd., Chipping Norton, N.S.W.

Greer, A. E. (1997). ''The Biology and Evolution of Australian Snakes.'' Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Gregory, P. T. (1974). Patterns of emergence of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. *Can. J. Zool.* **52:** 1063–1069.

Gregory, P. T. (1982). Reptilian hibernation. *In* ''Biology of the Reptilia. Volume 13, Physiology D, Physiological

Ecology" (C. Gans and F. H. Pough, Eds.), pp. 53–154. Academic Press, New York.

Gregory, P. T. (1984). Communal denning in snakes. *In* "Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch" (R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag, Eds.), pp. 57–75. Univ. Kansas Mus. Nat. Hist., Spec. Publ., Lawrence, KS.

Gregory, W. K. (1951). "Evolution Emerging. Vol. II." Macmillan Co., New York.

Griffiths, I. (1963). The phylogeny of the Salientia. *Biol. Rev.* **38:** 241–292, Plate I.

Griffiths, R. A. (1996). "Newts and Salamanders of Europe." Academic Press, London.

Grillitsch, B., and Chovanec, A. (1995). Heavy metals and pesticides in anuran spawn and tadpoles, water, and sediment. *Toxicol. Environ. Chem.* **50:** 131–155.

Grillitsch, B., Grillitsch, H., Häupl, M., and Tiedemann, F. (1983). "Lurche und Kriechtiere Niederösterreichs." Facultas Verlag, Vienna.

Grismer, L. L. (1988). Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. *In* "Phylogenetic Relationships of the Lizard Families" (R. Estes and G. Pregill, Eds.), pp. 369–469. Stanford Univ. Press, Stanford, CA.

Grismer, L. L., Ota, H., and Tanaka, S. (1994). Phylogeny, classification, and biogeography of *Goniurosaurus kuroiwae* (Squamata: Eublepharidae) from the Ryukyu Archipelago, Japan, with description of a new subspecies. *Zool. Sci.* **11:** 319–335.

Gross, M. R., and Shine, R. (1981). Parental care and mode of fertilization in ectothermic vertebrates. *Evolution* **35:** 775–793.

Groves, J. D. (1981). Observations and comments on the post-parturient behavior of some tropical boas of the genus *Epicrates*. *Br. J. Herpetol.* **6:** 89–91.

Grubb, P. (1971). The growth, ecology and population structure of giant tortoises on Aldabra. *Philos. Trans. R. Soc. London Ser. B* **260:** 327–372.

Guard, C. I. (1979). The reptilian digestive system: General characteristics. *In* "Comparative Physiology: Primitive Mammals" (K. Schmidt-Nielsen, L. Bolis, and C. R. Taylor, Eds.), pp. 43–51. Cambridge Univ. Press, New York.

Guillette, L. J., Jr. (1987). The evolution of viviparity in fishes, amphibians and reptiles: An endocrine approach. *In* "Hormones and Reproduction in Fishes, Amphibians, and Reptiles" (D. O. Norris and R. E. Jones, Eds.), pp. 523–569. Plenum, New York.

Guillette, L. J., Jr. (1995). Endocrine disrupting environmental contaminants and developmental abnormalities in embryos. *Human Ecol. Risk Assess.* **1995:** 25–36.

Guillette, L. J., Jr., and Gongora, G. L. (1986). Notes on oviposition and nesting in the high elevation lizard, *Sceloporus aeneus*. *Copeia* **1986:** 232–233.

Guillette, L. J., Jr., and Méndez-de la Cruz, F. (1993). The reproductive cycle of the viviparous Mexican lizard *Sceloporus torquatus*. *J. Herpetol.* **27:** 168–174.

Guillette, L. J., Jr., Jones, R. E., Fitzgerald, K. T., and Smith, H. M. (1980). Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetologica* **36:** 201–215.

Guillette, L. J., Jr., Arnold, S. F., and Mclachlan, J. A. (1996). Ecoestrogens and embryos-Is there a scientific basis for concern? *Anim. Reprod. Sci.* **42:** 13–24.

Guimond, R. W., and Hutchison, V. H. (1972). Pulmonary, brachial, and cutaneous gas exchange in the mudpuppy, *Necturus maculosus maculosus* (Rafinesque). *Comp. Biochem. Physiol.* **42A:** 367–392.

Guimond, R. W., and Hutchison, V. H. (1976). Gas exchange of the giant salamanders of North America. *In* "Respiration of Amphibious Vertebrates" (G. M. Hughes, Ed.) pp. 313–338. Academic Press, New York.

Gundappa, K. R., Balakrishna, R. T. A., and Shakuntala, K. (1981). Ecology of *Ichthyophis glutinosus* (Linn.) (Apoda, Amphibia). *Curr. Sci., Bangalore* **50:** 480–483.

Guttman, S. I. (1985). Biochemical studies of anuran evolution. *Copeia* **1985:** 292–309.

Guyer, C. (1991). Orientation and homing behavior as a measure of affinity for the home range in two species of iguanid lizards. *Amphibia-Reptilia* **12:** 373–384.

Guyer, C., and Savage, J. M. (1987). Cladistic relationships among anoles (Sauria: Iguanidae). *Syst. Zool.* **35:** 509–531.

Gyi, K. K. (1970). A revision of colubrid snakes of the subfamily Homalopsinae. *Univ. Kansas Publ., Mus. Nat. Hist.* **20:** 47–223.

Haas, G. (1973). Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. *In* "Biology of the Reptilia. Volume 4. Morphology D" (C. Gans and T. S. Parsons, Eds.), pp. 285–490. Academic Press, London.

Haddad, C. F. B., and Giaretta, A. A. (1999). Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). *J. Herpetol.* **55:** 324–333.

Hahn, W. E. (1967). Estradiol-induced vitellinogenesis and concomitant fat mobilization in the lizard *Uta stansburiana*. *Comp. Biochem. Physiol.* **23:** 83–93.

Hahn, W. E., and Tinkle, D. W. (1965). Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *J. Exp. Zool.* **158:** 79–86.

Hairston, N. G. (1983). Growth, survival and reproduction of *Plethodon jordani:* Trade-offs between selective pressures. *Copeia* **1983:** 1024–1035.

Hairston, N. G., Sr. (1996). Predation and competition in salamander communities. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 161–189. Academic Press, San Diego.

Hall, R. J., and Fitch, H. S. (1972). Further observations on the demography of the great plains skink (*Eumeces obsoletus*). *Trans. Kansas Acad. Sci.* **74:** 94–98.

Hallermann, J. (1994). Zur Morphologie der Ethmoidalregion der Iguania (Squamata)—Eine vergleichend-anatomische Untersuchung. *Bonn. Zool. Monog.* **35:** 1–133.

Hallermann, J. (1998). The ethmoidal region of *Dibamus taylori* (Squamata: Dibamidae), with a phylogenetic hypothesis on dibamid relationships within Squamata. *Zool. J. Linn. Soc.* **122:** 385–426.

Halliday, T. R. (1977). The courtship of European newts: An evolutionary perspective. *In* "Reproductive Biology of

Amphibians" (D. H. Taylor and S. I. Guttman, Eds.), pp. 185–232. Plenum Press, New York.

Halliday, T., and Adler, K., Eds. (1986). "The Encyclopedia of Reptiles and Amphibians." Facts on File Inc., New York.

Halliday, T. R., and Heyer, W. R. (1997). The case of the vanishing frogs. *MIT's Tech. Rev.* May/June: 56–63.

Halliday, T., and Tejedo, M. (1995). Intrasexual selection and alternative mating behaviour. *In* "Amphibian Biology. Volume 2, Social Behaviour" (H. Heatwole and B. K. Sullivan, Eds.), pp. 419–468. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Halpern, M. (1992). Nasal chemical senses in reptiles: Structure and function. *In* "Biology of the Reptilia. Volume 18, Physiology. Hormones, Brain, and Behavior" (C. Gans and D. Crews, Eds.), pp. 422–523. Univ. Chicago Press, Chicago.

Hamilton, J., and Coe, M. (1982). Feeding, digestion and assimilation of a population of giant tortoises (*Geochelone gigantea*) on Aldabra atoll. *J. Arid Environ.* **5:** 127–144.

Hanken, J. (1986). Developmental evidence for amphibian origins. *Evol. Biol.* **20:** 389–417.

Hanken, J. (1989). Development and evolution in amphibians. *Am. Sci.* **77:** 336–343.

Hanken, J., and Hall, B. K., Eds. (1993). "The Skull. Volumes 1–3." Univ. Chicago Press, Chicago.

Hanski, I., and Simberloff, D. (1997). The metapopulation approach, its history, conceptual domain, and application to conservation. *In* "Metapopulation Biology: Ecology, Genetics, and Evolution" (I. A. Hanski and M. E. Gilpen, Eds.), pp. 5–26. Academic Press, San Diego.

Hardy, D. L. (1994). A re-evaluation of suffocation as the cause of death during constriction by snakes. *Herp. Rev.* **25:** 45–47.

Hartline, P. H. (1967). The unbelievable fringed turtle. *Int. Turtle Tortoise Soc. J.* **1:** 24–29.

Hass, C. A., Hoffman, M. A., Densmore, L. D., and Maxson, L. R. (1992). Crocodilian evolution: Insights from immunological data. *Mol. Phylog. Evol.* **1:** 193–201.

Hass, C. A., Nussbaum, R. A., and Maxson, L. R. (1993). Immunological insights into the evolutionary history of caecilian (Amphibia: Gymnophiona): Relationships of the Seychellean caecilians and a preliminary report on family-level relationships. *Herpetol. Monog.* **7:** 56–63.

Hay, J. M., Ruvinsky, I., Hedges, S. B., and Maxson, L. R. (1995). Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Mol. Biol. Evol.* **12:** 928–937.

Hayashi, T., and Matsui, M. (1989). Preliminary study of phylogeny in the family Salamandridae: Allozyme data. *In* "Current Herpetology in East Asia" (M. Matsui, T. Hikida, and R. C. Goris, Eds.), pp. 157–167. Herpetol. Soc. Japan, Kyoto.

Hayes, M. P. (1983). Predation on the adults and prehatching stages of glass frogs (Centrolenidae). *Biotropica* **15:** 74–76.

Hayes, T. B., Coord. (1997a). Amphibian metamorphosis: An integrative approach. *Am. Zool.* **37:** 121–207.

Hayes, T. B. (1997b). Steroids as potential modulators of thyroid hormone activity in anuran metamorphosis. *Am. Zool.* **37:** 185–194.

Hayes, T. B., Wu, T. H., and Gill, T. N. (1997). DDT-like effects as a result of corticosterone treatment in an anuran amphibian: Is DDT a corticoid mimic or a stressor? *Environ. Toxicol. Chem.* **16:** 1948–1953.

Hayes, W. K., Kaiser, I. I., and Duvall, D. (1992). The mass of venom expended by prairie rattlesnakes when feeding on rodent prey. *In* "Biology of Pitvipers" (J. A. Campbell and E. D. Brodie, Jr., Eds.), pp. 383–388. Selva, Tyler, TX.

Heatwole, H. (1999). "Sea Snakes," 2nd ed. Krieger Publ. Co., Malabar, FL.

Heatwole, H., and Barthalmus, G. T. (1994). "Amphibian Biology. Volume 1. The Integument." Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Heatwole, H., and Cogger, H. G. (1993). Family Hydrophiidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 310–318. Australian Govern. Publ. Serv., Canberra.

Heatwole, H., and Guinea, M. L. (1993). Family Laticaudinae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 319–321. Australian Govern. Publ. Serv., Canberra.

Hecnar, S. J., and M'Closkey, R. T. (1996). Regional dynamics and the status of amphibians. *Ecology* **77:** 2091–2097.

Hedges, S. B. (1986). An electrophoretic analysis of Holarctic hylid frog evolution. *Syst. Zool.* **35:** 1–21.

Hedges, S. B., and Maxson, L. R. (1996). Re: Molecules and morphology in amniote phylogeny. *Mol. Phylog. Evol.* **6:** 312–314.

Hedges, S. B., and Poling, L. L. (1999). A molecular phylogeny of reptiles. *Science* **283:** 998–1001.

Hedges, S. B., Bezy, R. L., and Maxson, L. R. (1991). Phylogenetic relationships and biogeography of xantusiid lizards, inferred from mitochondrial DNA sequences. *Mol. Biol. Evol.* **8:** 767–780.

Hedges, S. B., Hass, C. A., and Maxson, L. R. (1993a). Relations of fish and tetrapods. *Nature* **363:** 501–502.

Hedges, S. B., Nussbaum, R. A., and Maxson, L. R. (1993b). Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes (Amphibia: Gymnophiona). *Herpetol. Monog.* **7:** 64–76.

Heise, P. J., Maxson, L. R., Dowling, H. G., and Hedges, S. B. (1995). Higher-level snake phylogeny inferred from mitochondrial DNA sequences of 12S rRNA and 16S rRNA genes. *Mol. Biol. Evol.* **12:** 259–265.

Hemmer, H., and Alcover, J. A., Eds. (1984). "Història Biològica del Ferreret" (Life History of the Mallorcan Midwife Toad). Editorial Moll, Palma de Mallorca.

Henderson, R. W. (1993). *Corallus. Catalog. Am. Amphib. Rept.* **572:** 1–2.

Hennig, W. (1966). "Phylogenetic Systematics." Univ. Chicago Press, Chicago.

Henrici, A. C. (1994). *Tephrodytes brassicarvalis,* new genus and species (Anura: Pelodytidae), from the Arikareean

Cabbage Patch Beds of Montana, USA, and pelodytid-pelobatid relationships. *Ann. Carnegie Mus. Nat. Hist.* **63:** 155–183.

Henrici, A. C. (1998). A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. *J. Vert. Paleontol.* **18:** 321–322.

Herbeck, L. A., and Larsen, D. R. (1999). Plethodontid salamander response to silvicultural practices in Missouri Ozark forest. *Conserv. Biol.* **13:** 623–632.

Herbst, L. H. (1994). Fibropapillomatosis of marine turtles. *Ann. Rev. Fish Diseases* **4:** 389–425.

Herbst, L. H., and Klein, P. A. (1995). Green turtle fibropapillomatosis: Challenges to assessing the role of environmental cofactors. *Environ. Health Perspect.* **103** (Suppl. 4): 27–30.

Hermann, H.-W., and Joger, U. (1997). Evolution of viperine snakes. *In* "Venomous Snakes, Ecology, Evolution and Snakebite" (R. S. Thorpe, W. Wüster, and A. Malhotra, Eds.), pp. 43–61. Zool. Soc., London.

Herrmann, H.-J. (1993). "Ruder-und Riedfrösche. Baumfrösche mit interessantem Verhalten für attraktive Terriarien." Tetra-Verlag, Melle, Germany.

Hertz, P. E., Huey, R. B., and Nevo, E. (1982). Fight versus flight: Body temperature influences defensive responses of lizards. *Anim. Behav.* **30:** 676–679.

Hertz, P. E., Huey, R. B., and Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *Am. Nat.* **142:** 796–818.

Hetherington, T. E. (1985). Role of the opercularis muscle in seismic sensitivity in the bullfrog *Rana catesbeiana. J. Exp. Zool.* **235:** 27–34.

Hetherington, T. E., Jaslow, A. P., and Lombard, R .E. (1986). Comparative morphology of the amphibian opercularis system: I. General design features and functional interpretation. *J. Morphol.* **190:** 43–61.

Heyer, W. R. (1967). A herpetofaunal study of an ecological transect through the Cordillera de Tilarán, Costa Rica. *Copeia* **1967:** 259–271.

Heyer, W. R. (1969). The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* **23:** 421–428.

Heyer, W. R. (1975). A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. *Smith. Contrib. Zool.* **199:** 1–55.

Heyer, W. R. (1979). Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smith. Contrib. Zool.* **301:** 1–43.

Heyer, W. R., and Liem, D. S. (1976). Analysis of the intergeneric relationships of the Australian frog family Myobatrachidae. *Smith. Contrib. Zool.* **233:** 1–29.

Heyer, W. R., Rand, A. S., Goncalvez da Cruz, C. A., and Peixoto, O. L. (1988). Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. *Biotropica* **20:** 230–235.

Heyer, W. R., Rand, A. S., Cruz, C. A. G. da, Peixoto, O. L., and Nelson, C. E. (1990). Frogs of Boracéia. *Arq. Zool.* **31:** 231–410.

Hillis, D. M. (1991). The phylogeny of amphibians: Current knowledge and the role of cytogenetics. *In* "Amphibian Cytogenetics and Evolution" (D. M. Green and S. K. Sessions, Eds.), pp. 7–31. Academic Press, San Diego.

Hillis, D. M., and Green, D. M. (1990). Evolutionary changes of heterogametic sex in the phylogenetic history of amphibians. *J. Evol. Biol.* **3:** 49–64.

Hillis, D. M., Mable, B. K., Larson, A., Davis, S. K., and Zimmer, E. A. (1996a). Nucleic acid IV: Sequencing and cloning. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 321–381. Sinauer Assoc., Inc., Sunderland, MA.

Hillis, D. M., Moritz, C., and Mable, B. K., Eds. (1996b). "Molecular Systematics, Second Edition." Sinauer Assoc., Inc., Sunderland, MA.

Himstedt, W. (1996). "Die Blindwühlen." Westarp Wissenschaften, Magdeburg.

Hirayama, R. (1994). Phylogenetic systematics of chelonioid sea turtles. *Island Arc* **3:** 270–284.

Hirayama, R. (1997). Distribution and diversity of Cretaceous chelonioids. *In* "Ancient Marine Reptiles" (J. M. Callaway and E. L. Nicholls, Eds.), pp. 225–241. Academic Press, San Diego.

Hirayama, R. (1998). Oldest known sea turtle. *Nature* **392:** 705–708.

Hirschfield, M. F., and Tinkle, D. W. (1975). Natural selection and the evolution of reproductive effort. *Proc. Natl. Acad. Sci.* **72:** 2227–2231.

Hödl, W. (1990). Reproductive diversity in Amazonian lowland frogs. *Fortschr. Zool.* **38:** 41–60.

Hoff, K. S., and Hillyard, S. D. (1991). Angiotension II stimulates cutaneous drinking in the toad, *Bufo punctatus:* A new perspective on the evolution of thirst in terrestrial vertebrates. *Physiol. Zool.* **64:** 1165–1172.

Hoffstetter, R. (1955). Rhynchocephalia, Squamata. Squamata de types modernes. *In* "Traité de Paléontologie V" (J. Piveteau, Ed.), pp. 556–605, 606–662, respectively. Masson et Cie, Édit., Paris.

Hoffstetter, R. (1962). Revue des récentes acquisitions concernant l'historire et la systématique des squamates. *Coll. Intern. C. N. R. S.* **104:** 243–279.

Hoffstetter, R., and Gasc, J.-P. (1969). Vertebrae and ribs of modern reptiles. *In* "Biology of the Reptilia. Volume 1. Morphology A" (C. Gans, A. d'A. Bellairs, and T. S. Parsons, Eds.), pp. 201–310. Academic Press, London.

Hofman, A., Maxson, L. R., and Arntzen, J. W. (1991). Biochemical evidence pertaining to the taxonomic relationships within the family Chamaeleonidae. *Amphibia-Reptilia* **12:** 245–265.

Höggren, M., and Tegelström, H. (1995). DNA fingerprinting shows within-season multiple paternity in the adder (*Vipera berus*). *Copeia* **1995:** 271–277.

Holman, J. A. (1995). "Pleistocene Amphibians and Reptiles in North America." Oxford Univ. Press, New York.

Holmberg, A. R. (1957). Lizard hunts on the north coast of Peru. *Fieldiana, Anthropol.* **36**: 203–220.

Holmstrom, W. F. (1978). Preliminary observations on prey herding in the matamata turtle, *Chelus fimbriatus* (Reptilia, Testudines, Chelidae*). J. Herpetol.* **12:** 573–674.

Honegger, R. E. (1981). List of amphibians and reptiles either known or thought to have become extinct since 1600. *Biol. Conserv.* **19:** 141–158.

Hoogmoed, M. S. (1969). Notes on the herpetofauna of Surinam. II. On the occurrence of *Allophryne ruthveni* Gaige (Amphibia, Salientia, Hylidae) in Surinam. *Zool. Mededel.* **44:** 75–81.

Hoogmoed, M. S., and Cadle, J. E. (1990). Natural history and distribution of *Agalychnis craspedopus* (Funkhouser, 1957) (Amphibia: Anura: Hylidae). *Zool. Mededel.* **65:** 129–142.

Hotton, N., MacLean, P. D., Roth, J. J., and Roth, E. C. (1986). "The Ecology and Biology of Mammal-like Reptiles." Smithsonian Inst. Press, Washington, DC.

Hotton, N., Olson, E. C., and Beerbower, R. (1997). Amniote origins and the discovery of herbivory. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 207–264. Academic Press, San Diego.

Houck, L. D., and Sever, D. M. (1994). Role of the skin in reproduction and behaviour. *In* "Amphibian Biology. Volume 1, The Integument" (H. Heatwole and G. T. Barthalmus, Eds.), pp. 351–381. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Houck, L. D., and Verrell, P. A. (1993). Studies of courtship behavior in plethodontid salamanders: A review. *Herpetologica* **49:** 175–184.

Hourdry, J., and Beaumont, A. (1985). "Les Métamorphoses des Amphibien." Masson, Paris.

Howard, R. D. (1978a). The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. *Ecology* **59:** 789–798.

Howard, R. D. (1978b). The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* **32:** 850–871.

Howard, R. R., and Brodie, E. D., Jr. (1973). A Batesian mimetic complex in salamanders: Responses of avian predators. *Herpetologica* **29:** 33–41.

Howland, J. M. (1992). Life history of *Cophosaurus texanus* (Sauria: Iguanidae): Environmental correlates and interpopulational variation. *Copeia* **1992:** 82–93.

Howland, J. M., Vitt, L. J., and Lopez, P. T. (1990). Life on the edge: The ecology and life history of the tropidurine iguanid lizard *Uranoscodon superciliosum. Can. J. Zool.* **68:** 1366–1373.

Hua, S., and Buffetaut, E. (1997). Part V: Crocodylia. Introduction. *In* "Ancient Marine Reptiles" (J. M. Callaway and E. L. Nicholls, Eds.), pp. 357–374. Academic Press, San Diego.

Huang, W.-S. (1997a). Reproductive cycle of the skink, *Sphenomorphus taiwanensis,* in central Taiwan. *J. Herpetol.* **31:** 287–290.

Huang, W.-S. (1997b). Reproductive cycle of the oviparous lizard *Japalura brevipes* (Agamidae: Reptilia) in Taiwan, Republic of China. *J. Herpetol.* **31:** 22–29.

Huang, W.-S. (1998). Reproductive cycles of the grass lizard, *Takydromus hsuehshanensis,* with comments on reproductive patterns of lizards from the central high elevation area of Taiwan. *Copeia* **1998:** 866–873.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. *In* "Biology of the Reptilia. Volume 12, Physiology C. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 25–91. Academic Press, London.

Huey, R. B., and Pianka, E. R. (1981a). Ecological consequences of foraging mode. *Ecology* **62:** 991–999.

Huey, R. B., and Pianka, E. R. (1981b). Natural selection for juvenile lizards mimicking noxious beetles. *Science* **195:** 201–203.

Huey, R. B., and Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *Quart. Rev. Biol.* **51:** 363–384.

Huey, R. B., and Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Am. Zool.* **19:** 357–366.

Huey, R. B., Bennett, A. F., John-Alder, H., and Nagy, K. A. (1984). Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* **32:** 41–50.

Huey, R. B., Peterson, C. R., Arnold, S. J., and Porter, W. P. (1989a). Hot rocks and not-so-hot rocks: Retreat-site selection by garter snakes and its thermal consequences. *Ecology* **70:** 931–944.

Huey, R. B., Niewiarowski, P. H., Kaufmann, J., and Herron, J. C. (1989b). Thermal biology of nocturnal ectotherms: Is sprint performance of geckos maximal at low body temperatures? *Physiol. Zool.* **62:** 488–504.

Hughes, G. M., Ed. (1976). "Respiration of Amphibious Vertebrates." Academic Press, London.

Hulse, A. C. (1976). Carapacial and plastral flora and fauna of the Sonora mud turtle, *Kinosternon sonoriense* Le Conte (Reptilia, Testudines, Kinosternidae). *J. Herpetol.* **10:** 45–48.

Humphries, R. L. (1956). An unusual aggregation of *Plethodon glutinosus* and remarks on its subspecific status. *Copeia* **1946:** 122–123.

Hunt, R. H., and Ogden, J. J. (1991). Selected aspects of the nesting ecology of American alligators in Okefenokee Swamp. *J. Herpetol.* **24:** 448–453.

Hutchinson, J. H. (1991). Early Kinosterninae (Reptilia: Testudines) and their phylogenetic significance. *J. Vert. Paleontol.* **11:** 145–167.

Hutchinson, J. H. (1992). Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications. *In* "Eocene-Oligocene Climatic and Biotic Evolution" (D. R. Prothero and W. A. Berggen, Eds.), pp. 451–463. Princeton Univ. Press, Princeton.

Hutchinson, M. N. (1992). Origins of the Australian scincid lizards: A preliminary report on the skinks of Riversleigh. *Beagle* **9:** 61–70.

Hutchinson, M. N. (1993). Family Scincidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 261–279. Aust. Govern. Publ. Serv., Canberra.

Hutchison, V. H. (1982). Physiological ecology of the telmatobiid frogs of Lake Titicaca. *Natl. Geog. Soc. Res. Rep.* **14:** 357–361.

Hutchison, V. H., and Dupré, R. K. (1992). Thermoregulation. *In* "Environmental Physiology of the Amphibia"

(M. E. Feder and W. W. Burggren, Eds.), pp. 206–249. Univ. Chicago Press, Chicago.

Hutchison, V. H., and Larimer, J. (1960). Reflectivity of the integuments of some lizards from different habitats. *Ecology* **41:** 199–209.

Hutchison, V. H., Dowling, H. G., and Vinegar, A. (1966). Thermoregulation in a brooding female Indian python, *Python molurus bivittatus. Science* **151:** 694–696.

Hutchison, V. H., Haines, H. B., and Engbretson, G. A. (1976). Aquatic life at high altitude: Respiratory adaptations in the Lake Titicaca frog, *Telmatobius culeus. Respir. Physiol.* **27:** 115–129.

Hutton, J. M. (1989). Production efficiency at crocodile rearing stations in Zimbabwe. *In* "Crocodiles. Proceedings of the 8th Working Meeting of the Crocodile Specialist Group, IUCN," pp. 1–15. The World Conservation Union, Gland, Switzerland.

Ineich, I. (1992). La parthenogenese chez les Gekkonidae (Reptilia, Lacertilia): Origine et evolution. *Bull. Soc. Nat. France* **117:** 253–266.

Inger, R. F. (1954). Systematics and zoogeography of Philippine Amphibia. *Fieldiana: Zool.* **33:** 181–531.

Inger, R. F. (1966). The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana: Zool.* **52:** 1–402.

Inger, R. F. (1967). The development of a phylogeny of frogs. *Evolution* **21:** 369–384.

Inger, R. F. (1980). Densities of floor-dwelling frogs and lizards in lowland forests of southeast Asia and Central America. *Am. Nat.* **115:** 761–770.

Inger, R. F. (1986). Diets of tadpoles living in a Bornean rain forest. *Alytes* **5:** 153–164.

Inger, R. F. (1996). Commentary on a proposed classification of the family Ranidae. *Herpetologica* **52:** 241–246.

Inger, R. F., and Bacon, J. P. (1968). Annual reproduction and clutch size in rain forest frogs from Sarawak. *Copeia* **3:** 602–606.

Inger, R. F., and Colwell, R. K. (1977). Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecol. Monog.* **47:** 229–253.

Inger, R. F., and Greenberg, B. (1966). Annual reproductive patterns of lizards from a Bornean rain forest. *Ecology* **47:** 1007–1021.

Inger, R. F., and Lian, T. F. (1996). "The Natural History of Amphibians and Reptiles in Sabah." Natural History Publ. (Borneo) Sdn. Bhd., Kota Kinabalu, Sabah.

Inger, R. R., and Stuebing, R. B. (1997). "A Field Guide to the Frogs of Borneo." Natural History Publ. (Borneo) Sdn. Bhd., Kota Kinabalu, Sabah.

Inger, R. F., Shaffer, H. B., Koshy, M., and Bakde, R. (1984). A report on a collection of amphibians and reptiles from the Ponmudi, Kerala, South India. *J. Bombay Nat. Hist. Soc.* **81:** 551–570.

Inger, R. F., Voris, H. K., and Frogner, K. J. (1986). Organization of a community of tadpoles in rain forest streams in Borneo. *J. Trop. Ecol.* **2:** 193–205.

Iordansky, N. N. (1973). The skull of the Crocodilia. *In* "Biology of the Reptilia. Volume 4. Morphology D" (C. Gans and T. S. Parsons, Eds.), pp. 201–262. Academic Press, London.

Irish, F. J., Williams, E. E., and Seling, E. (1988). Scanning electron microscopy of changes in epidermal structure occurring during the shedding cycle in squamate reptiles. *J. Morphol.* **197:** 105–126.

Irschick, D. J., Vitt, L. J., Zani, P. A., and Losos, J. B. (1997). A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology* **78:** 2191–2203.

Iskandar, D. T. (1995). Notes on the second specimen of *Barbourula kalimantanensis* (Amphibia: Anura: Discoglossidae). *Raffles Bull. Zool.* **43:** 309–311.

Iverson, J. B. (1979). Behavior and ecology of the rock iguana *Cyclura carinata. Bull. Florida State Mus., Biol. Sci.* **24:** 175–358.

Iverson, J. B. (1982). Adaptations to herbivory in iguanine lizards. *In* "Iguanas of the World: Their Behavior, Ecology, and Conservation" (G. M. Burghardt and A. S. Rand, Eds.), pp. 60–76. Noyes Publications, Park Ridge, NJ.

Iverson, J. B. (1990). Nesting and parental care in the mud turtle, *Kinosternon flavescens. Can. J. Zool.* **68:** 230–233.

Iverson, J. B. (1991a). Phylogenetic hypotheses for the evolution of modern kinosternine turtles. *Herpetol. Monog.* **5:** 1–27.

Iverson, J. B. (1991b). Life history and demography of the yellow mud turtle, *Kinosternon flavescens. Herpetologica* **47:** 373–395.

Iverson, J. B. (1992). "A Revised Checklist with Distribution Maps of the Turtles of the World." Privately Printed, Richmond, IN.

Iverson, J. B., Balgooyen, C. P., Byrd, K. K., and Lyddan, K. K. (1993). Latitudinal variation in egg and clutch size in turtles. *Can. J. Zool.* **71:** 2448–2461.

Iverson, J. B., Higgins, H., Sirulnik, A., and Griffiths, C. (1997). Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentina*). *Herpetologica* **53:** 96–117.

Izecksohn, E. (1993). Três novas espécies de *Dendrophryniscus* Jiménez de la Espada das regioes sudeste e sul do Brasil (Amphibia, Anura, Bufonidae). *Rev. Brasil. Zool.* **10:** 473–488.

Jackman, T. R., Applebaum, G., and Wake, D. B. (1997a). Phylogenetic relationships of bolitoglossine salamanders: A demonstration of the effects of combining morphological and molecular data sets. *Mol. Biol. Evol.* **14:** 883–891.

Jackman, T., Losos, J. B., Larson, A., and de Queiroz, K. (1997b). Phylogenetic studies of convergent adaptive radiations in Caribbean *Anolis* lizards. *In* "Molecular Evolution and Adaptive Radiation" (T. J. Givnish and K. J. Sytsma, Eds.), pp. 535–557. Cambridge Univ. Press, New York.

Jackson, C. G., Jr., and Davis, J. D. (1972). Courtship display behavior of *Chrysemys concinna suwanniensis. Copeia* **1972:** 385–387.

Jacobson, S. K. (1985). Reproductive behavior and male mating success in two species of glass frogs (Centrolenidae). *Herpetologica* **41:** 396–404.

Jaeger, C. B., and Hillman, D. E. (1976). Morphology of gustatory organs. *In* "Frog Neurobiology. A Handbook"

(R. Llinás and W. Precht, Eds.), pp. 588–606. Springer-Verlag, Berlin.

Jaeger, R. G. (1976). A possible prey-call window in anuran auditory perception. *Copeia* **1976:** 833–834.

Jaeger, R. G. (1981). Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.* **117:** 962–974.

Jaeger, R. G., and Forester, D. C. (1993). Social behavior of plethodontid salamanders. *Herpetologica* **49:** 163–175.

Jaeger, R. G., Kalvarsky, D., and Shimizu, N. (1982). Territorial behaviour of the red-backed salamander: Expulsion of intruders. *Anim. Behav.* **30:** 490–496.

Jaksíc, F. M., and Schwenk, K. (1983). Natural history observations on *Liolaemus magellanicus,* the southernmost lizard in the world. *Herpetologica* **39:** 457–461.

James, C. D. (1991). Annual variation in reproductive cycles of scincid lizards (*Ctenotus*) in central Australia. *Copeia* **1991:** 744–760.

James, C. D., and Shine, R. (1985). The seasonal timing of reproduction: A tropical-temperate comparison in Australian lizards. *Oecologia* **67:** 464–474.

James, C. D., and Shine, R. (1988). Life-history strategies of Australian lizards: A comparison between the tropics and the temperate zone. *Oecologia* **75:** 307–316.

James, F. C., and McCullough, C. E. (1985). Data analysis and the design of experiments in ornithology. *In* "Current Ornithology. Vol. 2" (R. F. Johnston, Ed.), pp. 1–63.

James, F. C., and McCullough, C. E. (1990). Multivariate analysis in ecology and systematics: Panacea or Pandora's box? *Ann. Rev. Ecol. Syst.* **21:** 129–166.

Jameson, D. L. (1955). The population dynamics of the cliff frog, *Syrrhophus marnocki. Am. Midl. Nat.* **54:** 342–381.

Janzen, F. J., and Paukstis, G. (1991). Environmental sex determination in reptiles: Ecology, evolution, and experimental design. *Quart. Rev. Biol.* **66:** 149–179.

Jenkins, F. A., and Walsh, D. M. (1993). An Early Jurassic caecilian with limbs. *Nature* **365:** 246–249.

Jenssen, T. A. (1970a). The ethoecology of *Anolis nebulosus* (Sauria: Iguanidae). *J. Herpetol.* **4:** 1–38.

Jenssen, T. A. (1970b). Female response to filmed displays of *Anolis nebulosus* (Sauria, Iguanidae). *Anim. Behav.* **18:** 640–647.

Jenssen, T. A., and Hover, E. L. (1976). Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behaviour* **57:** 227–240.

Jenssen, T. A., and Nunez, S. C. (1998). Spatial and breeding relationships of the lizard *Anolis carolensis:* Evidence of intrasexual selection. *Behaviour* **135:** 981–1003.

Joanen, T. (1969). Nesting ecology of alligators in Louisiana. *Proc. Ann. Conf. S. E. Assoc. Game Fish Comm.* **23:** 141–151.

Joanen, T., and McNease, L. (1980). Reproductive biology of the American alligator in southwest Louisiana. *In* "Reproductive Biology and Disease of Captive Reptiles" (J. B. Murphy and J. T. Collins, Eds.), pp. 153–159. Soc. Study Amphibians and Reptiles, Athens, OH.

Joger, U. (1991). A molecular phylogeny of agamid lizards. *Copeia* **1991:** 616–622.

Joglar, R. J., and Burrowes, P. A. (1996). Declining amphibian populations in Puerto Rico. *In* "Contribution to West Indian Herpetology. A Tribute to Albert Schwartz" (R. Powell and R. W. Henderson, Eds.), pp. 371–380. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Joglar, R. L., Burrowes, P. A., and Rios, N. (1996). Biology of the Puerto Rican cave-dwelling frog, *Eleutherodactylus cooki,* and some recommendations for conservation. *In* "Contributions to West Indian Herpetology: A Tribute to Albert Schwartz" (R. Powell and R. W. Henderson, Eds.), pp. 251–258. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Johnson, C. R. (1969). Aggregation as a means of water conservation in juvenile *Limnodynastes* from Australia. *Herpetologica* **25:** 275–276.

Johnston, G. R., and Richards, S. J. (1993). Observations on the breeding biology of a microhylid frog (genus *Oreophryne*) from New Guinea. *Trans. Roy. Soc. S. Aust.* **117:** 105–107.

Joly, J. (1968). Données écologiques sur la salamandre tachetée *Salamandra salamandra. Ann. Sci. Nat., Zool., Ser. 12* **10:** 301–366.

Jones, D. R. (1996). The crocodilian central circulation: Reptilian or avian? *Verh. Dtsch. Zool. Ges.* **89**(2): 209–218.

Jones, T. R., Kluge, A. G., and Wolf, A. J. (1993). When theories and methodology clash: A phylogenetic reanalysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). *Syst. Biol.* **42:** 92–102.

Jorgensen, C. B. (1992). Growth and reproduction. *In* "Environmental Physiology of the Amphibia" (M. E. Feder and W. W. Burggren, Eds.). Univ. Chicago Press, Chicago.

Juncá, F. A. (1998). Reproductive biology of *Colostethus stepheni* and *Colostethus marchesianus* (Dendrobatidae), with the description of a new anuran mating behavior. *Herpetologica* **54:** 377–387.

Juncá, F. A., Altig, R., and Gascon, C. (1994). Breeding biology of *Colostethus stepheni,* a dendrobatid frog with a nontransported nidicolous tadpole. *Copeia* **3:** 747–750.

Jungfer, K.-H. (1996). Reproduction and parental care of the coronated treefrog, *Anotheca spinosa* (Steindachner, 1864) (Anura: Hylidae). *Herpetologica* **52:** 25–32.

Jungfer, K.-H., and Schiesari, L. C. (1995). Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura, Hylidae), with oophagous tadpoles. *Alytes* **13:** 1–13.

Jungfer, K.-H., and Weygoldt, P. (1999). Biparental care in the tadpole-feeding Amazonian treefrog *Osteocephalus oophagus. Amphibia-Reptilia* **20:** 235–249.

Junqueira, L. C. U., Jared, C., and Antoniazzi, M. M. (1999). Structure of the caecilian *Siphonops annulatus* (Amphibia, Gymnophiona): General aspect of the body, disposition of the organs and structure of the mouth, esophagus and stomach. *Acta Zool.* **80:** 75–84.

Justus, J. T., Sandomir, M., Urquhart, T., and Ewan, B. O. (1977). Developmental rates of two species of toads from the desert Southwest. *Copeia* **1977:** 592–594.

Kachigan, S. K. (1982). "Multivariate Statistical Analysis. A Conceptual Introduction." Radius Press, New York.

Kalb, H. J., and Zug, G. R. (1990). Age estimates for a population of American toads, *Bufo americanus* (Salientia: Bufonidae), in northern Virginia. *Brimleyana* **16:** 79–86.

Kaminsky, S. D., Linsenmair, K. E., and Grafe, T. U. (1999). Reproductive timing, nest construction and tadpole guidance in the African pig-nosed frog, *Hemisus marmoratus. J. Herpetol.* **33:** 119–123.

Kardong, K. V. (1992). "Vertebrates. Comparative Anatomy, Function, and Evolution." Wm. C. Brown, Publ., Dubuque, IA.

Kardong, K. V. (1995). "Vertebrates: Comparative Anatomy, Function, Evolution." Wm. C. Brown Publ., Dubuque, IA.

Kardong, K. V. (1997). Squamates at geological boundaries: Unbounded evolution. *Zoology* **100:** 152–163.

Kardong, K. (1998). "Vertebrates. Comparative Anatomy, Function, Evolution. Second Edition." McGraw-Hill, New York.

Kats, L. B., Petranka, J. W., and Sih, A. (1988). Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* **69:** 1865–1870.

Katz, U. (1989). Strategies of adaptation to osmotic stress in anuran Amphibia under salt and burrowing conditions. *Comp. Biochem. Physiol.* **93A:** 499–503.

Kennett, R., Christian, K., and Pritchard, D. (1993a). Underwater nesting of the tropical freshwater turtle, *Chelodina rugosa. Aust. J. Zool.* **41:** 47–52.

Kennett, R., Georges, A., and Palmer-Allen, M. (1993b). Early developmental arrest during immersion of eggs of a tropical freshwater turtle, *Chelodina rugosa* (Testudinata: Chelidae), from northern Australia. *Aust. J. Zool.* **41:** 37–45.

Keogh, J. S. (1998). Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biol. J. Linn. Soc.* **63:** 177–203.

Kiester, A. R., Gorman, G. C., and Arroyo, D. C. (1975). Habitat selection behavior of three species of *Anolis* lizards. *Ecology* **56:** 220–225.

King, D., and Green, B. (1993). "Goanna. The Biology of Varanid Lizards." New S. Wales Univ. Press, Kensington, N.S.W.

King, M., and Horner, P. (1993). Family Gekkonidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 221–233. Aust. Govern. Publ. Serv., Canberra.

Kinkead, R. (1997). Episodic breathing in frogs: Converging hypotheses on neural control of respiration in air breathing vertebrates. *Am. Zool.* **37:** 31–40.

Kizirian, D. A. (1996). A review of Ecuadorian *Proctoporus* (Squamata: Gymnophthalmidae) with descriptions of nine new species. *Herpetol. Monog.* **10:** 85–155.

Klauber, L. M. (1982). "Rattlesnakes. Their Habits, Life Histories, and Influence on Mankind," abridged ed. Univ. California Press, Berkeley.

Klaver, C. J. J., and Böhme, W. (1986). Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. *Bonn. Zool. Beitr.* **22:** 1–64.

Klaver, C. J. J., and Böhme, W. (1997). Chamaeleonidae. *Das Tierreich* **109:** 1–306.

Kluge, A. G. (1974). A taxonomic revision of the lizard family Pygopodidae. *Misc. Publ. Mus. Zool. Univ. Michigan* **147:** 1–221.

Kluge, A. G. (1976). Phylogenetic relationships in the lizard family Pygopodidae: An evaluation of theory, methods and data. *Misc. Publ. Mus. Zool. Univ. Michigan* **152:** 1–72.

Kluge, A. G. (1981). The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Misc. Publ. Mus. Zool. Univ. Michigan* **160:** 1–170.

Kluge, A. G. (1987). Cladistic relationships among the Gekkonoidea (Squamata, Sauria). *Misc. Publ. Mus. Zool. Univ. Michigan* **173:** 1–54.

Kluge, A. G. (1989). Progress in squamate classification. *Herpetologica* **45:** 368–379.

Kluge, A. G. (1991a). Boine snake phylogeny and research cycles. *Misc. Publ. Mus. Zool. Univ. Michigan* **178:** 1–58.

Kluge, A. G. (1991b). Checklist of gekkonoid lizards. *Smith. Herpetol. Info. Serv.* **85:** 1–35.

Kluge, A. G. (1993a). *Aspidites* and the phylogeny of pythonine snakes. *Rec. Aust. Mus., Suppl.* **19:** 1–77.

Kluge, A. G. (1993b). *Calabaria* and the phylogeny of erycine snakes. *Zool. J. Linn. Soc.* **107:** 293–351.

Kluge, A. G., and Farris, J. S. (1969). Quantitative phyletics and the evolution of anurans. *Syst. Zool.* **18:** 1–32.

Kobel, H. R., Loumont, C., and Tinsley, R. C. (1996). The extant species. *In* "The Biology of *Xenopus*" (R. C. Tinsley and H. R. Kobel, Eds.), pp. 9–33. Zool. Soc. London, London.

Kochva, E. (1978). Phylogeny of oral glands in reptiles as related to the origin and evolution of snakes. *In* "Toxins: Animal, Plant and Microbal" (P. Rosenberg, Ed.), pp. 29–37. Pergamon Press, Oxford.

Kofron, C. P. (1983). Female reproductive cycle of the neotropical snail-eating snake *Sibon sanniola* in northern Yucatan, Mexico. *Copeia* **1983:** 963–969.

Kofron, C. P. (1988). The Central and South American blindsnakes of the genus *Anomalepis. Amphibia-Reptilia* **9:** 7–14.

Köhler, J., Glaw, F., and Vences, M. (1997). Notes on the reproduction of *Rhombophryne* (Anura: Microhylidae) at Nosy Be, northern Madagascar. *Rev. Fr. Aquariol.* **24:** 1–2.

Kok, D., du Preez, L. H., and Channing, A. (1989). Channel construction by the African bullfrog: Another anuran parental care strategy. *J. Herpetol.* **23:** 435–437.

Komnick, H. (1986). Chloride cells and salt glands. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 499–516. Springer Verlag, Berlin.

Kraus, F., and Brown, W. M. (1998). Phylogenetic relationships of colubroid snakes based on mitochondrial DNA sequences. *Zool. J. Linn. Soc.* **122:** 455–487.

Kraus, F., Mink, D. G., and Brown, W. M. (1996). Crotaline intergeneric relationships based on mitochondrial DNA sequence data. *Copeia* **1996:** 763–773.

Kropach, C. (1971). Sea snake (*Pelamis platurus*) aggregations on slicks in Panama. *Herpetologica* **27:** 131–135.

Krügel, P., and Richter, S. (1995). *Syncope antenori*—A bromeliad breeding frog with free-swimming, nonfeeding tadpoles (Anura, Microhylidae). *Copeia* **1995:** 955–963.

Kuchling, G. (1998). Managing the last survivors: Integration of *in situ* and *ex situ* conservation of *Pseudemydura umbrina*. *In* "Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference" [1997] (J. V. Abbema, Ed.), pp. 339–344. New York Turtle and Tortoise Society, New York.

Kuchling, G. (1999). "The Reproductive Biology of the Chelonia." Springer-Verlag, Berlin.

Kusano, T. (1980). Breeding and egg survival of a population of a salamander, *Hynobius nebulosus tokyoensis* Tago. *Res. Popul. Ecol.* **21:** 181–196.

Kuzmin, S. L. (1995). "The Clawed Salamanders of Asia." Westarp Wissenschaften, Magdeburg.

Lambiris, A. J. L. (1989). The frogs of Zimbabwe. *Mus. Region. Sci. Nat. Monog.* **10:** 1–247.

Lancini, A. R., and Kornacker, P. M. (1989). "Die Schlangen von Venezuela." Verlag Armitano Ed. C. A., Carcas.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34:** 292–305.

Landmann, L. (1975). The sense organs in the skin of the head of Squamata (Reptilia). *Israel J. Zool.* **24:** 99–135.

Landmann, L. (1986). Epidermis and dermis. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 150–187. Springer Verlag, Berlin.

Lang, J. W. (1976). Amphibious behavior of *Alligator mississippiensis:* Roles of a circadian rhythm and light. *Science* **191:** 575–577.

Lang, J. W. (1989). Social behavior. *In* "Crocodiles and Alligators" (C. A. Ross, Ed.), pp. 102–117. Golden Press Pty Ltd., Silverwater, N.S.W.

Lang, J. W., and Andrews, H. V. (1994). Temperature-dependent sex determination in crocodilians. *J. Exp. Zool.* **270:** 28–44.

Lang, J. W., Whitaker, R., and Andrews, H. (1986). Male parental care in Mugger Crocodiles. *Natl. Geog. Res.* **2:** 519–525.

Lang, M. (1989a). Notes on the genus *Bombina* Oken (Anura: Bombinatoridae): III. Anatomy, systematics, hybrization, fossil record and biogeography. *Br. Herpetol. Soc. Bull.* **28:** 43–49.

Lang, M. (1989b). Phylogenetic and biogeographic patterns of basiliscine iguanians (Reptilia: Squamata: "Iguanidae"). *Bonn. Zool. Monog.* **28:** 1–172.

Lang, M. (1991). Genetic relationships within the Cordyliformes (Reptilia: Squamata). *Bull. Inst. Roy. Sci. Nat. Belgique, Biol.* **61:** 121–188.

Lanka, V., and Vit, Z. (1985). "Reptiles et Amphibiens." Gründ, Paris.

Lannoo, M. J. (1987a). Neuromast topography in anuran amphibians. *J. Morphol.* **191:** 115–129.

Lannoo, M. J. (1987b). Neuromast topography in urodele amphibians. *J. Morphol.* **191:** 247–263.

Lanza, B., Vanni, S, and Brizzi, R. (1992). Le discoglosse Sarde. & Le discoglosse Corse. *In* "Atlas de Repartition des Batraciens et Reptiles de Corse" (M. Delaugerre and M. Cheylan, Eds.), pp. 29–32. Parc Naturel Regional de Corse, Bastia.

Lanza, B., Caputo, V., Nascetti, G., and Bullini, L. (1995). Morphologic and genetic studies of the European plethodontid salamanders: Taxonomic inferences (genus *Hydromantes*). *Mus. Reg. Sci. Nat.-Torino Monog.* **14:** 1–366.

Largen, M. J. (1991). A new genus and species of petropedetine frog (Amphibia Anura Ranidae) from high altitude in the mountains of Ethiopia. *Trop. Zool.* **4:** 139–152.

Larson, A. (1991). A molecular perspective on the evolutionary relationships of the salamander families. *Evol. Biol.* **25:** 211–277.

Larson, A., and Dimmick, W. W. (1993). Phylogenetic relationships of the salamander families: An analysis of congruence among morphological and molecular characters. *Herpetol. Monog.* **7:** 77–93.

Larson, J. H., Jr., and Guthrie, D. J. (1985). The feeding system of terrestrial tiger salamanders (*Ambystoma tigrinum melanostictum* Baird). *J. Morphol.* **147:** 137–154.

Lasiewski, R. C., and Bartholomew, G. A. (1969). Condensation as a mechanism for water gain in nocturnal desert poikilotherms. *Copeia* **1969:** 405–407.

Lathrop, A. (1997). Taxonomic review of the megophryid frogs (Anura: Pelobatoidea). *Asiatic Herpetol. Res.* **7:** 68–79.

Lauder, G., and Gillis, G. B. (1997). Origin of the amniote feeding mechanism: Experimental analyses of outgroup clades. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 169–206. Academic Press, San Diego.

Laurance, W. F. (1996). Catastrophic declines of Australian rainforest frogs: Is unusual weather responsible? *Biol. Conserv.* **77:** 203–212.

Laurance, W. F., McDonald, K. R., and Speare, R. (1996). Epidemic disease and the catastrophic decline of Australian rainforest frogs. *Conserv. Biol.* **10:** 406–413.

Laurent, R. F. (1954). Aperçu de la biogéographie des batraciens et des reptiles de la région des grands lacs. *Bull. Soc. Zool. France* **79:** 290–310.

Laurent, R. F. (1986). Sous classe des lissamphibiens (Lissamphibia). Systématique. *In* "Traité de Zoologie. Anatomie, Systématique, Biologie. Amphibiens. Tome XI, Fasc. I-B" (P.-P. Grassé, Ed.), pp. 594–797.

Laurent, R. F., and Teran, E. M. (1981). Lista de los anfibios y reptiles de la provincia de Tucumán. *Fundac. Miguel Lillo Misc.* **71:** 1–15.

Laurin, M., and Reisz, R. R. (1995). A re-evaluation of early amniote phylogeny. *Zool. J. Linn. Soc.* **113:** 165–223.

Laurin, M., and Reisz, R. R. (1997). A new perspective on tetrapod phylogeny. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 9–59. Academic Press, San Diego.

Lawler, S. P. (1989). Behavioural responses to predators and predation risk in four species of larval anurans. *Anim. Behav.* **38:** 1039–1047.

Lawler, S. P., Dritz, D., Strange, T., and Holyoak, M. (1999). Effects of introduced mosquitofish and bullfrogs on the threatened California red-legged frog. *Conserv. Biol.* **13:** 613–622.

Lee, J. C. (1975). The autecology of *Xantusia henshawi henshawi* (Sauria: Xantusiidae). *Trans. San Diego Soc. Nat. Hist.* **17:** 259–278.

Lee, J. C. (1996). "The Amphibians and Reptiles of the Yucatán Peninsula." Comstock Publ. Assoc., Ithaca, NY.

Lee, M. S. Y. (1993). The origin of the turtle body plan: Bridging a famous morphological gap. *Science* **261:** 1716–1720.

Lee, M. S. Y. (1995). Historical burden in systematics and the interrelationships of 'parareptiles.' *Biol. Rev.* **70:** 459–547.

Lee, M. S. Y. (1997). Pareiasaur phylogeny and the origin of turtles. *Zool. J. Linn. Soc.* **120:** 197–280.

Lee, M. S. Y. (1998). Convergent evolution and character correlation in burrowing reptiles: Towards a resolution of squamate relationships. *Biol. J. Linn. Soc.* **65:** 369–453.

Legler, J. M. (1993). Morphology and physiology of the Chelonia. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 42–152. Australian Govern. Publ. Serv., Canberra.

Legler, J. M., and Fitch, H. S. (1957). Observations on hibernation and nests of the collared lizard, *Crotaphytus collaris. Copeia* **1957:** 305–307.

Legler, J. M., and Georges, A. (1993). Family Chelidae. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 120–128. Australian Govern. Publ. Serv., Canberra.

Lemos-Espinal, J., Smith, G. R., and Ballinger, R. E. (1997a). Natural history of the Mexican knob-scaled lizard, *Xenosaurus rectocollaris. Herpetol. Nat. Hist.* [1996] **4:** 151–154.

Lemos-Espinal, J., Smith, G. R., and Ballinger, R. E. (1997b). Neonate-female associations in *Xenosaurus newmanorum:* A case of parental care in a lizard? *Herpetol. Rev.* **28:** 22–23.

Leonard, W. P., Brown, H. A., Jones, L. L. C., McAllister, K. R., and Storm, R. M. (1993). "Amphibians of Washington and Oregon." Seattle Audubon Soc., Seattle.

Lescure, J. (1979). Étude taxonomique et éco-éthologique d'un ampihibien des petites Antilles *Leptodactylus fallax* Muller, 1926 (Leptodactylidae). *Bull. Mus. Natl. Hist. Nat., Paris* **1:** 757–774.

Lescure, J. (1986a). La vie sociale de l'adulte. *In* "Traité de Zoologie. Anatomie, Systématique, Biologie. Tome XIV. Batraciens" (P.-P. Grassé and M. Delsol, Eds.), pp. 525–537. Masson, Paris.

Lescure, J. (1986b). Histoire de la classification des cecilies (Amphibia: Gymnophiona). *Mém. Soc. Zool. France* **43:** 11–19.

Lescure, J., Renous, S., and Gasc, J.-P. (1986). Proposition d'une nouvelle classification des amphibiens gymnopiones. *Mém. Soc. Zool. France* **43:** 145–177.

Liebman, P. A., and Granda, A. M. (1971). Microspectrophotometric measurements of visual pigments in two species of turtle, *Trachemys scripta* and *Chelonia mydas. Vision Res.* **11:** 105–114.

Liem, K. F., Marx, H., and Rabb, G. R. (1971). The viperid snake *Azemiops:* Its comparative cephalic anatomy and phylogenetic position in relation to Viperinae and Crotalinae. *Fieldiana Zool.* **59:** 1–126.

Liem, S. S. (1970). The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Fieldiana Zool.* **57:** 1–145.

Likens, G., Ed. (1989). "Long-Term Studies in Ecology." Springer-Verlag, New York.

Lillywhite, H. B. (1970). Behavioral thermoregulation in the bullfrog. *Copeia* **1970:** 158–168.

Lillywhite, H. B. (1987). Temperature, energetics, and physiological ecology. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 422–477. Macmillan, New York.

Lillywhite, H. B., and Maderson, P. F. A. (1982). Skin structure and permeability. *In* "Biology of the Reptilia. Volume 12. Physiology C" (C. Gans and F. H. Pough, Eds.), pp. 397–442. Academic Press, London.

Limpus, C. J. (1993). Family Dermochelyidae. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 139–141. Aust. Govern. Publ. Serv., Canberra.

Limpus, C. J., and Miller, J. D. (1993). Family Cheloniidae. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia" (C. J. Glasby, G. J. B. Ross, and P. I. Beesley, Eds.), pp. 133–138. Aust. Govern. Publ. Serv., Canberra.

Lindquist, E. D., and Hetherington, T. E. (1996). Field studies of visual and acoustic signaling in the "earless" Panamanian golden frog, *Atelopus zeteki. J. Herpetol.* **30:** 347–354.

Lips, K. R. (1998). Decline of a tropical montane amphibian fauna. *Conserv. Biol.* **12:** 106–117.

Lips, K. R. (1999). Mass mortality and population declines of anurans at an upland site in western Panama. *Conserv. Biol.* **13:** 117–125.

Little, C. (1990). "The Terrestrial Invasion. An Ecophysiological Approach to the Origins of Land Animals." Cambridge Univ. Press, Cambridge.

Littlejohn, M. J., Roberts, J. D., Watson, G. F., and Davies, M. (1993). The Myobatrachidae. *In* "Fauna of Australia. Volume 2A, Amphibia & Reptilia." (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 41–57. Aust. Govern. Publ. Serv., Canberra.

Liu, C.-Z., and Hu, S.-Q. (1961). "The Anura of China." Science Press, Beijing. [In Chinese]

Llinás, R., and Precht ,W., Eds. (1976). "Frog Neurobiology. A Handbook." Springer-Verlag, Berlin.

Lloyd, M., Inger, R. F., and King, F. W. (1968). On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* **102:** 497–515.

Lohmann, K. J. (1992). How sea turtles navigate. *Sci. Am.* 266:100–106.

Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F., and Salmon, M. (1966) Orientation, navigation, and natal beach homing in sea turtles. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 107–135. CRC Press, Boca Raton, FL.

Lombard, R. E., and Sumida, S. S. (1992). Recent progress in understanding early tetrapods. *Am. Zool.* **32:** 609–622.

Lombard, R. E., and Wake, D. B. (1976). Tongue evolution in the lungless salamanders, family Plethodontidae I. Introduction, theory, and a general model of dynamics. *J. Morphol.* **148:** 265–286.

Lombard, R. E., and Wake, D. B. (1977). Tongue evolution in the lungless salamanders, family Plethodontidae II. Function and evolutionary diversity. *J. Morphol.* **153:** 39–79.

Lopez, C. H., and Brodie, E. D., Jr. (1977). The function of costal grooves in salamanders (Amphibia, Urodela). *J. Herpetol.* **11:** 372–374.

López, P., Salvador, A., and W. E. Cooper, Jr. (1997). Discrimination of self from other males by chemosensory cues in the amphisbaenian (*Blanus cinereus*). *J. Comp. Psychol.* **111:** 105–109.

Losos, J. B. (1992). The evolution of convergent structure in Caribbean *Anolis* communities. *Syst. Biol.* **41:** 403–420.

Losos, J. B. (1994). Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Ann. Rev. Ecol. Syst.* **25:** 467–493.

Lötters, S. (1996). "The Neotropical Toad Genus *Atelopus*. Checklist-Biology-Distribution" (M. Vences and F. Glaw, Eds.). Verlags GbR, Cologne.

Louw, G. N., and Holm, E. (1972). Physiological, morphological and behavioural adaptations of the ultrapsammophilous, Namib Desert lizard *Aporosaura anchietae* (Bocage). *Madoqua, Ser. II* **1:** 67–81.

Lowe, C. H., Schwalbe, C. R., and Johnson, T. B. (1986). "The Venomous Reptiles of Arizona." Arizona Fish & Game Dept., Phoenix.

Lue, K. Y. (1991). "The Amphibians of Taiwan." Taiwan Prov. Dept. Education, Taipei.

Luiselli, L., Capula, M., and Shine, R. (1996). Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca,* in the eastern Italian Alps. *Oecologia* **106:** 100–110.

Luiselli, L., Capula, M., and Shine, R. (1997). Food habits, growth rates, and reproductive biology of grass snakes, *Natrix natrix* (Colubridae) in the Italian Alps. *J. Zool., London* **241:** 371–380.

Luppa, H. (1977). Histology of the digestive tract. *In* "Biology of the Reptilia. Volume 6. Morphology E" (C. Gans and T. S. Parsons, Eds.), pp. 225–313. Academic Press, London.

Luthardt, G., and Roth, G. (1979). The relationship between stimulus orientation and stimulus movement pattern in the prey catching behavior of *Salamandra salamandra. Copeia* **1979:** 442–447.

Lynch, J. D. (1971). Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Mus. Nat. Hist., Univ. Kansas* **53:** 1–238.

Lynch, J. D. (1973). The transition from archaic to advanced frogs. *In* "Evolutionary Biology of the Anurans" (J. L. Vial, Ed.), pp. 133–182. Univ. Missouri Press, Columbia, MO.

Lynch, J. D., Ruiz, P. M., and Rueda, J. V. (1983). Notes on the distribution and reproductive biology of *Centrolene geckoideum* Jimenez de la Espada in Colombia and Ecuador (Amphibia: Centrolenidae). *Stud. Neotrop. Fauna Environ.* **18:** 239–243.

Lynn, W. G. (1970). The thyroid. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 201–234. Academic Press, London.

MacArthur, R. H., and Pianka, E. R. (1966). On optimal use of a patchy environment. *Am. Nat.* **100:** 603–609.

MacArthur, R. H., and Wilson, E. O. (1967). "The Theory of Island Biogeography." Princeton Univ. Press, Princeton, NJ.

MacDonald, L. A., and Mushinsky, H. R. (1988). Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. *Herpetologica* **44**: 345–353.

Macey, J. R., Larson, A., Ananjeva, N. B., and Papenfuss, T. J. (1997). Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* **44:** 660–674.

Maderson, P. F. A. (1965). The structure and development of the squamate epidermis. *In* "Biology of the Skin and Hair Growth" (A. G. Lyne and B. F. Short, Eds.), pp. 129–153. Angus & Robertson, Sydney.

Maderson, P. F. A., Rabinowitz, T., Tandler, B., and Alibardi, L. (1998). Ultrastructural contributions to an understanding of the cellular mechanisms involved in lizard skin shedding with comments on the function and evolution of a unique lepidosaurian phenomenon. *J. Morphol.* **236:** 1–24.

Madison, D. M. (1969). Homing behavior of the red-cheeked salamander, *Plethodon jordani. Anim. Behav.* **17:** 25–39.

Madison, D. M., and Shoop, C. R. (1970). Homing behavior, orientation, and home range of salamanders tagged with Tantalum-182. *Science* **168:** 1484–1487.

Madsen, T. (1984). Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* **1984:** 707–713.

Madsen, T., and Shine, R. (1993). Male mating success and body size in European grass snakes. *Copeia* **1993:** 561–564.

Madsen, T., and Shine, R. (1994). Components of lifetime reproductive success in adders, *Vipera berus. J. Anim. Ecol.* **63:** 561–568.

Madsen, T., and Shine, R. (1996a). Determinants of reproductive output in female water pythons (*Liasis fuscus:* Pythonidae). *Herpetologica* **52:** 146–159.

Madsen, T., and Shine, R. (1996b). Seasonal migration of predators and prey—A study of pythons and rats in tropical Australia. *Ecology* **77:** 149–156.

Madsen, T., and Shine, R. (1998). Spatial subdivision within a population of tropical pythons (*Liasis fuscus*) in a superficially homogeneous habitat. *Aust. J. Ecol.* **23:** 340–348.

Madsen, T., Shine, R., Loman, J., and Hakansson, T. (1992). Why do female adders copulate so frequently? *Nature* **355:** 440–441.

Maeda, N., and Matsui, M. (1989). "Frogs and Toads of Japan." Bun-Ichi Sogo Shuppan Co., Tokyo.

Mägdefrau, H. (1997). Biologie, Haltung und Zucht der Krododilschwanz-Höcherechse (*Shinisaurus crocodilurus*). *Zeits. Kölner Zoo* **2:** 55–60.

Maglia, A. M. (1996). Ontogeny and feeding ecology of the red-backed salamander, *Plethodon cinereus. Copeia* **1996:** 576–586.

Maglia, A. M. (1998). Phylogenetic relationships of extant pelobatoid frogs (Anura: Pelobatoidea): Evidence from adult morphology. *Sci. Pap., Nat. Hist. Mus. Univ. Kansas* **10:** 1–19.

Magnusson, W. E. (1980). Hatching and creche formation by *Crocodylus porosus. Copeia* **1980:** 359–362.

Magnusson, W. E., Vliet, K. A., Pooley, A. C., and Whitaker, R. (1989). Reproduction. *In* "Crocodiles and Alligators" (C. A. Ross, Ed.), pp. 118–135. Golden Press Pty Ltd., Silverwater, N.S.W.

Mahmoud, I. Y., and Klicka, J. (1979). Feeding, drinking, and excretion. *In* "Turtles, Perspectives and Research" (M. Harless and H. Morlock, Eds.), pp. 229–243. John Wiley and Sons, New York.

Main, A. R., and Bull, C. M. (1996). Mother-offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii. Anim. Behav.* **52:** 193–200.

Maiorana, V. C. (1977). Tail autotomy, functional conflicts and their resolution by a salamander. *Nature* **265:** 533–535.

Malkmus, R. (1995). "Die Amphibien und Reptilien Portugals, Madeiras und der Azoren." Westarp Wissenschaften, Magdeburg.

Manley, G. A. (1990). "Peripheral Hearing Mechanisms in Reptiles and Birds." Springer-Verlag, Berlin.

Manthey, U., and Grossman, W. (1997). "Amphibien & Reptilien Südostasiens." Natur und Tier Verlag, Münster.

Markwick, P. J. (1998). Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: Implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeog. Palaeoclimatol. Palaeoecol.* **137:** 205–271.

Márquez, R. (1990). Sea turtles of the world. An annotated and illustrated catalogue of sea turtles species known to date. *FAO Fish. Synop.* **125**(11): 1–81.

Márquez, R. (1992). Terrestrial paternal care and short breeding seasons: Reproductive phenology of the midwife toads *Alytes obstetricans* and *A. cisternasii. Ecography* **15:** 279–288.

Márquez, R. (1995). Female choice in the midwife toads (*Alytes obstetricans* and *A. cisternasii*). *Behaviour* **132:** 151–161.

Marquis, R. J., Donnelly, M. A., and Guyer, C. (1986). Aggregations of calling males of *Agalychnis calcifer* Boulenger (Anura: Hylidae) in a Costa Rican lowland wet forest. *Biotropica* **18:** 173–175.

Martin, J. (1992). "Masters of Disguise: A Natural History of Chameleons." Facts on File, Inc., New York.

Martin, J. A., and Salvador, A. (1993). Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola. Behav. Ecol. Sociobiol.* **32:** 185–189.

Martin, K. L. M., and Nagy, K. A. (1997). Water balance and the physiology of the amphibian to amniote transition. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 399–423. Academic Press, San Diego.

Martin, L. D. (1991). Mesozoic birds and the origin of birds. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 485–540. Comstock Publ. Assoc., Ithaca, NY.

Martin, L. D., and Rothschild, B. M. (1989). Paleopathology and diving mosasaurs. *Am. Sci.* **77:** 460–467.

Martin, W. F., and Gans, C. (1972). Muscular control of the vocal tract during release signaling in the toad *Bufo valliceps. J. Morphol.* **137:** 1–28.

Martins, E. P. (1993). Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus. Anim. Behav.* **45:** 25–36.

Martins, E. P. (1994). Phylogenetic perspectives on the evolution of lizard territoriality. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Ed.), pp. 118–144. Princeton Univ. Press, Princeton, NJ.

Martof, B. S. (1953). Home range and movements of the green frog, *Rana clamitans. Ecology* **34:** 529–543.

Martof, B. S. (1972). *Pseudobranchus* Gray. *Catalog. Am. Amphib. Rept.* **118:** 1–4.

Martof, B. S. (1974). *Siren* Linnaeus. *Catalog. Am. Amphib. Rept.* **152:** 1–2.

Marvin, G. A. (1996). Life history and population characteristics of the salamander *Plethodon kentucki* with a review of *Plethodon* life histories. *Am. Midl. Nat.* **136:** 385–400.

Maslin, T. P. (1950). The production of sound in caudate Amphibia. *Univ. Colorado Stud., Ser. Biol. No.* **1:** 29–45.

Mason, R. T. (1992). Reptilian pheromones. *In* "Biology of the Reptilia. Volume 18, Physiology. Hormones, Brain, and Behavior" (C. Gans and D. Crews, Eds.), pp. 114–228. Univ. Chicago Press, Chicago.

Mason, R. T., and D. Crews. (1985). Female mimicry in garter snakes. *Nature* **316:** 59–60.

Mason, R. T., and D. Crews. (1986). Pheromone mimicry in garter snakes. *In* "Chemical Signals in Vertebrates. Volume 4. Ecology, Evolution, and Comparative Biology" (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, Eds.), pp. 279–283. Plenum Press, New York.

Masood-Parveez, U., and Nadkarni, V. B. (1993). The ovarian cycle in an oviparous gymnophione amphibian *Ichthyophis beddomei* (Peters). *J. Herpetol.* **27:** 59–63.

Massey, A. (1988). Sexual interactions in red-spotted newt populations. *Anim. Behav.* **36:** 205–210.

Mathis, A. (1991). Territories of male and female terrestrial salamanders: Costs, benefits, and intersexual spatial associations. *Oecologia* **86:** 433–440.

Mathis, A., Jaeger, R. G., Keen, W. H., Ducey, P. K., Walls, S. C., and Buchanan, B. W. (1995). Aggression and territoriality by salamanders and a comparison with the territorial behaviour of frogs. *In* "Amphibian Biology. Volume 2, Social Behaviour" (H. Heatwole and B. K. Sullivan, Eds.), pp. 633–676. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Mautz, W. J., and Lopez-Forment, W. (1978). Observations on the activity and diet of the cavernicolous lizard *Lepidophyma smithii. Herpetologica* **34**: 311–313.

Mautz, W. J., and Nagy, K. A. (1987). Ontogenetic changes in diet, field metabolic rate, and water flux in the herbivorous lizard *Dipsosaurus dorsalis. Physiol. Zool.* **60**: 640–658.

Maxson, L. R., and Maxson, R. D. (1990). Proteins II: Immunological techniques. *In* "Molecular Systematics" (D. M.

Hillis and C. Moritz, Eds.), pp. 127–155. Sinauer Assoc., Inc., Sunderland, MA.

Maxson, L. R., and Ruibal, R. (1988). Relationships of frogs in the leptodactylid subfamily Ceratophryinae. *J. Herpetol.* **22:** 228–231.

Maxson, R. D., and Maxson, L. R. (1986). Micro-complement fixation: A quantitative estimator of protein evolution. *Mol. Biol. Evol.* **3:** 375–388.

Mayer, W., and Benyr, G. (1994). Albumin-evolution und phylogenese in der Familie Lacertidae (Reptilia: Sauria). *Ann. Naturhist. Mus. Wien* **96B:** 621–648.

Mayer, W., and Bishoff, W. (1996). Beiträge zur taxonomischen Revision der Gattung *Lacerta* (Reptilia: Lacertidae). Teil 1: *Zootoca, Omanosaura, Timon* and *Teira* als eigenständige Gattungen. *Salamandra* **32:** 163–170.

Mayr, E., and Ashlock, S. D. (1991). "Principles of Systematic Zoology." McGraw-Hill Book Co., New York.

Mazzotti, F. J., and Dunson, W. A. (1989). Osmoregulation in crocodilians. *Am. Zool.* **29:** 903–920.

McCarthy, C. J. (1985). Monophyly of elapid snakes (Serpentes: Elapidae), an assessment of the evidence. *Zool. J. Linn. Soc.* **83:** 79–93.

McCarthy, C. J. (1986). Relationships of the laticaudine sea snakes (Serpentes: Elapidae: Laticaudinae). *Bull. Br. Mus. Nat. Hist. (Zool.)* **50:** 127–162.

McClanahan, L. L., Jr., and Baldwin, R. (1969). Rate of water uptake through the integument of the desert toad, *Bufo punctatus. Comp. Biochem. Physiol.* **28:** 381–389.

McClanahan, L. L., Jr., Shoemaker, V. H., and Ruibal, R. (1976). Structure and function of the cocoon of a ceratophryd frog. *Copeia* **1976:** 179–185.

McClanahan, L. L., Jr., Stinner, J. N., and Shoemaker, V. H. (1978). Skin lipids, water loss, and metabolism in a South American tree frog (*Phyllomedusa sauvagei*). *Physiol. Zool.* **51:** 179–187.

McClanahan, L. L., Jr., Ruibal, R., and Shoemaker, V. H. (1983). Rate of cocoon formation and its physiological correlates in a ceratophryd frog. *Physiol. Zool.* **56:** 430–435.

McCoy, C. J. (1968). Reproductive cycles and viviparity in Guatemalan *Corythophanes percarinatus* (Reptilia: Iguanidae). *Herpetologica* **24:** 175–178.

McDiarmid, R. W. (1978). Evolution of parental care in frogs. *In* "The Development of Behavior: Comparative and Evolutionary Aspects" (G. M. Burghardt and M. Bekoff, Eds.), pp. 127–147. Garland STPM Press, New York.

McDiarmid, R. W., Campbell, J. A., and Touré, T. A. (1999). "Snake Species of the World. A Taxonomic and Geographic Reference. Volume 1." The Herpetologists' League, Washington, DC.

McDonald, K. R., and Tyler, M. J. (1984). Evidence of gastric brooding in the Australian leptodactylid frog *Rheobatrachus vitellinus. Trans. Roy. Soc. S. Aust.* **108:** 226.

McDowell, S. B., Jr. (1964). Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. *Proc. Zool. Soc. London* **143:** 239–279.

McDowell, S. B. (1969). Notes on the Australian sea-snake *Ephalophis greyi* M. Smith (Serpentes: Elapidae, Hydrophiinae) and the origin and classification of sea-snakes. *Zool. J. Linn. Soc.* **48:** 333–349.

McDowell, S. B. (1974). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum, part I. Scolecophidia. *J. Herpetol.* **8:** 1–128.

McDowell, S. B. (1987). Systematics. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Siegel, J. T. Collins, and S. S. Novak, Eds.), pp. 3–50. Macmillan Publ. Co., New York.

McGowan, C. (1991). "Dinosaurs, Spitfires, and Sea Dragons." Harvard Univ. Press, Cambridge, MA.

McGowan, G., and Evans, S. E. (1995). Albanerpetontid amphibians from the Cretaceous of Spain. *Nature* **373:** 143–145.

McGregor, J. H., and Teska, W. R. (1989). Olfaction as an orientation mechanism in migrating *Ambystoma maculatum. Copeia* **1989:** 779–781.

McGuire, J. A. (1996). Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). *Bull. Carnegie Mus. Nat. Hist.* **32:** 1–143.

McIlhenny, E. A. (1935). "The Alligator's Life History." Christopher Publ. House, Boston.

McPherson, R. J., and Marion, K. R. (1981). The reproductive biology of female *Sternotherus odoratus* in an Alabama population. *J. Herpetol.* **15:** 389–396.

McVey, M. E., Zahary, R. G., Perry, D., and MacDougal, J. (1981). Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). *Copeia* **1981:** 1–8.

Means, D. B. (1996). *Amphiuma pholeter* Neill. *Catalog. Am. Amphib. Rept.* **622:** 1–2.

Means, D. B., Palis, J. G., and Baggett, M. (1996). Effects of slash pine silviculture on a Florida population of flatwoods salamanders. *Conserv. Biol.* **10:** 426–437.

Medica, P. A., and Turner, F. B. (1984). Natural longevity of lizards in southern Nevada. *Herpetol. Rev.* **15:** 34–35.

Medica, P. A., Bury, R. B., and Luckenbach, R. A. (1980). Drinking and construction of water catchments by the desert tortoise, *Gopherus agassizii,* in the Mojave Desert. *Herpetologica* **36:** 301–304.

Meffe, G. K., Carroll, C. R., and Contributors (1994a). "Principles of Conservation Biology." Sinauer Associates, Inc., Sunderland, MA.

Meffe, G. K., Carroll, C. R., and Pimm, S. L. (1994b). Community-level conservation: Species interactions, disturbance regimes, and invading species. *In* "Principles of Conservation Biology" (G. K. Meffe, C. R. Carroll, et al., Eds.), pp. 209–236. Sinauer Associates, Inc., Sunderland, MA.

Melisch, R. (1998). Wildlife trade, sustainable use, and conservation implications from a WWF and TRAFFIC perspective. *In* "Conservation, Trade and Sustainable Use of Lizards and Snakes in Indonesia" (W. Erdelen, Ed.), pp. 1–8. Mertensiella no. 7, Rheinbach, Germany.

Menzies, J. I. (1976). "Handbook of Common New Guinea Frogs." Wau Ecological Institute Handbook no. 1, Wau, Papua New Guinea.

Mertens, R., and Wermuth, H. (1960). "Die Amphibien und Reptilien Europas." Verlag Waldemar Kramer, Frankfurt am Main.

Metter, D. E. (1968). *Ascaphus* and *A. truei*. *Catalog. Am. Amphib. Rept.* **69:** 1–2.

Meylan, P. A. (1987). The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). *Bull. Am. Mus. Nat. Hist.* **186:** 1–110.

Meylan, P. A. (1996). Skeletal morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoi* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. *J. Vert. Paleontol.* **16:** 20–33.

Meylan, P. A., and Gaffney, E. S. (1989). The skeletal morphology of the Cretaceous cryptodiran turtle, *Adocus,* and the relationships of the Trionychoidea. *Am. Mus. Novitates* **2941:** 1–60.

Middendorf, G. A., III, and Sherbrooke, W. C. (1992). Canid elicitation of blood squirting in a horned lizard. *Copeia* **1992:** 519–527.

Miller, J. D. (1996). Reproduction in sea turtles. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 51–81. CRC Press, Boca Raton, FL.

Miller, M. R. (1954). Further observations on reproduction in the lizard *Xantusia vigilis*. *Copeia* **1954:** 38–40.

Miller, M. R., and Lagios, M. D. (1970). The pancreas. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 319–346. Academic Press, London.

Mills, M. S., Hudson, C. L., and Berna, H. J. (1995). Spatial ecology and movements of the brown water snake (*Nerodia taxispilota*). *Herpetologica* **51:** 412–423.

Milner, A. C. (1980). A review of them Nectridea (Amphibia). *In* "The Terrestrial Environment and the Origin of Land Vertebrates" (A. L. Panchen, Ed.), pp. 377–405. Academic Press, London.

Milner, A. C (1988). The relationships and origin of living amphibians. *In* "The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds" (M. J. Benton, Ed.), pp. 59–102. Clarendon Press, Oxford.

Milner, A. C. (1994). Late Triassic and Jurassic amphibians: Fossil record and phylogeny. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 23–37. Cambridge Univ. Press, New York.

Milner, A. R. (1993). The Paleozoic relatives of lissamphibians. *Herpetol. Monog.* **7:** 8–27.

Milner, A. R., Smithson, T. R., Milner, A. C., Coates, M. I., and Rolfe, W. D. I. (1986). The search for early tetrapods. *Modern Geol.* **10:** 1–28.

Milton, T. H., and T. A. Jenssen. (1979). Description and significance of vocalizations by *Anolis grahami*. *Copeia* **1979:** 481–489.

Minnich, J. E. (1979). Reptiles. *In* "Comparative Physiology of Osmoregulation in Animals" (G. M. Hughes, Ed.), pp. 391–641. Academic Press, London.

Minnich, J. E. (1982). The use of water. *In* "Biology of the Reptilia. Volume 12, Physiology C, Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 325–395. Academic Press, London.

Mitchell, J. C. (1988). Population ecology and life histories of the freshwater turtles, *Chrysemys picta* and *Sternotherus odoratus* in an urban lake. *Herpetol. Monog.* **2:** 40–61.

Mitchell, J. C. (1994). "The Reptiles of Virginia." Smithsonian Inst. Press, Washington, DC.

Mitchell, J. C., and Beck, R. A. (1992). Free-ranging domestic cat predation on native vertebrates in rural and urban Virginia. *Virginia J. Sci.* **43:** 197–207.

Mitchell, S. L., and Altig, R. (1983). The feeding ecology of *Sooglossus gardineri*. *J. Herpetol.* **17:** 281–282.

Mlynarski, M. (1976). "Testudines. Handbuch der Paläoherpetologie, 7." Gustav Fischer Verlag, Stuttgart.

Modha, M. L. (1967). The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *East Afr. Wildl. J.* **5:** 74–95.

Moler, P. E., and Kezer, J. (1993). Karyology and systematics of the salamander genus *Pseudobranchus* (Sirenidae). *Copeia* **1993:** 39–47.

Moll, D. (1989). Food and feeding behavior of the turtle, *Dermatemys mawei,* in Belize. *J. Herpetol.* **23:** 445–447.

Moll, D. (1990). Population sizes and foraging ecology in a tropical freshwater stream turtle community. *J. Herpetol.* **24:** 48–53.

Moll, D., and Klemens, M. W. (1996). Ecological characteristics of the pancake tortoise, *Malacochersus tornieri,* in Tanzania. *Chelonian Conserv. Biol.* **2:** 26–35.

Moll, E. O. (1980). Natural history of the river terrapin, *Batagur baska* (Gray) in Malaysia. *Malays. J. Sci.* **6**: 23–62.

Monagas, W. R., and Gatten, R. E., Jr. (1983). Behavioural fever in the turtles *Terrapene carolina* and *Chrysemys picta*. *J. Therm. Biol.* **8:** 285–288.

Mook, C. C. (1921). Notes on the postcranial skeleton in Crocodilia. *Bull. Am. Mus. Nat. Hist.* **44:** 67–100.

Morales, V. R., and McDiarmid, R. W. (1996). Annotated checklist of the amphibians and reptiles of Pakita, Manu National Park Reserve Zone, with comments on the herpetofauna of Madre de Dios. *In* "Manu. The Biodiversity of Southeastern Peru" (D. E. Wilson and A. Sandoval, Eds.), pp. 503–522. Smithsonian Inst., Washington, DC.

Morey, S. R. (1990). Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. *J. Herpetol.* **24:** 292–296.

Morin, P. J. (1987). Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. *Ecology* **68:** 675–683.

Moritz, C., and Hillis, D. M. (1996). Molecular systematics: Context and controversies. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 1–13. Sinauer Assoc., Inc., Sunderland, MA.

Morreale, S. J., Ruiz, G. J., Spotila, J. R., and Standora, E. A. (1982). Temperature-dependent sex determination: Current practices threaten conservation of sea turtles. *Science* **216:** 1245–1247.

Moskovits, D. K., and Bjorndal, K. A. (1990). Diet and food preferences of the tortoises *Geochelone carbonaria* and

G. denticulata in northwestern Brazil. *Herpetologica* **46**: 207–218.

Mouton, P. le F. N. (1997). Family Cordylidae. *In* "Proceedings of the Fitzsimons Commemorative Symposium" (J. H. van Dyke, Ed.), pp. 19–23. Herpetol. Assoc. Africa, Matieland, South Africa.

Mrosovsky, N. (1983). "Conserving Sea Turtles." British Herpetological Society, London.

Mrosovsky, N. (1994). Sex ratios in sea turtles. *J. Exp. Zool.* **270:** 16–27.

Murphy, J. B., Quinn, H., and Campbell, J. A. (1977). Observations on the breeding habits of the aquatic caecilian *Typhlonectes compressicaudus. Copeia* **1977:** 66–69.

Murphy, J. C., and Voris, H. K. (1994). A key to the homalopsine snakes. *Snake* **26:** 123–133.

Murphy, R. W., Sites, J. W., Buth, D. G., and Haufler, C. H. (1996). Proteins: Isozyme electrophoresis. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 51–120. Sinauer Assoc., Inc., Sunderland, MA.

Mushinsky, H. R., Hebrard, J. J., and Vodopich, D. S. (1982). Ontogeny of water snake foraging ecology. *Ecology* **63:** 1624–1629.

Myers, C. W., and Daly, J. W. (1983). Dart-poison frogs. *Sci. Am.* **248:** 120–133.

Myers, C. W., and Rand, A. S. (1969). Checklist of amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. *Smith. Contrib. Zool.* **10:** 1–11.

Myers, C. W., Paolillo O., A., and Daly, J. W. (1991). Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: Phylogenetic significance of a new genus and species from the Venezuelan Andes. *Am. Mus. Novitates* **3022:** 1–33.

Nagy, K. A. (1972). Water and electrolyte budgets of a free-living desert lizard, *Sauromalus obesus. J. Comp. Physiol. B* **79:** 39–62.

Nagy, K. A. (1977). Cellulose digestion and nutrient assimilation in *Sauromalus obesus,* a plant-eating lizard. *Copeia* **1977:** 355–362.

Nagy, K. A. (1983a). The doubly labeled water (^{3}H^{18}O) method: A guide to its use. *UCLA Publ.* **12–1417:** 1–45.

Nagy, K. A. (1983b). Ecological energetics. *In* "Lizard Ecology: Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 24–54. Harvard Univ. Press, Cambridge, MA.

Nagy, K. A., Huey, R. B., and Bennett, A. F. (1984). Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology* **65:** 588–596.

Nanayakkara, G. L. A. (1988). An analysis of the defensive behaviour of the Sri Lankan pipe snake, *Cylindrophis maculatus* (Linne, 1758). *Snake* **20:** 81–83.

National Research Council (1990). "Decline of the Sea Turtles." National Academy Press, Washington, DC.

Nelsen, O. E. (1953). "Comparative Embryology of the Vertebrates." Blakiston Co., Inc., New York.

Newman, D. G. (1987). Burrow use and population densities of tuatara (*Sphenodon punctatus*) and how they are influenced by fairy prions (*Pachyptila turtur*) on Stephens Island, New Zealand. *Herpetologica* **43:** 336–344.

Newton, W. D., and Trauth, S. E. (1992). Ultrastructure of the spermatozoon of the lizard *Cnemidophorus sexlineatus* (Sauria: Teiidae). *Herpetologica* **48:** 330–343.

Nickerson, M. A., and May, C. E. (1973). The hellbenders: North American giant salamanders. *Milwaukee Public Mus., Publ. Biol. Geol.* **1:** 1–106.

Niewiarowski, P. H. (1994). Understanding geographic life-history variation in lizards. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 31–49. Princeton Univ. Press, Princeton, NJ.

Niewiarowski, P. H., Congdon, J. D., Dunham, A. E., Vitt, L. J., and Tinkle, D. W. (1997). Tales of lizard tails: Effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana. Can. J. Zool.* **75:** 542–548.

Noble, G. K. (1922). The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny. *Bull. Am. Mus. Nat. Hist.* **46:** 1–87.

Noble, G. K. (1931). "The Biology of the Amphibia." McGraw-Hill Book Co., New York.

Noble, G. K., and Bradley, H. T. (1933). The mating behavior of lizards; its bearing on the theory of sexual selection. *Ann. N. Y. Acad. Sci.* **35:** 25–100.

Noble, G. K., and Clausen, H. J. (1936). The aggregation behavior of *Storeria dekayi* and other snakes, with special reference to the sense organs involved. *Ecol. Monog.* **6:** 271–316.

Noble, G. K., and Mason, E. R. (1933). Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus. Am. Mus. Novitates* **619:** 1–29.

Nöllert, A. (1990). "Die Knoblauchkröte." A. Ziemsen Verlag, Wittenberg Lutherstadt.

Norell, M. A. (1989). The higher level relationships of the extant Crocodylia. *J. Herpetol.* **23:** 325–335.

Norell, M. A., and de Queiroz, K. (1991). The earliest iguanine lizard (Reptilia: Squamata) and its bearing on iguanine phylogeny. *Am. Mus. Novitates* **2997:** 1–16.

Norell, M. A., and Gao, K. (1997). Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert and the recognition of a new clade of lizards. *Am. Mus. Novitates* **3211:** 1–25.

Norell, M. A., Clark, J. M., and Hutchison, J. H. (1994). The Late Cretaceous alligatoroid *Brachychamps Montana* [sic] (Crocodylia): New material and putative relationships. *Am. Mus. Novitates* **3116:** 1–26.

Norris, K. S., and Dawson, W. R. (1964). Observations on the water economy and electrolyte excretion of chuckwallas (Lacertilia, *Sauromalus*). *Copeia* **1964:** 638–646.

Nussbaum, R. A. (1976). Geographic variation and systematics of salamanders of the genus *Dicamptodon* Strauch (Ambystomatidae). *Misc. Publ. Mus. Zool. Univ. Michigan* **149:** 1–94.

Nussbaum, R. A. (1977). Rhinatrematidae: A new family of caecilians (Amphibia: Gymnophiona). *Occas. Pap. Mus. Zool. Univ. Michigan* **682:** 1–30.

Nussbaum, R. A. (1979). The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. *Occas. Pap. Mus. Zool. Univ. Michigan* **687:** 1–20.

Nussbaum, R. A. (1980). Phylogenetic implications of amplectic behavior in sooglossid frogs. *Herpetologica* **36:** 1–5.

Nussbaum, R. A. (1984). Amphibians of the Seychelles. *In* "Biogeography and Ecology of the Seychelles Islands" (D. R. Stoddart, Ed.), pp. 378–415. W. Junk, The Hague.

Nussbaum, R. A. (1985a). Systematics of caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae. *Occas. Pap. Mus. Zool. Univ. Michigan* **713:** 1–49.

Nussbaum, R. A. (1985b). Amphibian fauna of the Seychelles Archipelago. *Natl. Geog. Soc. Res. Rep.* **1977:** 53–62.

Nussbaum, R. A., and Hinkel, H. (1994). Revision of East African caecilians of the genera *Afrocaecilia* Taylor and *Boulengerula* Tornier (Amphibia: Gymnophiona: Caeciliaidae). *Copeia* **1994:** 750–760.

Nussbaum, R. A., and Tait, C. K. (1977). Aspects of the life history and ecology of the Olympic salamander, *Rhyacotriton olympicus* (Gaige). *Am. Midl. Nat.* **98:** 176–199.

Nussbaum, R. A., and Wilkinson, M. (1989). On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. *Herpetol. Monog.* **3:** 1–42.

Nussbaum, R. A., and Wu, S. H. (1995). Distribution, variation, and systematics of the Seychelles treefrog, *Tachycnemis seychellensis* (Amphibia: Anura: Hyperoliidae). *J. Zool., London* **236:** 383–406.

Nussbaum, R. A., Jaslow, A., and Watson, J. (1982). Vocalization in frogs of the family Sooglossidae. *J. Herpetol.* **16:** 198–204.

Nussbaum, R. A., Brodie, E. D., Jr., and Storm, R. M. (1983). "Amphibians and Reptiles of the Pacific Northwest." Univ. Press Idaho, Moscow, ID.

Odinchenko, V. I., and Latyshev, V. A. (1996). Keeping and breeding in captivity the Mexican burrowing python *Loxocemus bicolor* (Cope, 1861) at Moscow Zoo. *Russ. J. Herpetol.* **3:** 95–97.

Oelrich, T. M. (1956). The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Publ. Mus. Zool., Univ. Michigan* **94:** 1–122. [59 figures]

Olsson, M., and Madsen, T. (1998). Sexual selection and sperm competition in reptiles. *In* "Sexual Selection and Sperm Competition" (T. Birkhead and A. P. Moller, Eds.), pp. 503–577. Academic Press, London.

Olsson, M., and Shine, R. (1997). The limits of reproductive output: Offspring size versus number in the sand lizard (*Lacerta agilis*). *Am. Nat.* **149:** 179–188.

Olsson, M., Shine, R., and Madsen, T. (1996). Sperm selection by females. *Nature* **383:** 585.

Olsson, M., Madsen, T., and Shine, R. (1997). Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus. Proc. Roy. Soc. London B* **264:** 455–459.

Oosterbrock, P. (1987). More appropriate definitions of paraphyly and polyphyly, with a comment on the Farris 1974 model. *Syst. Zool.* **36:** 103–108.

Organ, J. A. (1961). Studies of the local distribution, life history, and population dynamics of the salamander genus *Desmognathus* in Virginia. *Ecol. Monog.* **31:** 189–220.

Orlov, N. L. (1997). Viperid snakes (Viperidae Bonaparte, 1840) of Tam-Dao mountain ridge (Vinh-Phu and Bac-Thai Provinces, Vietnam). *Russ. J. Herpetol.* **4:** 64–74.

Ortega, C. E., Stranc, D. S., Casal, M. P., Hallman, G. M., and Muchlinski, A. E. (1991). A positive fever response in *Agama agama* and *Sceloporus orcutti* (Reptilia, Agamidae and Iguanidae). *J. Comp. Physiol. B* **161:** 377–381.

Orton, G. L. (1953). The systematics of vertebrate larvae. *Syst. Zool.* **2:** 63–75.

O'Shea, M. (1996). "A Guide to the Snakes of Papua New Guinea." Independent Publ. Publishing, Port Moresby.

Ostrom, J. H. (1991). The question of the origin of birds. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 467–484. Comstock Publ. Assoc., Ithaca, NY.

Ottaviani, G., and Tazzi, A. (1977). The lymphatic system. *In* "Biology of the Reptilia. Volume 6. Morphology E" (C. Gans and T. S. Parsons, Eds.), pp. 315–462. Academic Press, London.

Ouboter, P. E., and Nanhoe, L. M. R. (1989). Notes on nesting and parental care in *Caiman crocodilus crocodilus* in northern Suriname and an analysis of crocodilian nesting habitats. *Amphibia-Reptilia* **8:** 331–348.

Overall, K. L. (1994). Lizard egg environments. *In* "Lizard Ecology: Historical and Experimental Perspectives" (L. J. Vitt and E. R. Pianka, Eds.), pp. 51–72. Princeton Univ. Press, Princeton, NJ.

Packard, G. C., and Kilgore, D. L., Jr. (1968). Internal fertilization: Adaptive value to early amniotes. *J. Theoret. Biol.* **20:** 245–248.

Packard, G. C., and Packard, M. J. (1980). Evolution of the cleidoic egg among reptilian antecedents of birds. *Am. Zool.* **20:** 351–362.

Packard, G. C., and Packard, M. J. (1988). The physiological ecology of reptilian eggs and embryos. *In* "Biology of the Reptilia. Volume 16, B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 523–605. Alan R. Liss, Inc., New York.

Packard, G. C., Tracy, C. R., and Roth, J. J. (1977). The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. *Biol. Rev.* **52:** 71–105.

Packard, G. C., Taigen, T. L., Packard, M. J., and Boardman, T. J. (1981). Changes in mass of eggs of softshell turtles (*Trionyx spiniferus*) incubated under hydric conditions simulating those of natural nests. *J. Zool., London* **193:** 81–90.

Packard, G. C., Packard, M. J., and Benigan, L. (1991). Sexual differentiation, growth, and hatching success by embryonic painted turtles incubated in wet and dry environments at fluctuation temperatures. *Herpetologica* **47:** 125–132.

Packard, M. J. (1994). Patterns of mobilization and deposition of calcium in embryos of oviparous, amniotic vertebrates. *Israel J. Zool.* **40:** 481–492.

Packard, M. J., and DeMarco, V. G. (1991). Eggshell structure and formation in eggs of oviparous reptiles. *In* "Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles" (D. C. Deeming and M. W. J. Ferguson, Eds.), pp. 53–69. Cambridge Univ. Press, Cambridge.

Packard, M. J., and Seymour, R. S. (1997). Evolution of the amniote egg. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 265–290. Academic Press, San Diego.

Packard, M. J., Packard, G. C., and Boardman, T. J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica* **38:** 136–155.

Paine, F. L., Miller, J. D., Crawshaw, G., Johnson, B., Lacy, R., Smith, C. R., and Tolson, P. J. (1989). Status of the Puerto Rican crested toad. *Int. Zoo Yearb.* **28:** 53–58.

Paladino, F. V., O'Connor, M. P., and Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344:** 858.

Palmer, B. D., Demarco, V., and Guillette, L. J., Jr. (1993). Oviductal morphology and eggshell formation in the lizard, *Sceloporus woodi. J. Morphol.* **217:** 205–217.

Palumbi, S. R. (1996). Nucleic acids II: The polymerase chain reaction. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 205–247. Sinauer Assoc., Inc., Sunderland, MA.

Panchen, A. L. (1991). The early tetrapods: Classification and the shape of cladograms. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 110–144. Comstock Publ. Assoc., Ithaca, NY.

Panchen, A. L., and Smithson, T. R. (1988). The relationships of the earliest tetrapods. *In* "The Phylogeny and Classification of the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds" (M. J. Benton, Ed.), pp. 1–32. Clarendon Press, Oxford.

Pang, P. K. T., and Schreibman, M. P., Eds. (1986). "Vertebrate Endocrinology: Fundamentals and Biomedical Implications. Vol. 1. Morphological Considerations." Academic Press, Orlando.

Pappenfuss, T. J. (1982). The ecology and systematics of the amphisbaenian genus *Bipes. Occas. Pap. Calif. Acad. Sci.* **136:** 1–42.

Pappenfuss, T. J. (1986). Amphibian and reptile diversity along elevational transects in the White-Inyo Range. *In* "Natural History of the White-Inyo Range, Eastern California and Western Nevada and High Altitude Physiology" (C. A. Hall, Jr., and D. J. Young, Eds.), pp. 129–136. Univ. California White Mnt. Res. Stat. Sympos., Bishop, CA.

Parham, J. F., and Fastovsky, D. E. (1998). The phylogeny of cheloniid sea turtles revisited. *Chelonian Conserv. Biol.* [1997] **2:** 548–554.

Parker, E. D., and Selander, R. K. (1976). The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tesselatus. Genetics* **84:** 791–805.

Parker, H. W. (1934). "A Monograph of the Frogs of the Family Microhylidae." The British Museum, London.

Parker, M. S. (1994). Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* **1994:** 705–718.

Parker, W. S., and Brown, W. S. (1980). Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola,* in northern Utah. *Milwaukee Public Mus., Publ. Biol. Geol.* **7:** 1–104.

Parmenter, C. J. (1985). Reproduction and survivorship of *Chelodina longicollis* (Testudinata: Chelidae). *In* "Biology of Australian Frogs and Reptiles" (G. Grigg, R. Shine, and H. Ehmann, Eds.), pp. 53–61. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Parmley, D., and Holman, J. A. (1995). Hemphillian (Late Miocene) snakes from Nebraska, with comments on Arikareean through Blancan snakes of midcontinental North America. *J. Vert. Paleontol.* **15:** 79–95.

Parrish, J. M. (1997). Evolution of the archosaurs. *In* "The Complete Dinosaur" (J. O. Farlow and M. K. Brett-Surman, Eds.), pp. 191–203. Indiana Univ. Press, Bloomington.

Parsons, T. S. (1970). The nose and Jacobson's organ. *In* "Biology of the Reptilia. Volume 2. Morphology B" (C. Gans and T. S. Parsons, Eds.), pp. 99–191. Academic Press, London.

Passmore, N., and Carruthers, S. V. (1995). "South African Frogs. A Complete Guide," Rev. ed. Southern Books & Witwatersrand Univ. Press, Johannesburg.

Patchell, F. C., and Shine, R. (1986a). Feeding mechanisms in pygopodid lizards: How can *Lialis* swallow such large prey? *J. Herpetol.* **20:** 59–64.

Patchell, F. C., and Shine, R. (1986b). Food habitas and reproductive biology of the Australian legless lizards Pygopodidae. *Copeia* **1986:** 30–39.

Pearman, P. B. (1997). Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conserv. Biol.* **11:** 1211–1225.

Pearson, O. P., and Bradford, D. F. (1976). Thermoregulation of lizards and toads at high altitudes in Peru. *Copeia* **1976:** 155–169.

Pechmann, J. H. K., and Semlitsch, R. D. (1986). Diel activity patterns in the breeding migrations of winter-breeding anurans. *Can. J. Zool.* **64:** 1116–1120.

Pechmann, J. H. K., and Wake, D. B. (1997). Declines and disappearances of amphibian populations. *In* "Principles of Conservation Biology" (G. K. Meffe, C. R. Carroll, and Contributors), pp. 135–137. Sinauer Associates, Inc., Sunderland, MA.

Pechmann, J. H. K., and Wilbur, H. M. (1994). Putting declining amphibian populations in perspective: Natural fluctuations and human impacts. *Herpetologica* **50:** 65–84.

Pechmann, J. H. K., Scott, D. E., Gibbons, J. W., and Semlitsch, R. D. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecol. Manag.* **1:** 3–11.

Pechmann, J. H. K., Scott, D. E., Semlitsch, R. D., Caldwell, J. P., Vitt, L. J., and Gibbons, J. W. (1991). Declining amphibian populations: The problem of separating human impacts from natural fluctuations. *Science* **253:** 892–895.

Pefaur, J. E., and Duellman, W. E. (1980). Community structure in high Andean herpetofaunas. *Trans. Kansas Acad. Sci.* **83:** 45–65.

Perez-Higareda, G., Rangel-Rangel, A., Smith, H. M., and Chiszar, D. (1989). Comments on the food and feeding habits of Morelet's crocodile. *Copeia* **1989:** 1039–1041.

Pérez-Santos, C., and Moreno, A. G. (1991). Serpientes de Ecuador. *Mus. Reg. Sci. Nat.-Torino Monog.* **11:** 1–538.

Perret, J.-L. (1966). Les amphibiens du Cameroun. *Zool. Jb., Abt. Syst. Ökol. Geog. Tiere* **93:** 289–464.

Perry, G. (1999). The evolution of search modes: Ecological versus phylogenetic perspectives. *Am. Nat.* **153:** 98–109.

Perry, G., and Pianka, E. R. (1997). Animal foraging: Past, present, and future. *Trends Ecol. Evol.* **12:** 360–364.

Perry, G., Lampl, I., Lerner, A., Rothenstein, D., Shani, E., Sivan, N., and Werner, Y. L. (1990). Foraging mode in lacertid lizards: Variation and correlates. *Amphibia-Reptilia* **11:** 373–384.

Perry, S. F. (1983). Reptilian lungs. Functional anatomy and evolution. *Adv. Anat. Embryol. Cell Biol.* **29:** 1–81.

Perry, S. F. (1998). Lungs: Comparative anatomy, functional morphology, and evolution. *In* "Biology of the Reptilia. Volume 19, Morphology G" (C. Gans and A. S. Gaunt, Eds.), pp. 1–92. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Peters, G. (1971). Die intragenerischen Gruppen und die Phylogenese der Schetterlingsagamen (Agamidae: *Leiolepis*). *Zool. Jb. Syst.* **98:** 11–130

Peterson, C. C. (1996). Anhomeostasis: Seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. *Physiol. Zool.* **69:** 1324–1358.

Peterson, C. L., Wilkinson, R. F., Topping, M. S., and Metter, D. E. (1983). Age and growth of the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*). *Copeia* **1983:** 225–231.

Petranka, J. W. (1998). "Salamanders of the United States and Canada." Smithsonian Inst. Press, Washington, DC.

Petranka, J. W., Kats, L. B., and Sih, A. (1987). Predator-prey interactions among fish and larval amphibians: Use of chemical cues to detect predatory fish. *Anim. Behav.* **35:** 420–425.

Petranka, J. W., Brannon, M. P., Hopey, M. E., and Smith, C. K. (1994). Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecol. Manag.* **67:** 135–147.

Petren, K., Bolger, D., and Case, T. J. (1993). Mechanisms in the competitive success of an invading sexual gecko over an asexual native. *Science* **259:** 354–358.

Petriella, S., Reboreda, J. C., Otero, M., and Segura, E. T. (1989). Antidiuretic responses to osmotic cutaneous stimulation in the toad, *Bufo arenarum*. *J. Comp. Physiol.* **159B:** 91–95.

Pfingsten, R. A., and Downs, F. L., Eds. (1989). Salamanders of Ohio. *Bull. Ohio Biol. Survey* **7:** 1–315.

Phillips, J. B., and Borland, S. C. (1994). Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*. *J. Exp. Biol.* **188:** 275–291.

Pianka, E. R. (1966). Convexity, desert lizards and spatial heterogeneity. *Ecology* **47:** 1055–1059.

Pianka, E. R. (1970). On 'r' and 'K' selection. *Am. Nat.* **104:** 592–597.

Pianka, E. R. (1973). The structure of lizard communities. *Ann. Rev. Ecol. Syst.* **4:** 53–74.

Pianka, E. R. (1975). Niche relations of desert lizards. *In* "Ecology and Evolution of Communities" (M. Cody and J. Diamond, Eds.), pp. 292–314. Harvard Univ. Press, Cambridge, MA.

Pianka, E. R. (1985). Some intercontinental comparisons of desert lizards. *Natl. Geog. Soc. Res. Rep.* **1:** 490–504.

Pianka, E. R. (1986). "Ecology and Natural History of Desert Lizards. Analyses of the Ecological Niche and Community Structure." Princeton Univ. Press, Princeton.

Pianka, E. R. (1988). "Evolutionary Ecology." Harper & Row, New York.

Pianka, E. R. (1992). The state of the art in community ecology. *In* "Herpetology: Current Research on the Biology of Amphibians and Reptiles" (K. Adler, Ed.), pp. 141–162. SSAR, Oxford, OH.

Pianka, E. R. (1994a). Biodiversity of Australian desert lizards. *In* "Biodiversity and Terrestrial Ecosystems" (C. I. Peng and C. H. Chou, Eds.), pp. 259–281. Inst. Botany, Academia Sinica Monog. no. 14, Taipei.

Pianka, E. R. (1994b). Comparative ecology of *Varanus* in the Great Victoria Desert. *Aust. J. Ecol.* **19:** 395–408.

Pianka, E. R. (1995). Evolution of body size: Varanid lizards as a model system. *Am. Nat.* **146:** 398–414.

Pianka, E. R. (1996). Long-term changes in lizard assemblages in the Great Victoria Desert: Dynamic habitat mosaics in response to wildfires. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 191–215. Academic Press, San Diego.

Pianka, E. R., and Parker, W. S. (1975). Ecology of horned lizards: A review with special reference to *Phrynosoma platyrhinos*. *Copeia* **1975:** 141–162.

Pieau, C. (1971). Sur la proportion sexuelle chez les embryons de deux chéloniens (*Testudo graeca* L. et *Emys orbicularis* L.) issus d'oeufs incubés artificiellement. *C. R. Acad. Sci. Paris* **274:** 3071–3074.

Pieau, C. (1975). Temperature and sex differentiation in embryos of two chelonians, *Emys orbicularis* L., and *Testudo graeca* L. *In* "Intersexuality in the Animal Kingdom" (R. Reinboth, Ed.), pp. 332–339. Springer-Verlag, New York.

Pilorge, T. (1987). Density, size structure, and reproductive characteristics of three populations of *Lacerta vivipara*. *Herpetologica* **43:** 345–356.

Pitman, C. R. S. (1974). "A Guide to the Snakes of Uganda. Revised Edition." Wheldon & Wesley, Ltd., Codicote, UK.

Platenberg, R. J., and Griffiths, R. A. (1999). Translocation of slow-worms (*Anguis fragilis*) as a mitigation strategy: A case study from south-east England. *Biol. Conserv.* **90:** 125–132.

Pledge, N. S. (1992). The Curramulka local fauna: A new Late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *Beagle* **9:** 115–142.

Plummer, M. V. (1976). Some aspects of nesting success in the turtle, *Trionyx muticus. Herpetologica* **32:** 353–359.

Plummer, M. V. (1977a). Activity, habitat and population structure in the turtle, *Trionyx muticus. Copeia* **1977:** 431–440.

Plummer, M. V. (1977b). Reproduction and growth in the turtle *Trionyx muticus. Copeia* **1977:** 440–447.

Plummer, M. V. (1985). Growth and maturity in green snakes (*Opheodrys aestivus*). *Herpetologica* **41:** 28–33.

Plummer, M. V., and Shirer, H. W. (1975). Movement patterns in a river population of the softshell turtle, *Trionyx muticus. Occas. Pap. Mus. Nat. His. Univ. Kansas* **43:** 1–26.

Poe, S. (1997). Data set incongruence and the phylogeny of crocodilians. *Syst. Biol.* [1996] **45:** 393–414.

Poinar, G. R., Jr., and Cannatella, D. C. (1987). An Upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. *Science* **237:** 1215–1216.

Polisar, J. (1996). Reproductive biology of a flood-season nesting freshwater turtle of the northern Neotropics: *Dermatemys mawii* in Belize. *Chelonian Conserv. Biol.* **2:** 13–25.

Pombal, J. P., Jr., Sazima, I., and Haddad, C. F. B. (1994). Breeding behavior of the pumpkin toadlet, *Brachycephalus ephippium* (Brachycephalidae). *J. Herpetol.* **28:** 516–519.

Pombal, J. P., Jr., Wistuba, E. M., and Bornshein, M. R. (1998). A new species of brachycephalid (Anura) from the Atlantic rain forest of Brazil. *J. Herpetol.* **32:** 70–74.

Pooley, A. C. (1974). Parental care in the Nile crocodile: a preliminary report on behaviour of a captive female. *Lammergeyer* **3:** 22–44.

Pooley, A. C. (1977). Nest opening response of the Nile crocodile *Crocodylus niloticus. J. Zool., London* **182:** 17–26.

Porter, W. P., and Gates, D. M. (1969). Thermodynamic equilibria of animals with environment. *Ecol. Monog.* **39:** 227–244.

Pough, F. H. (1988). Mimicry and related phenomenona. *In* "Biology of the Reptilia. Volume **16:** Ecology B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 153–234. Alan R. Liss, Inc., New York.

Pough, F. H., and Gans, C. (1982). The vocabulary of reptilian thermoregulation. *In* "Biology of the Reptilia. Volume 12, Physiology C. Physiological Ecology" (C. Gans and F. H. Pough, Eds.), pp. 17–23. Academic Press, New York.

Pough, F. H., and Taigen, T. L. (1990). Metabolic correlates of the foraging and social behaviour of dart-poison frogs. *Anim. Behav.* **39:** 145–155.

Pough, F. H., and Wilson, R. E. (1977). Acid precipitation and reproductive success of *Ambystoma* salamanders. *Water Air Soil Pollution* **7:** 307–316.

Pough, F. H., Taigen, T. L., Stewart, M. M., and Brussard, P. F. (1983). Behavioral modification of evaporative water loss by a Puerto Rican frog. *Ecology* **64:** 244–252.

Pough, F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Savitzky, A. H., and Wells, K. D. (1998). "Herpetology." Prentice Hall, Upper Saddle River, NJ.

Pound, J. A., and Crump, M. L. (1994). Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. *Conserv. Biol.* **8:** 72–85.

Pound, J. A., Fogden, M. P. L., Savage, J. M., and Gorman, G. C. (1997). Test of null models for amphibian declines on a tropical mountain. *Conserv. Biol.* **11:** 1307–1322.

Poynton, J. C. (1964). The Amphibia of Southern Africa: a faunal study. *Ann. Natal Mus.* **17:** 1–334.

Poynton, J. C. (1996). Diversity and conservation of African bufonids (Anura): some preliminary findings. *Afr. J. Herpetol.* **45:** 1–7.

Poynton, J. C., and Broadley, D. G. (1985–1991). Amphibia Zambesiaca. Parts 1–5 *Ann. Natal Mus.* **26:** 503–553; **27:** 115–181; **28:** 161–229; **29:** 447–490; **32:** 221–277.

Prasad, G. V. R., and Rage, J.-C. (1991). A discoglossid frog in the latest Cretaceous (Maastrichtian) of India. Further evidence for a terrestrial route between India and Laurasia in the latest Cretaceous. *C. R. Acad. Sci. Paris* **313:** 273–278.

Prasad, G. V. R., and Rage, J.-C. (1995). Amphibians and squamates from the Maastrichtian of Naskal, India. *Cretaceous Res.* **16:** 95–107.

Pregill, G. K., Gauthier, J. A., and Greene, H. W. (1986). The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Trans. San Diego Soc. Nat. Hist.* **21:** 167–202.

Presch, W. (1974). Evolutionary relationships and biogeography of the macroteiid lizards (Family Teiidae, Subfamily Teiinae). *Bull. S. Calif. Acad. Sci.* **73:** 23–32.

Presch, W. (1988). Phylogenetic relationships of the Scincomorpha. *In* "Phylogenetic Relationships of the Lizard Families" (R. Estes and G. Pregill, Eds.), pp. 471–492. Stanford Univ. Press, Stanford, CA.

Price, T. D. (1984). The evolution of sexual size dimorphism in Darwin's finches. *Am. Nat.* **123:** 500–518.

Primack, R. B. (1995). "A Primer of Conservation Biology." Sinauer Assoc. Inc., Sunderland, MA.

Pritchard, P. C. H., and Trebbau, P. (1984). "The Turtles of Venezuela." Soc. Study Amphibians and Reptiles, Athens, OH.

Proud, K. R. S. (1978). Some notes on a captive earless monitor lizard *Lanthanotus borneensis. Sarawak Mus. J.* **26:** 235–242.

Pyke, G. H., and Osborne, W. S., Eds. (1996). The green & golden bell frog *Litoria aurea*. Biology and conservation. *Aust. Zool.* **30:** 132–258.

Qualls, C. P., and Shine, R. (1995). Maternal body-volume as a constraint on reproductive output in lizards: Evidence from the evolution of viviparity. *Oecologia* **103:** 73–78.

Quay, W. B. (1972). Integument and the environment: glandular composition, function, and evolution. *Am. Zool.* **12:** 95–108.

Quay, W. B. (1979). The parietal eye-pineal complex. *In* "Biology of the Reptilia. Volume 9. Neurology A" (C. Gans, R. G. Northcutt, and P. Ulinski, Eds.), pp. 245–406. Academic Press, London.

Quay, W. B. (1986). Glands. *In* "Biology of the Integument. 2. Vertebrates" (J. Bereiter-Hahn, A. G. Matoltsy, and K. S. Richards, Eds.), pp. 188–193. Springer Verlag, Berlin.

Rabb, G. B., and Rabb, M. S. (1960). On the mating and egg-laying behavior of the Surinam toad, *Pipa pipa. Copeia* **1960:** 271–276.

Rabb, G. B., and Rabb, M. S. (1963a). Additional observations on breeding behavior of the Surinam toad, *Pipa pipa*. *Copeia* **1963:** 636–642

Rabb, G. B., and Rabb, M. S. (1963b). On the behavior and breeding biology of the African pipid frog *Hymenochirus boettgeri*. *Z. Tierpsychol.* **20:** 215–241.

Rabb, G. B., and Snediger, R. (1960). Observations on breeding and development of the Surinam toad, *Pipa pipa*. *Copeia* **1960:** 40–44.

Radtkey, R. R., Donnellan, S. C., Fisher, R. N., Moritz, C., Hanley, K. A., and Case, T. J. (1995). When species collide: The origin and spread of an asexual species of gecko. *Proc. Roy. Soc. London B* **259:** 145–152.

Rage, J.-C. (1984). "Serpentes. Handbuch der Paläoherpetologie, 11." Gustav Fischer Verlag, Stuttgart.

Rage, J.-C. (1986). Le plus ancien amphibien apode (Gymnophiona) fossile. Remarques sur la répartiition et l'histoire paléobiogéographique des gymnophiones. *C. R. Acad. Sci., Paris* **302:** 1033–1036.

Rage, J.-C. (1987). Fossil history. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 51–76. Macmillan Publ. Co., New York.

Rage, J.-C. (1996). Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: Témoins gondwaniens d'une dispersion transtéthysienne. *C. R. Acad. Sci., Paris, Ser. IIa* **322:** 603–608.

Rage, J.-C., and Richter, A. (1994). A snake from the Lower Cretaceous (Barremian) of Spain: The oldest known snake. *N. Jb. Geol. Paläont. Mh.* **1994:** 561–565.

Rage, J.-C., and Rocek, Z. (1989). Redescription of *Triadobatrachus massinoti* (Piveteau, 1936), an anuran from the Early Triassic. *Palaeontographica Abt. A* **206:** 1–16.

Rage, J.-C., Marshall, L. G., and Gayet, M. (1993). Enigmatic Caudata (Amphibia) from the Upper Cretaceous of Gondwana. *Geobios* **26:** 515–519.

Rajendran, M. V. (1985). "Studies in Uropeltid Snakes." Publ. Div., Madurai Kamaraj Univ., Madurai, India.

Ralph, C. L. (1983). Evolution of pineal control of endocrine function in lower vertebrates. *Am. Zool.* **23:** 597–605

Rand, A. S. (1982). Clutch and egg size in Brazilian iguanid lizards. *Herpetologica* **38:** 171–178.

Rand, A. S., Dugan, B. A., Monteza, H., and Vianda, D. (1990). The diet of a generalized folivore: *Iguana iguana* in Panama. *Copeia* **1990**: 211–214.

Rand, W. M., and Rand, A. S. (1976). Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. *Z. Tierpsychol.* **40:** 279–299.

Rao, D.-Q., and Yang, D.-T. (1992). Phylogenetic systematics of Pareinae (Serpentes) of southeastern Asia and adjacent islands with relationship between it and the geology change. *Acta Zool. Sinica* **38:** 139–150.

Rao, D.-Q., and Yang, D.-T. (1997). The karyotypes of Megophryidae (Pelobatoidea) with a discussion on their classification and phylogenetic relationships. *Asiatic Herpetol. Res.* **7:** 93–102.

Rashid, S. M. A., and Swingland, I. R. (1998). On the ecology of some freshwater turtles in Bangladesh. *In* "Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference" [1997] (J. Van Abbema, Ed.), pp. 224–242. New York Turtle & Tortoise Soc., Purchase, NY.

Rasmussen, A. R. (1997). Systematics of sea snakes: a critical review. *In* "Venomous Snakes, Ecology, Evolution and Snakebite" (R. S. Thorpe, W. Wüster, and A. Malhotra, Eds.), pp. 15–30. Zoological Society of London, Oxford.

Raup, D. M. (1991). "Extinction: Bad Genes or Bad Luck?" W. W. Norton & Co., New York.

Reagan, D. P. (1991). The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. *Biotropica* **23:** 468–474.

Rebouças-Spieker, R., and Vanzolini, P. E. (1978). Parturition in *Mabuya macrorhyncha* Hoge, 1946 (Sauria, Scincidae), with a note on the distribution of maternal behavior in lizards. *Pap. Av. Zool. (S. Paulo)* **32:** 95–99.

Reeder, T. W. (1995). Phylogenetic relationships among phrynosomatid lizards as inferred from mitochondrial ribosomal DNA sequences: Substitutional bias and information content of transitions relative to transversions. *Mol. Phylog. Evol.* **4:** 203–222.

Reeder, T. W., and Wiens, J. J. (1996). Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. *Herpetol. Monog.* **10:** 43–84.

Reid, K. J. (1955). Reproduction and development in the northern diamondback terrapin, *Malaclemys terrapin terrapin*. *Copeia* **1955:** 310–311.

Reilly, S. M., and Brandon, R. A. (1994). Partial paedomorphosis in the Mexican stream ambystomatids and the taxonomic status of the genus *Rhyacosiredon* Dunn. *Copeia* **1994:** 656–662.

Reilly, S. M., Wiley, E. O., and Meinhardt, D. J. (1997). An integrative approach to heterochrony: The distinction between interspecific and intraspecific phenomena. *Biol. J. Linn. Soc.* **60:** 119–143.

Reinert, H. K. (1991). Translocations as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. *Herpetologica* **47:** 357–363.

Reisz, R. R., and Laurin, M. (1991). *Owenetta* and the origin of turtles. *Nature* **349:** 324–326.

Reno, H. W., Gehlbach, F. R., and Turner, R. A. (1972). Skin and aestivational cocoon of the aquatic amphibian, *Siren intermedia* Le Conte. *Copeia* **1972:** 625–631.

Richards, C. M., and Moore, W. S. (1998). A molecular phylogenetic study of the Old World treefrog family Rhacophoridae. *Herpetol. J.* **8:** 41–46.

Richards S. J., McDonald, K. R., and Alford, R. A. (1993). Declines in populations of Australia's endemic tropical rainforest frogs. *Pacific Conserv. Biol.* **1:** 66–77.

Richardson, B. J., Baverstock, P. R., and Adams, M. (1986). "Allozyme Electrophoresis. A Handbook for Animal Systematics and Population Studies." Academic Press, Sydney.

Riemer, W. J. (1957). The snake *Farancia abacura:* an attended nest. *Herpetologica* **13:** 31–32.

Rieppel, O. (1988). A review of the origin of snakes. *Evol. Biol.* **22:** 37–130.

Rieppel, O. (1993). Euryapsid relationships: a preliminary analysis. *N. Jb. Geol. Paläont. Abh.* **188:** 241–264.

Rieppel, O. (1994). The Lepidosauromorpha: an overview with special emphasis on the Squamata. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 23–37. Cambridge Univ. Press, New York.

Rieppel, O., and Crumly, C. (1997). Paedomorphosis and skull structure in Malagasy chamaeleons (Reptilia: Chamaeleoninae). *J. Zool., London* **243:** 351–380.

Rieppel, O., and deBraga, M. (1996). Turtles as diapsid reptiles. *Nature* **384:** 453–455.

Riley, J., Stimson, A. F., and Winch, J. M. (1985). A review of Squamata ovipositing in ant and termite nests. *Herpetol. Rev.* **16:** 38–43.

Ripa, D. (1999). Keys to understanding the bushmasters (genus *Lachesis* Daudin, 1803). *Bull. Chicago Herpetol. Soc.* **34:** 45–92.

Robb, J. (1986). "New Zealand Amphibians and Reptiles in Colour. Revised." Collins, Auckland.

Roberts, J. D., Horwitz, P, Wardell-Johnson, G., Maxson, L. R., and Mahony, J. (1997). Taxonomy, relationships and conservation of a new genus and species of myobatrachid frog from the high rainfall region of southwestern Australia. *Copeia* **1997:** 373–381.

Robinson, M. D., and Cunningham, A. B. (1978). Comparative diets of two Namib Desert sand lizards. *Madoqua* **11**: 41–45.

Rocek, Z. (1994a). A review of the fossil Caudata of Europe. *Abh. Ber. Naturk.* **17:** 51–56.

Rocek, Z. (1994b). Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* V. Meyer, 1843. *Geobios* **27:** 717–751.

Rocek, Z., and Lamaud, P. (1995). *Thaumastosaurus bottii* de Stefano, 1903, an anuran with Gondwanan affinities from the Eocene of Europe. *J. Vert. Palaeontol.* **15:** 506–515.

Rocek, Z., and Nessov, L. A. (1993). Cretaceous anurans from Central Asia. *Palaeontographica Abt. A* **226:** 1–54.

Rocha, C. F. D. (1990). Reproductive effort in the Brazilian sand lizard *Liolaemus lutzae* (Sauria: Iguanidae). *Cienc. Cult.* **42:** 1203–1206.

Rocha, C. F. D., and Bergallo, H. G. (1990). Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. Evol.* **2:** 263–268.

Rodda, G. H. (1984). The orientation and navigation of juvenile alligators: Evidence of magnetic sensitivity. *J. Comp. Physiol.* **154A:** 649–658.

Rodda, G. H. (1985). Navigation in juvenile alligators. *Z. Tierpsychol.* **68:** 65–77.

Rodda, G. H., and Fritts, T. H. (1992). The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam's lizards. *J. Herpetol.* **26:** 166–174.

Rodda, G. H., and Phillips, J. B. (1992). Navigational systems develop along similar lines in amphibians, reptiles, and birds. *Ethol. Ecol. Evol.* **4:** 43–51.

Rödel, M.-O. (1996). "Amphibien der westafrikanischen Savanne." Edition Chimaira, Frankfurt am Main.

Rödel, M.-O. (1998). A reproductive mode so far unknown in African ranids: *Phrynobatrachus guineensis* Guibé & Lamotte, 1961, breeds in tree holes (Anura: Ranidae). *Herpetozoa* **11:** 19–26.

Rödel, M.-O., Spieler, M., Grabow, K., and Böckheler, C. (1995). *Hemisus marmoratus* (Peters, 1854) (Anura: Hemisotidae), Fortpflanzungsstrategien eines Savannenfrosches. *Bonn. Zool. Beitr.* **45:** 191–207.

Rodriguez, L. B., and Cadle, J. E. (1990). A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru. *In* "Four Neotropical Rainforests" (A. H. Gentry, Ed.), pp. 410–425. Yale Univ. Press, New Haven, CT.

Roman, J., Santhuff, S. D., Moler, P. R., and Bowen, B. W. (1999). Population structure and cryptic evolutionary units in the alligator snapping turtle. *Conserv. Biol.* **13:** 135–142.

Rome, L. C., Stevens, D. E., and John-Adler, H. B. (1992). The influence of temperature and thermal acclimation on physiological function. *In* "Environmental Physiology of the Amphibians" (M. E. Feder and W. W. Burggren, Eds.), pp. 183–205. Univ. Chicago Press, Chicago.

Romer, A. S. (1956). "Osteology of the Reptiles." Univ. Chicago Press, Chicago.

Romer, A. S. (1966). "Vertebrate Paleontology. Third Edition." Univ. Chicago Press, Chicago.

Rose, B. (1982). Lizard home ranges: Methodology and functions. *J. Herpetol.* **16:** 253–269.

Rose, W. (1962). "The Reptiles and Amphibians of Southern Africa." Maskew Miller, Ltd., Cape Town, South Africa.

Rosenberg, D. K., Noon, B. R., and Meslow, E. C. (1997). Biological corridors, form, function, and efficacy. *BioScience* **47:** 677–687.

Rosenberg, D. K., Noon, B. R., Megahan, J. W., and Meslow, E. C. (1998). Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: A field experiment. *Can. J. Zool.* **76:** 117–133.

Rosenberg, H. I., and Russell, A. P. (1980). Structural and functional aspects of tail squirting: A unique defense mechanism of *Diplodactylus* (Reptilia: Gekkonidae). *Can. J. Zool.* **58:** 865–881.

Rosenberg, H. I., Russell, A. P., and Kapoor, M. (1984). Preliminary characterization of the defensive secretion of *Diplodactylus* (Reptilia: Gekkonidae). *Copeia* **1984:** 1025–1028.

Rösler, H. (1995). "Geckos der Welt. Alle Gattungen." Urania-Verlag, Leipzig.

Ross, C. A., Ed. (1989). "Crocodiles and Alligators." Golden Press Pty. Ltd., Silverwater, N.S.W.

Ross, C. A. (1990). *Crocodylus raninus* S. Müller and Schlegel, a valid species of crocodile (Reptilia: Crocodylidae) from Borneo. *Proc. Biol. Soc. Washington* **103:** 955–961.

Rossi, J. V. (1983). The use of olfactory cues by *Bufo marinus*. *J. Herpetol.* **17:** 72–73.

Rossman, D. A., and Williams, K. L. (1966). Defensive behavior of the South American colubrid snakes *Pseustes sulphureus* (Wagler) and *Spilotes pullatus* (Linnaeus). *Proc. Louisiana Acad. Sci.* **29:** 152–156.

Rossman, D. A., Ford, N. B., and Seigel, R. A., Eds. (1996). "The Garter Snakes: Evolution and Ecology." Univ. Oklahoma Press, Norman.

Roth, G. (1986). Neural mechanisms of prey recognition: an example in amphibians. *In* "Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates" (M. E. Feder and G. V. Lauder, Eds.), pp. 42–68. Univ. Chicago Press, Chicago.

Roth, G. (1987). "Visual Behavior in Salamanders." Springer-Verlag, New York.

Roughgarden, J. (1995). "Anolis Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics." Oxford Univ. Press, New York.

Rowe, C. L., and Dunson, W. A. (1995). Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. *Oecologia* **102:** 397–403.

Roze, J. A. (1996). "Coral Snakes of the Americas: Biology, Identification, and Venoms." Krieger Publ. Co., Malabar, FL.

Ruben, J. A., Hillenius, W. J., Geist, N. R., Leitch, A., Jones, T. D., Currie, P. J., Horner, J. R., and Espe, G. (1996). The metabolic status of some Late Cretaceous dinosaurs. *Science* **273:** 1204–1207.

Rubio, M. (1998). "Rattlesnakes: Portrait of a Predator." Smithsonian Inst. Press, Washington, DC.

Ruby, D. E. (1978). Seasonal changes in the territorial behavior of the iguanid lizard, *Sceloporus jarrovi. Copeia* **1978:** 430–438.

Ruby, D. E. (1981). Phenotypic correlates of male reproductive success in the lizard, *Sceloporus jarrovi. In* "Natural Selection and Social Behavior" (R. D. Alexander and D. W. Tinkle, Eds.), pp. 96–107. Chiron Press, New York.

Ruby, D. E. (1984). Male breeding success and differential access to females in *Anolis carolinensis. Herpetologica* **40:** 272–280.

Ruby, D. E., and Baird, D. I. (1993). Effects of sex and size on agonistic encounters between juvenile and adult lizards, *Sceloporus jarrovi. J. Herpetol.* **27:** 100–103.

Ruby, D. E., and Dunham, A. E. (1987). Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami. Oecologia* **71:** 473–480.

Ruby, D. E., and Niblick, H. A. (1994). A behavioral inventory of the desert tortoise: development of an ethogram. *Herpetol. Monog.* **8:** 88–102.

Rugh, R. (1951). "The Frog. Its Reproduction and Development." McGraw-Hill Book Co., New York.

Ruibal, R., and Shoemaker, V. (1984). Osteoderms in anurans. *J. Herpetol.* **18:** 313–328.

Ruiz-Carrnaza, P. M., and Lynch, J. D. (1991) Ranas Centrolenidae de Colombia. I. Propuesta de una nueva clasificación genérica. *Lozania* **57:** 1–30.

Runkle, L. S., Wells, K. D., Robb, C. C., and Lance, S. L. (1994). Individual, nightly, and seasonal variation in calling behavior of the gray treefrog, *Hyla versicolor:* implications for energy expenditure. *Behav. Ecol.* **5:** 318–325.

Russell, A. P. (1988). Limb muscles in relation to lizard systematics: a reappraisal. *In* "Phylogenetic Relationships of the Lizard Families" (R. Estes and G. Pregill, Eds.), pp. 493–568. Stanford Univ. Press, Stanford, CA.

Russell, A. P., and Wu, X.-C. (1997). The Crocodylomorpha at and between geological boundaries: The Baden-Powell approach to change? *Zoology* **100:** 164–182.

Russell, A. P., Bauer, A. M., and Laroiya, R. (1997). Morphological correlates of the secondarily symmetrical pes of gekkotan lizards. *J. Zool., London* **241:** 767–790.

Ruvinsky, I., and Maxson, L. R. (1996). Phylogenetic relationships among bufonoid frogs (Anura: Neobatrachia) inferred from mitochondrial DNA sequences. *Mol. Phylog. Evol.* **5:** 533–547.

Ryan, M. J. (1985). "The Túngara Frog. A Study in Sexual Selection and Communication." Univ. Chicago Press, Chicago.

Ryan, M. J., and Rand, A. S. (1995). Female responses to ancestral advertisement calls in Túngara frogs. *Science* **269:** 390–392.

Ryan, M. J., Tuttle, M. D., and Taft, L. K. (1981). The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.* **8:** 273–278.

Ryan, M. J., Tuttle, M. D., and Rand, A. S. (1982). Bat predation and sexual advertisement in a Neotropical frog. *Am. Nat.* **119:** 136–139.

Ryan, P. (1988). "Fiji's Natural Heritage." Southwestern Publ. Co., Auckland.

Sabater-Pi, J. (1985). Contribution to the biology of the giant frog (*Conraua goliath,* Boulenger). *Amphibia-Reptilia* **6:** 143–153.

Sage, R. D., Prager, E. M., and Wake, D. B. (1982). A Cretaceous divergence time between pelobatid frogs (*Pelobates* and *Scaphiopus*): immunological studies of serum albumin. *J. Zool., London* **198:** 481–494.

Saint-Aubain, M. L. de (1985). Blood flow patterns of the respiratory systems in larval and adult amphibians: Functional morphology and phylogenetic significance. *Zeits. Zool. Syst. Evol.* **23:** 229–240.

Saint Girons, H. (1970). The pituitary gland. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 135–199. Academic Press, London.

Saint Girons, H. (1988). Les glandes céphaliques exocrines des reptiles. I. Données anatomiques et histologiques. *Ann. Sci. Nat., Zool., Paris 13^e^ Ser.* **9:** 221–255.

Saint Girons, H. (1992). Strategies reproductrices des Viperidae dans les zones temperees fraiches et froides. *Bull. Soc. Zool. France* **117:** 267–278.

Saint Girons, M.-C. (1970). Morphology of the circulating blood cells. *In* "Biology of the Reptilia. Volume 3. Morphology C" (C. Gans and T. S. Parsons, Eds.), pp. 73–91. Academic Press, London.

Sakaluk, S. K., and Belwood J. J. (1984). Gecko phonotaxis to cricket calling song: A case of satellite predation. *Anim. Behav.* **32:** 659–662.

Salthe, S. N. (1969). Reproductive modes and the numbers and sizes of ova in the urodeles. *Am. Midl. Nat.* **81:** 467–490.

Salthe, S. N. (1973a). *Amphiuma means* Garden. *Catalog. Am. Amphib. Rept.* **148:** 1–2.

Salthe, S. N. (1973b). *Amphiuma tridactylum* Cuvier. *Catalog. Am. Amphib. Rept.* **149:** 1–2.

Salthe, S. N., and Duellman, W. E. (1973). Quantitative constraints associated with reproductive mode in anurans. *In* "Evolutionary Biology of the Anurans" (J. L. Vial, Ed.), pp. 229–249. Univ. Missouri Press, Columbia.

Salthe, S. N., and Mecham, J. S. (1974). Reproduction and courtship patterns. *In* "Physiology of the Amphibia, Volume 2" (B. Lofts, Ed.), pp. 309–521. Academic Press, New York.

Salvador, A. (1985). "Guia de Campo de los Anfibios y Reptiles de la Peninsula Iberica, Islas Baleares y Canarias." Privately printed, Madrid.

Salvador, A., Martín, J., López, P., and Veiga, J. P. (1996). Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). *Copeia* **1996:** 208–209.

Salvidio, S. (1993). Life history of the European plethodontid salamander *Speleomantes ambrosii* (Amphibia, Caudata). *Herpetol. J.* **3:** 55–59.

Sanchiz, B., and Rocek, Z. (1996). An overview of the anuran fossil record. *In* "The Biology of *Xenopus*" (R. C. Tinsley and H. R. Kobel, Eds.), pp. 317–328. Zool. Soc. London, London.

Sartorius, S. S., Vitt, L. J., and Colli, G. R. (1999). Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biol. Conserv.* **90:** 91–101.

Savage, J. M. (1995). Systematics and the biodiversity crisis. *BioScience* **45:** 673–679.

Savage, J., and Guyer, C. (1989). Infrageneric classification and species composition of the anole genera, *Anolis, Ctenonotus, Dactyloa, Norops,* and *Semiurus* (Sauria: Iguanidae). *Amphibia-Reptilia* **10:** 105–116.

Savage, J. M., and Lips, K. R. (1993). A review of the status and biogeography of the lizard genera *Celestus* and *Diploglossus* (Squamata: Anguidae), with description of two new species from Costa Rica. *Rev. Biol. Trop.* **41:** 817–842.

Savidge, J. A. (1987). Extinction of an island forest avifauna by an introduced snake. *Ecology* **68:** 660–668.

Savitzky, A. H. (1983). Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. *Am. Zool.* **23:** 397–409.

Sazima, I. (1991). Caudal luring in two neotropical pitvipers, *Bothrops jararaca* and *B. jararacussu*. *Copeia* **1991:** 245–248.

Sazima, I., and Abe, A. S. (1991). Habits of five Brazilian snakes with coral-snake pattern, including a summary of defensive tactics. *Stud. Neotrop. Fauna Environ.* **26:** 159–164.

Scalia, F. (1976). Structure of the olfactory and accessory olfactory systems. *In* "Frog Neurobiology. A Handbook" (R. Llinás and W. Precht, Eds.), pp. 213–233. Springer-Verlag, Berlin.

Scanlon, J. D. (1992). A new large madtsoiid snake from the Miocene of the Northern Territory. *Beagle* **9:** 49–60.

Schaeffel, R., and de Queiroz, A. (1990). Alternative mechanisms of enhanced underwater vision in the garter snake *Thamnophis melanogaster* and *T. couchii*. *Copeia* **1990:** 50–58.

Schaffner, F. (1998). The liver. *In* "Biology of the Reptilia. Volume 19, Morphology G" (C. Gans and A. S. Gaunt, Eds.), pp. 485–531. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Schall, J. J. (1983). Lizard malaria: Parasite-host ecology. *In* "Lizard Ecology. Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 84–100. Harvard Univ. Press, Cambridge, MA.

Schall, J. J. (1992). Parasite-mediated competition in *Anolis* lizards. *Oecologia* **92:** 58–64.

Schall, J. J., and Pianka, E. R. (1980). Evolution of escape behavior diversity. *Am. Nat.* **115:** 551–566.

Schauinsland, H. (1903). Beiträge zur Entwickelungsgechichte und Anatomie der Wirbeltiere. I. *Sphenodon, Callorhynchus, Chamäleo. Abh. Ges. Zool.* **39:** 1–95.

Schiesari, L. C., Grillitsch, B., and Vogl, C. (1996). Comparative morphology of phytotelmonous and pond-dwelling larvae of four neotropical treefrog species (Anura, Hylidae, *Osteocephalus oophagus, Osteocephalus taurinus, Phrynohyas resinifictrix, Phrynohyas venulosa). Alytes* **13:** 109–139.

Schiotz, A. (1963). The Amphibia of Nigeria. *Vidensk. Medd. Dansk Naturh. Foren.* **125:** 1–92, plates 1–4.

Schiotz, A. (1967). The treefrogs (Rhacophoridae) of West Africa. *Spolia Zool. Mus. Hauniensis* **25:** 1–346.

Schiotz, A. (1975). "The Treefrogs of East Africa." Steenstrupia, Copenhagen.

Schmalhausen, I. I. (1968). "The Origin of Terrestrial Vertebrates." Academic Press, New York.

Schmitt, M. (1989). Claims and limits of phylogenetic systematics. *Z. Zool. Syst. Evol.-Forsch.* **27:** 181–190.

Schmuck, R., and Linsemair, K. E. (1988). Adaptations of the reed frog, *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its environment: III. Aspects of nitrogen metabolism and osmoregulation in the reed frog, *Hyperolius viridiflavus taeniatus,* with special reference to the role of iridophores. *Oecologia* **75:** 354–361.

Schoener, T. W. (1974a). Resource partitioning in ecological communities. *Science* **185:** 27–38.

Schoener, T. W. (1974b). Theory of feeding strategies. *Ann. Rev. Syst. Ecol.* **2:** 369–404.

Schoener, T. W. (1979). Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* **60:** 1110–1115.

Schoener, T. W. (1986). Overview: Kinds of ecological communities-Ecology becomes pluralistic. *In* "Community Ecology" (J. Diamond and T. J. Case, Eds.), pp. 467–479. Harper and Row, New York.

Schoener, T. W., and Schoener, A. (1980). Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* **1980:** 839–850.

Schoener, T. W., and Schoener, A. (1982). The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* **39:** 1–16.

Schreibman, M. P. (1986). Pituitary gland. *In* "Vertebrate Endocrinology: Fundamentals and Biomedical Implications. Vol. 1. Morphological Considerations" (P. K. T.

Pang and M. P. Schreibman, Eds.), pp. 11–55. Academic Press, Orlando.

Schubauer, J. P., Gibbons, J. W., and Spotila, J. R. (1990). Home range and movement patterns of slider turtles inhabiting Par Pond. *In* "Life History and Ecology of the Slider Turtle" (J. W. Gibbons, Ed.), pp. 223–232. Smithsonian Inst. Press, Washington, DC.

Schultze, H.-P. (1991). A comparison of controversial hypotheses on the origin of tetrapods. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 29–67. Comstock Publ. Assoc., Ithaca, NY.

Schultze, H.-P. (1994). Comparison of hypotheses on the relationships of sarcopterygians. *Syst. Biol.* **43:** 155–173.

Schultze, H.-P., and Trueb, L., Eds. (1991). "Origins of the Higher Groups of Tetrapods. Controversy and Consensus." Comstock Publ. Assoc., Ithaca, NY.

Schwartz, A., and Henderson, R. W. (1991). "Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History." Univ. Florida Press, Gainesville, FL.

Schwartz, E. R., Schwartz, C. W., and Kiester, A. R. (1984). The three-toed box turtle in central Missouri, part II: A nineteen-year study of home range, movements and population. *Missouri Dept. Conserv., Terrest.* **12:** 1–28.

Schwenk, K. (1985). Occurrence, distribution and functional significance of taste buds in lizards. *Copeia* **1985:** 91–101.

Schwenk, K. (1986). Morphology of the tongue in the tuatara, *Sphenodon punctatus* (Reptilia: Lepidosauria), with comments on function and phylogeny. *J. Morphol.* **188:** 129–156.

Schwenk, K. (1988) Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. *In* "Phylogenetic Relationships of the Lizard Families" (R. Estes and G. Pregill, Eds.), pp. 569–598. Stanford Univ. Press, Stanford, CA.

Schwenk, K. (1993). The evolution of chemoreception in squamate reptiles: A phylogenetic approach. *Brain Behav. Evol.* **41:** 124–137.

Schwenk, K. (1994a). Why snakes have forked tongues. *Science* **263:** 1573–1577.

Schwenk, K. (1994b). Systematics and subjectivity: The phylogeny and classification of iguanian lizards revisited. *Herpetol. Rev.* **25:** 53–57.

Schwenk, K. (1995). Of tongues and noses: Chemoreception in lizards and snakes. *Trends Ecol. Evol.* **10:** 7–12.

Schwenk, K., and Greene, H. W. (1987). Water collection and drinking in *Phrynocephalus helioscopus:* a possible condensation mechanism. *J. Herpetol.* **21:** 134–139.

Scott, A. C. (1980). The ecology of some Upper Palaeozoic floras. *In* "The Terrestrial Environment and the Origin of Land Vertebrates" (A. L. Panchen, Ed.), pp. 87–115. Academic Press, London.

Scott, D. E. (1990). Effects of larval density in *Ambystoma opacum:* An experiment in large-scale field enclosures. *Ecology* **71:** 296–306.

Scott, D. E. (1994). The effect of larval density on adult demographic traits in *Ambystoma opacum. Ecology* **75:** 1383–1396.

Scott, N. J., Jr. (1976). The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* **8:** 41–58.

Seben, K. P. (1987). The ecology of indeterminate growth in animals. *Ann. Rev. Ecol. Syst.* **18:** 371–407.

Secor, S. M. (1994). Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes. Copeia* **1994:** 631–645.

Secor, S. M., and Nagy, K. A. (1994). Bioenergetic correlates of foraging for the snakes *Crotalus cerastes* and *Masticophis flagellum. Ecology* **75:** 1600–1614.

Secor, S. M., Jayne, B. C., and Bennett, A. F. (1992). Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes. J. Exp. Biol.* **163:** 1–14.

Seddon, J. M., Georges, A., Baverstock, P. R., and McCord, W. (1997). Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA gene sequence variation. *Mol. Phylog. Evol.* **7:** 55–61.

Seigel, R. A. (1983). Natural survival of eggs and tadpoles of the wood frog, *Rana sylvatica. Copeia* **1983:** 1096–1098.

Seigel, R. A., and Ford, N. B. (1987). Reproductive ecology. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 210–252. Macmillan Publ. Co., New York.

Seigel, R. A., and Ford N. B. (1991). Phenotypic plasticity in the reproductive characteristics of an oviparous snake, *Elaphe guttata:* implications for life history studies. *Herpetologica* **47:** 301–307.

Seigel, R. A., Fitch, H. S., and Ford, N. B. (1986). Variation in relative clutch mass on snakes among and within species. *Herpetologica* **42:** 179–185.

Seigel, R. A., Huggins, M. M., and Ford, N. B. (1987). Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* **73:** 481–485.

Seigel, R. A., Loraine, R. K., and Gibbons, J. W. (1995). Reproductive cycles and temporal variation in fecundity in the black swamp snake, *Seminatrix pygaea. Am. Midl. Nat.* **134:** 371–377.

Selcer, K. W. (1990). Egg-size relationships in a lizard with fixed clutch size: Variation in a population of the Mediterranean gecko. *Herpetologica* **46:** 15–21.

Semlitsch, R. D. (1980). Geographic and local variation in population parameters of the slimy salamander *Plethodon glutinosus. Herpetologica* **36:** 6–16.

Semlitsch, R. D. (1981). Effects of implanted tantalum-182 wire tags on the mole salamander, *Ambystoma talpoideum. Copeia* **1981:** 735–737.

Semlitsch, R. D. (1985a). Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum. Copeia* **1985:** 477–489.

Semlitsch, R. D. (1985b). Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum. Oecologia* **65:** 305–313.

Semlitsch, R. D. (1987). Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum. Copeia* **1987:** 61–69.

Semlitsch, R. D. (1998). Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conserv. Biol.* **12:** 1113–1119.

Semlitsch, R. D., and Gibbons, J. W. (1988). Fish predation in size-structured populations of treefrog tadpoles. *Oecologia* **75:** 321–326.

Semlitsch, R. D., and West, C. A. (1983). Aspects of the life history and ecology of Webster's salamander, *Plethodon websteri. Copeia* **1983:** 339–346.

Semlitsch, R. D., Scott, D. E., and Pechmann, J. H. K. (1988). Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum. Ecology* **69:** 184–192.

Semlitsch, R. D., Gibbons, J. W., and Tuberville, T. D. (1995). Timing of reproduction and metamorphosis in the Carolina gopher frog (*Rana capito capito*) in South Carolina. *J. Herpetol.* **29:** 612–614.

Semlitsch, R. D., Scott, D. E., Pechmann, J. H. K., and Gibbons, J. W. (1996). Structure and dynamics of an amphibian community. Evidence from a 16–year study of a natural pond. *In* "Long-Term Studies of Vertebrate Communities" (M. L. Cody and J. A. Smallwood, Eds.), pp. 217–248. Academic Press, San Diego.

Sessions, S. K. (1996). Chromosomes: Molecular cytogenetics. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 121–168. Sinauer Assoc., Inc., Sunderland, MA.

Sever, D. M. (1991a). Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). I. Evolution at the family level. *Herpetologica* **47:** 165–193.

Sever, D. M. (1991b). Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). II. Cryptobranchidae, Hynobiidae, and Sirenidae. *J. Morphol.* **207:** 283–301.

Sever, D. M. (1992). Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). VI. Ambystomatidae and Dicamptodontidae. *J. Morphol.* **212:** 305–322.

Sever, D. M., Rania, L. C., and Krenz, J. D. (1996a). Annual cycle of sperm storage in spermathecae of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Salamandridae). *J. Morphol.* **227:** 155–170.

Sever, D. M., Rania, L. C., and Krenz, J. D. (1996b). Reproduction of the salamander *Siren intermedia* Le Conte with especial reference to oviductal anatomy and mode of fertilization. *J. Morphol.* **227:** 335–348.

Sexton, O. J. (1959). Spatial and temporal movements of a population of the painted turtle *Chrysemys picta marginata* (Agassiz). *Ecol. Monog.* **29:** 113–140.

Sexton, O. J., Ortleb, E. P., Hathaway, L. M., and Ballinger, R. E. (1971). Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. *Ecology* **52:** 201–215.

Sexton, O. J., Phillips, C., and Bramble, J. F. (1990). The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum). Copeia* **1990:** 781–787.

Seymour, R. S., and Bradford, D. F. (1995). Respiration of amphibian eggs. *Physiol. Zool.* **68:** 1–25.

Shaffer, H. B. (1993). Phylogenetics of model organisms: The laboratory axolotl, *Ambystoma mexicanum. Syst. Biol.* **42:** 508–522.

Shaffer, H. B., and McKnight, M. L. (1996). The polytypic species revisited: Genetic differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. *Evolution* **50:** 417–433

Shaffer, H. B., Clark, J. M., and Kraus, F. (1991). When molecules and morphology clash: A phylogenetic analysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). *Syst. Zool.* **40:** 284–303.

Shaffer, H. B., Meylan, P., and McKnight, M. L. (1997). Tests of turtle phylogeny: Molecular, morphological, and paleontological approaches. *Syst. Biol.* **46:** 235–268.

Shaffer, M. L. (1981). Minimum population sizes for species conservation. *BioScience* **31:** 131–134.

Shaldybin, S. L. (1981). Wintering and number of amphibians and reptiles of Lazo State Nature Reserve. *In* "Herpetological Investigations in Siberia and the Far East" (L. J. Borkin, Ed.), pp. 123–124. Acad. Sci. USSR, Zool. Inst., Leningrad.

Shea, G. M. (1993). Family Pygopodidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 234–239. Aust. Govern. Publ. Serv., Canberra.

Shea, G., Shine, R., and Covacevich, J. C. (1993). Family Elapidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 295–309. Aust. Govern. Publ. Serv., Canberra.

Sherbrooke, W. C. (1981). "Horned Lizards. Unique Reptiles of Western North America." Southw. Parks & Monument Assoc., Globe, AZ.

Sherbrooke, W. C. (1990). Rain-harvesting in the lizard, *Phrynosoma cornutum:* Behavior and integumental morphology. *J. Herpetol.* **24:** 302–308.

Sherbrooke, W. C., and Montanucci, R. R. (1988). Stone mimicry in the round-tailed horned lizard, *Phrynosoma modestum* (Sauria: Iguanidae). *J. Arid Environ.* **14:** 275–284.

Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia* **33:** 269–277.

Shine, R. (1979). Sexual selection and sexual dimorphism in the Amphibia. *Copeia* **1979:** 297–306.

Shine, R. (1980a). Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): Evidence for convergence with the Viperidae. *Herpetologica* **36:** 281–289.

Shine, R. (1980b). Reproduction, feeding and growth in the Australian burrowing snake *Vermicella annulata. J. Herpetol.* **14:** 71–77.

Shine, R. (1980c). "Costs" of reproduction in reptiles. *Oecologia* **46:** 92–100.

Shine, R. (1983). Reptilian viviparity in cold climates: Testing the assumptions of an evolutionary hypothesis. *Oecologia* **57:** 397–405.

Shine, R. (1985a). The reproductive biology of Australian reptiles: A search for general patterns. *In* "Biology of the Australian Frogs and Reptiles" (G. Grigg, R. Shine, and H.

Ehmann, Eds.), pp. 297–303. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Shine, R. (1985b). The evolution of viviparity in reptiles: An ecological analysis. *In* "Biology of the Reptilia. Volume 15, Developmental Biology B" (C. Gans and F. Billett, Eds.), pp. 677–680. John Wiley & Sons, Inc., New York.

Shine, R. (1986a). Ecology of a low-energy specialist: Food habits and reproductive biology of the Arafura filesnake (Acrochordidae). *Copeia* **1986:** 424–437.

Shine, R. (1986b). Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* **69:** 260–267.

Shine, R. (1987). The evolution of viviparity: Ecological correlates of reproductive mode within a genus of Australian snakes (*Pseudechis:* Elapidae). *Copeia* **1987:** 551–563.

Shine, R. (1988). Parental care in reptiles. *In* "Biology of the Reptilia. Vol. 16, Ecology B. Defense and Life History" (C. Gans and R. B. Huey, Eds.), pp. 275–329. Alan R. Liss, Inc., New York.

Shine, R. (1991a). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am. Nat.* **138:** 103–122.

Shine, R. (1991b). "Australian Snakes. A Natural History." Cornell Univ. Press, Ithaca, NY.

Shine, R. (1994). Sexual dimorphism in snakes revisited. *Copeia* **1994:** 326–346.

Shine, R., and Bull, J. J. (1979). The evolution of life-bearing in lizards and snakes. *Am. Nat.* **113:** 905–923.

Shine, R., and Fitzgerald, M. (1996). Large snakes in a mosaic rural landscape: The ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. *Biol. Conserv.* **76:** 113–122.

Shine, R., and Harlow, P. S. (1996). Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* **77:** 1808–1817.

Shine, R., and Houston, D. (1993). Family Acrochordidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 322–324. Aust. Govern. Publ. Serv., Canberra.

Shine, R., and Lambeck, R. (1985). A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes: Acrochordidae). *Herpetologica* **41:** 351–361.

Shine, R., and Schwaner, T. (1985). Prey constriction by venomous snakes: A review, and new data on Australian species. *Copeia* **1985:** 1067–1071.

Shine, R., and Schwarzkopf, L. (1992). The evolution of reproductive effort in lizards and snakes. *Evolution* **46:** 62–75.

Shine, R., and Slip, D. J. (1990). Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* **46:** 283–290.

Shine, R., Branch, W. R., Harlow, P. S., and Webb, J. K. (1996a). Sexual dimorphism, reproductive biology, and food habits of two species of African filesnakes (*Mehelya,* Colubridae). *J. Zool., London* **240:** 327–340.

Shine, R., Haagner, G. V., Branch, W. R., Harlow, P. S., and Webb, J. K. (1996b). Natural history of the African shield-nose snake *Aspidelaps scutatus* (Serpentes, Elapidae). *J. Herpetol.* **30:** 361–366.

Shine, R., Harlow, P. S., Branch, W. R., and Webb, J. K. (1996c). Life on the lowest branch: Sexual dimorphism, diet, and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia* **1996:** 290–299.

Shine, R., Harlow, P. S., and Keogh, J. S. (1996d). Commercial harvesting of giant lizards: The biology of water monitors *Varanus salvator* in southern Sumatra. *Biol. Conserv.* **77:** 125–134.

Shine, R., Schwarzkopf, L., and Caley, M. J. (1997). Energy, risk, and reptilian reproductive effort: A reply to Niewiarowski and Dunham. *Evolution* **50:** 2111–2114.

Shoemaker, V. H. (1992). Exchange of water, ions, and respiratory gases in terrestrial amphibians. *In* "Environmental Physiology of the Amphibians" (M. E. Feder and W. W. Burggren, Eds.), pp. 125–150. Univ. Chicago Press, Chicago.

Shoemaker, V. H., and Bickler, P. E. (1979). Kidney and bladder function in a uricotelic treefrog (*Phyllomedusa sauvagei*). *J. Comp. Physiol.* **133:** 211–218.

Shoemaker, V. H., and McClanahan, L. L. (1980). Nitrogen excretion and water balance in amphibians of Borneo. *Copeia* **1980:** 446–451.

Shoemaker, V. H., and McClanahan, L. L. (1982). Enzymatic correlates and uricotelism in tree frogs of the genus *Phyllomedusa*. *J. Exp. Zool.* **220:** 163–169.

Shoemaker, V. H., and Nagy, K. A. (1977). Osmoregulation in amphibians and reptiles. *Ann. Rev. Physiol.* **39:** 449–471.

Shoemaker, V. H., Baker, M. A., and Loveridge, J. P. (1989). Effect of water balance on thermoregulation in waterproof frogs (*Chiromantis* and *Phyllomedusa*). *Physiol. Zool.* **62:** 133–146.

Shoop, C. R. (1960). The breeding habits of the mole salamander, *Ambystoma talpoideum* (Holbrook), in southeastern Louisiana. *Tulane Stud. Zool.* **8:** 65–82.

Shoop, C. R. (1968). Migratory orientation of *Ambystoma maculatum*. Movements near breeding ponds and displacements of migrating individuals. *Biol. Bull.* **135:** 230–238.

Shubin, N. H., and Jenkins, F. A., Jr. (1995). An Early Jurassic jumping frog. *Nature* **377:** 49–52.

Simon, C. A. (1975). The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology* **56:** 993–998.

Simon, M. P. (1983). The ecology of parental care in a terrestrial breeding frog from New Guinea. *Behav. Ecol. Sociobiol.* **14:** 61–67.

Simon, M. P., and Toft, C. A. (1991). Diet specialization in small vertebrates: Mite eating in frogs. *Oikos* **61:** 263–278.

Simpson, G. G. (1961). "Principles of Animal Taxonomy." Columbia Univ. Press, New York.

Sinch, U. (1990). Migration and orientation in anuran amphibians. *Ethol. Ecol. Evol.* **2:** 65–79.

Sites, J. W., Jr., and Crandall, K. A. (1997). Testing species boundaries in biodiversity studies. *Conserv. Biol.* **11:** 1289–1297.

Sites, J. W., Jr., Archie, J. W., Cole, C. J., and Flores Villela, O. (1992). A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): Implications for ecological and evolutionary studies. *Bull. Am. Mus. Nat. Hist.* **213:** 1–110.

Sites, J. W., Jr., Davis S. K., Guerra, T., Iverson, J. B., and Snell, H. L. (1996). Character congruence and phylogenetic signal in molecular and morphological data sets: A case study in the living iguanas (Squamata, Iguanidae). *Mol. Biol. Evol.* **13:** 1087–1105.

Slade, N. A., and Wassersug, R. J. (1975). On the evolution of complex life cycles. *Evolution* **29:** 568–571.

Slowinski, J. B., Knight, A., and Rooney, A. P. (1997). Inferring species trees from gene trees: A phylogenetic analysis of the Elapidae (Serpentes) based on the amino acid sequences of venom proteins. *Mol. Phylog. Evol.* **8:** 349–362.

Smatresk, N. J. (1994). Respiratory control in the transition from water to air breathing in vertebrates. *Am. Zool.* **34:** 264–279.

Smith, C. C., and Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *Am. Nat.* **108:** 499–506.

Smith, H. M., Smith, R. B., and Sawin, H. L. (1977). A summary of snake classification (Reptilia, Serpentes) *J. Herpetol.* **11:** 115–121.

Smith, M. A. (1943). "The Fauna of British India, Ceylon and Burma. Vol. III. Serpentes." Taylor and Francis, London.

Smith, S. M. (1975). Innate recognition of coral snake pattern by a possible avian predator. *Science* **187:** 759–760.

Smith, S. M. (1977). Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* **265:** 535–536.

Snell, H. L., and Tracy C. R. (1985). Behavioral and morphological adaptations by Galapagos land iguanas (*Conolophus subcristatus*) to water and energy requirements of eggs and neonates. *Am. Zool.* **25:** 1009–1018.

Sokal, R. R. (1986). Phenetic taxonomy: Theory and methods. *Ann. Rev. Evol. Syst.* **17:** 423–442.

Somma, L. A., and Fawcett, J. D. (1989). Brooding behaviour of the prairie skink, *Eumeces septentrionalis,* and its relationship to the hydric environment of the nest. *Zool. J. Linn. Soc.* **95:** 245–256.

Spellerberg, I. F. (1988). Ecology and management of *Lacerta agilis* L. populations in England. *Mertensiella* **1:** 113–121.

Spinar, Z. V. (1972). "Tertiary Frogs from Central Europe." W. Junk N. V., The Hague.

Spotila, J. R., O'Connor, M. P., and G. S. Bakken. (1992). Biophysics of heat and mass transfer. *In* "Environmental Physiology of the Amphibians" (M. E. Feder and W. W. Burggren, Eds.), pp. 59–80. Univ. Chicago Press, Chicago, IL.

Spotila, J. R., O'Connor, M. P., and Paladino, F. V. (1997). Thermal biology. *In* "The Biology of Sea Turtles" (P. L. Lutz and J. A. Musick, Eds.), pp. 297–314. CRC Press, Boca Raton, FL.

Spotila, J. R., Dunham, A. E., Leslie, A. J., Steyermark, A. C., Plotkin, P. T., and Paladino, F. V. (1998). Worldwide population decline of *Dermochelys coriacea:* Are leatherback seaturtles going extinct? *Chelonian Conserv. Biol.* **2:** 209–222.

Sprawl, S., and Branch, B. (1995). "The Dangerous Snakes of Africa." Ralph Curtis Books, Sanibel, FL.

Spray, D. C. (1976). Pain and temperature receptors of anurans. *In* "Frog Neurobiology. A Handbook" (R. Llinás and W. Precht, Eds.) pp. 607–628. Springer-Verlag, Berlin.

Stamps, J. A. (1977). Social behavior and spacing patterns in lizards. *In* "Biology of the Reptilia. Volume 7. Ecology and Behavior" (C. Gans and D. W. Tinkle, Eds.), pp. 265–334. Academic Press, New York.

Stamps, J. A. (1978). A field study on the ontogeny of social behavior in the lizard *Anolis aeneus. Behaviour* **64:** 1–31.

Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territoriality. *In* "Lizard Ecology. Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 169–204. Harvard Univ. Press, Cambridge.

Stamps, J., and Krishnan, V. V. (1997). Sexual bimaturation and sexual size dimorphism in animals with asymptotic growth after maturity. *Evol. Ecol.* **11:** 21–39.

Stamps, J. A., Krishnan, V. V., and Andrews, R. M. (1994). Analyses of sexual size dimorphism using null growth-based models. *Copeia* **1994:** 598–613.

Stamps, J. A., Mangel, M., and Phillips, J. A. (1998). A new look at relationships between size at maturity and asymptotic size. *Am. Nat.* **152:** 470–479.

Starace, F. (1998). "Guide des serpents et amphisbènes de Guyana française." Ibis Rouge Editions, Guadeloupe.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Quart. Rev. Biol.* **51:** 3–47.

Stearns, S. C. (1977). The evolution of life history traits: A critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8:** 145–171.

Stebbins, R. C. (1954). "Amphibians and Reptiles of Western North America." McGraw-Hill Book Co., Inc., New York.

Stebbins, R. C., and Cohen, N. W. (1995). "A Natural History of Amphibians." Princeton Univ. Press, Princeton.

Steel, R. (1973). "Crocodylia. Handbuch der Paläoherpetologie, 16." Gustav Fischer Verlag, Stuttgart.

Steubing, R. (1994). A new species of *Cylindrophis* (Serpentes: Cylindrophiidae) from Sarawak, western Borneo. *Raffles Bull. Zool.* **42:** 967–973.

Stewart, J. R. (1989). Facultative placentotrophy and the evolution of squamate placentation: Quality of eggs and neonates in *Virginia striatula. Am. Nat.* **133:** 111–137.

Stewart, J. R., and Thompson, M. B. (1996). Evolution of reptilian placentation: Development of extraembryonic membranes of the Australian scincid lizards, *Bassiana duperreyi* (oviparous) and *Pseudemoia entrecasteauxii* (viviparous). *J. Morphol.* **227:** 349–370.

Stewart, M. M. (1967). "Amphibians of Malawi." State Univ. New York Press, Albany.

Stewart, M. M., and Pough, F. H. (1983). Population density of tropical forest frogs: Relation to retreat sites. *Science* **221:** 570–571.

Steyn, W. (1963). *Angolocaurus* [sic] *skoogi* (Andersson)—A new record from south west Africa. *Cimbebasia* **6:** 8–11.

Stickel, L. F. (1950). Populations and home range relationships of the box turtle *Terrapene c. carolina* (Linnaeus). *Ecol. Monog.* **20:** 351–378.

Stickel, L. F. (1989). Home range behavior among box turtles (*Terrapene c. carolina*) of a bottomland forest in Maryland. *J. Herpetol.* **23:** 40–44.

Storrs, G. W. (1993). Function and phylogeny in sauropterygian (Diapsida) evolution. *Am. J. Sci.* **293–A:** 63–90.

Sues, H.-D., Clark, J. M., and Jenkins, F. A., Jr. (1994). A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest. *In* "In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods" (N. C. Fraser and H.-D. Sues, Eds.), pp. 284–294. Cambridge Univ. Press, New York.

Sullivan , B. K. (1989). Desert environments and the structure of anuran mating systems. *J. Arid Environ.* **17:** 175–183.

Sullivan, B. K., Ryan, M. J., and Verrell, P. A. (1995). Female choice and mating system structure. *In* "Amphibian Biology. Volume 2, Social Behaviour" (H. Heatwole and B. K. Sullivan, Eds.), pp. 468–517. Surrey Beatty & Sons, Chipping Norton, N.S.W.

Sullivan, R. M., and Estes, R. (1997). A reassessment of the fossil Tupinambinae. *In* "Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia" (R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn, Eds.), pp. 100–112. Smithsonian Inst. Press, Washington, DC.

Sullivan, R. M., and Holman, J. A. (1996). Squamata. *In* "The Terrestrial Eocene-Oligocene Transition in North America" (D. R. Prothero and R. J. Emry, Eds.), pp. 354–372. Cambridge Univ. Press, New York.

Sumida, S. S. (1997). Locomotor features of taxa spanning the origin of amniotes. *In* "Amniote Origins. Completing the Transition to Land" (S. S. Sumida and K. L. M. Martin, Eds.), pp. 353–398. Academic Press, San Diego.

Summers, A. P., and O'Reilly, J. C. (1997). A comparative study of locomotion in the caecilians *Dermophis mexicanus* and *Typhlonectes natans* (Amphibia: Gymnophiona). *Zool. J. Linn. Soc.* **121:** 65–76.

Summers, K., and Amos, W. (1997). Behavioral, ecological, and molecular genetic analyses of reproductive strategies in the Amazonian dart-poison frog, *Dendrobates ventrimaculatus. Behav. Ecol.* **8:** 260–267.

Swingland, I. R. (1977). Reproductive effort and life history strategy of the Aldabran giant tortoise. *Nature* **269:** 402–404.

Swingland, I. R., and Klemens, M. W., Eds. (1989). The conservation biology of tortoises. *Occas. Pap. IUCN Species Surv. Commis.* **1:** 1–202.

Swofford, D. L., Olsen, G. J., Waddell, P. J., and Hillis, D. M. (1996). Phylogenetic inference. *In* "Molecular Systematics, Second Edition" (D. M. Hillis, C. Moritz, and B. K. Mable, Eds.), pp. 321–381. Sinauer Assoc., Inc., Sunderland, MA.

Sylber, C. K. (1988). Feeding habits of the lizards *Sauromalus varius* and *S. hispidus* in the Gulf of California. *J. Herpetol.* **22**: 413–424.

Szczerbak, N. N., and Golubev, M. L. (1997). "Gecko Fauna of the USSR and Contiguous Regions." Soc. Study Amphibians and Reptiles, Ithaca, NY.

Taigen, T. L., Pough, F. H., and Stewart, M. M. (1984). Water balance of terrestrial anuran (*Eleutherodactylus coqui*) eggs: Importance of parental care. *Ecology* **65:** 248–255.

Taigen, T. L., Wells, K. D., and Marsh, R. L. (1985). The enzymatic basis of high metabolic rates in calling frogs. *Physiol. Zool.* **58:** 719–726.

Tanaka, K. (1989). Mating strategy of male *Hynobius nebulosus. In* "Current Herpetology in East Asia" (M. Matsui et al., Eds.), pp. 437–448. Herpetol. Soc. Japan, Kyoto.

Tarsitano, S., and Hecht, M. K. (1980). A reconsideration of the reptilian relationships of *Archeopteryx. Zool. J. Linn. Soc.* **69:** 149–182.

Tarsitano, S., and Riess, J. (1982). Plesiosaur locomotion-Underwater flight versus rowing. *N. Jb. Geol. Paläont. Abh.* **164:** 188–192.

Tarsitano, S. F., Frey, E., and Riess, J. (1989). The evolution of the Crocodilia: A conflict between morphological and biochemical data. *Am. Zool.* **29:** 843–856.

Taylor, D. H., and Adler, K. (1973). Spatial orientation by salamanders using plane polarized light. *Science* **181:** 285–287.

Taylor, E. H. (1968). "The Caecilians of the World. A Taxonomic Review." Univ. Kansas Press, Lawrence, KS.

Tchernov, E. (1986). "Évolution des Crocodiles en Afrique du Nord et de l'Est." Édit. Centre Natl. Rech. Sci., Paris.

Teather, K. L. (1991). The relative importance of visual and chemical cues for foraging on newborn blue-striped garter snakes (*Thamnophis sirtalis similis*). *Behaviour* **117:** 255–261.

Temple, S. A. (1991). Conservation biology: new goals and new patterns for managers of biological resources. *In* "Challenges in the Conservation of Biological Resources: A Practitioner's Guide" (D. J. Decker et al., Eds.), pp. 45–54. Westview Press, Boulder, CO.

Templeton A. L. (1986). Coadaptation and outbreeding depression. *In* "Conservation Biology: The Science of Scarcity and Diversity" (M. E. Soulé, Ed.), pp. 105–116.

Thomas, R. (1965). A congregation of the blind snake, *Typhlops richardi. Herpetologica* **21:** 309.

Thomson, K. S. (1980). The ecology of Devonian lobe-finned fishes. *In* "The Terrestrial Environment and the Origin of Land Vertebrates" (A. L. Panchen, Ed.), pp. 187–122. Academic Press, London.

Thomson, K. S. (1993). The origin of the tetrapods. *Am. J. Sci.* **293–A:** 33–62.

Thorbjarnarson, J. B. (1990). Notes on the feeding behavior of the gharial (*Gavialis gangeticus*) under semi-natural conditions. *J. Herpetol.* **24:** 99–100

Thorbjarnarson, J. (1992). "Crocodiles: An Action Plan for Their Conservation." IUCN, Gland.

Thorbjarnarson, J. (1996). Reproductive characteristics of the order Crocodylia. *Herpetologica* **52:** 8–24.

Thorbjarnarson, J. (1999). Crocodile tears and skins: International trade, economic constraints, and limits to the sustainable use of crocodilians. *Conserv. Biol.* **13:** 465–470.

Thorpe, R. S. (1976) Biometric analysis of geographic variation and racial affinities. *Biol. Rev.* **51:** 407–452.

Thorpe, R. S. (1987). Geographic variation: A synthesis of cause, data, pattern and congruence in analysis and phylogenesis. *Boll. Zool.* **54:** 3–11.

Thorpe, R. S., Wüster, W., and Malhotra, A., Eds. (1997). "Venomous Snakes. Ecology, Evolution and Snakebite." Zool. Soc. London, London.

Thurow, G. R. (1994). Experimental return of wood frogs to west-central Illinois. *Trans. Illinois State Acad. Sci.* **87:** 83–97.

Thurow, G. R. (1997). Ecological lessons from two-lined salamander translocations. *Trans. Illinois State Acad. Sci.* **90:** 79–88.

Tiebout, H. M., and Cary, J. R. (1987). Dynamic spatial ecology of the water snake, *Nerodia sipedon*. *Copeia* **1987:** 1–18.

Tiedemann, F., Coord. (1990). "Lurche und Kriechtiere Wiens." J & V Editions, Vienna.

Tihen, J. A. (1965). Evolutionary trends in frogs. *Am. Zool.* **5:** 309–318.

Tilley, S. G. (1980). Life histories and comparative demography of two salamander populations. *Copeia* **1980:** 806–812.

Tilley, S. G., and Bernardo, J. (1993). Life history evolution in plethodontid salamanders. *Herpetologica* **49:** 154–163.

Tilley, S. G., Lundrigan, B. L., and Brower, L. P. (1982) Erythrism and mimicry in the salamander *Plethodon cinereus*. *Herpetologica* **38:** 409–417.

Tinkle, D. W. (1967). The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publ. Mus. Zool. Univ. Michigan* **132:** 1–182.

Tinkle, D. W., and Gibbons, J. W. (1977). The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool. Univ. Michigan* **154:** 1–55.

Tinkle, D. W., and Hadley, N. F. (1973). Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. *Copeia* **1973:** 272–277.

Tinkle, D. W., and Hadley, N. F. (1975). Lizard reproductive effort: Caloric estimates and comments on its evolution. *Ecology* **56:** 427–434.

Tinkle, D. W., Wilbur, H. M., and Tilley, S. G. (1970). Evolutionary strategies in lizard reproduction. *Evolution* **24:** 55–74.

Tinkle, D. W., Congdon, J. D., and Rosen, P. C. (1981). Nesting frequency and success: Implications for the demography of painted turtles. *Ecology* **62:** 1426–1432.

Tinsley, R. C. (1990). The influence of parasite infection on mating success in spadefoot toad, *Scaphiopus couchii*. *Am. Zool.* **30:** 313–324.

Tinsley, R. C., and Kobel, H. R., Eds. (1996). "The Biology of *Xenopus*." Zool. Soc. London, London.

Tinsley, R. C., Loumont, C., and Kobel, H. R. (1996). Geographic distribution and ecology. *In* "The Biology of *Xenopus*" (R. C. Tinsley and H. R. Kobel, Eds.), pp. 34–59. Zool. Soc. London, London.

Titus, T. A., and Frost, D. R. (1996). Molecular homology assessment and phylogeny in the lizard family Opluridae (Squamata: Iguania). *Mol. Phylog. Evol.* **6:** 49–62.

Titus, T. A., and Larson, A. (1995). A molecular phylogenetics perspective on the evolutionary radiation of the salamander family Salamandridae. *Syst. Biol.* **44:** 125–151.

Titus, T. A., and Larson, A. (1997). Molecular phylogenetics of desmognathine salamanders (Caudata: Plethodontidae): A reevaluation of evolution in ecology, life history, and morphology. *Syst. Biol.* [1996] **45:** 451–472.

Toft, C. A. (1980). Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* **45:** 131–134.

Toft, C. A. (1985). Resource partitioning in amphibians and reptiles. *Copeia* **1985:** 1–21.

Toft, C. A. (1995). Evolution of diet specialization in poison-dart frogs (Dendrobatidae). *Herpetologica* **51:** 202–216.

Tokar, A. A. (1989). A revision of the genus *Eryx* (Serpentes, Boidae), based upon osteological data. *Vestnik Zool.* **1989:** 46–55.

Tokar, A. A. (1996). Taxonomic revision of the genus *Gongylophis* Wagler 1830: *G. colubrinus* (L. 1758) (Serpentes Boidae). *Trop. Biol.* **9:** 1 17.

Tokarz, R. R. (1992). Male mating preferences for unfamiliar females in the lizard *Anolis sagrei*. *Anim. Behav.* **44:** 843–849.

Tokarz, R. R. (1995). Mate choice in lizards: A review. *Herpetol. Monog.* **9:** 17–40.

Tolson, P. J., and Henderson, R. W. (1993) "The Natural History of West Indian Boas." R&A Publishing, Ltd., Taunton, UK.

Tome, M. A., and Pough, F. H. (1982). Responses of amphibians to acid precipitation. *In* "Acid Rain/Fisheries. Proceedings of an International Symposium on Acidic Precipitation and Fishery Impacts in Northeastern North America" (R. E. Johnson, Ed.), pp. 245–254. American Fisheries Society, Bethesda, MD.

Tong, H., Gaffney, E. S., and Buffetaut, E. (1998). *Foxemys,* a new side-neck turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *Am. Mus. Novitates* **3251:** 1–19.

Townsend, D. S., and Stewart, M. M. (1985). Direct development in *Eleutherodactylus coqui* (Anura: Leptodactylidae): A staging table. *Copeia* **1985:** 423–436.

Townsend, D. S., Stewart, M. M., Pough, F. H., and Brussard, P. F. (1981). Internal fertilization in an oviparous frog. *Science* **212:** 469–471.

Tracy, C. R. (1971). Evidence for the use of celestial cues by dispersing immature California toads (*Bufo boreas*). *Copeia* **1971:** 145–147.

Tracy, C. R. (1999). Differences in body size among chuckwalla (*Sauromalus obesus*) populations. *Ecology* **80:** 259–271.

Tracy, C. R., and Dole, J. W. (1969). Orientation of displaced California toads, *Bufo boreas,* to their breeding sites. *Copeia* **1969:** 693–700.

Trauth, S. E., Cooper, J., Vitt, L. J., and Perrill, S. A. (1987). Cloacal anatomy of the broad-headed skink, *Eumeces lati-*

ceps, with a description of a female pheromonal gland. *Herpetologica* **43:** 458–466.

Trivers, R. L. (1972). Parental investment and sexual selection. *In* "Sexual Selection and the Descent of Man" (B. Campbell, Ed.), pp. 136–179. Aldine, Chicago.

Trivers, R. L. (1976). Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution* **30:** 253–269.

Troyer, K. (1984a). Structure and function of the digestive tract of an herbivorous lizard *Iguana iguana*. *Physiol. Zool.* **57:** 1–8.

Troyer, K. (1984b). Behavioral acquisition of the hindgut fermentation system by hatchling *Iguana iguana*. *Behav. Ecol. Sociobiol.* **14:** 189–193.

Troyer, K. (1991). Role of microbial cellulose degradation in reptile nutrition. *In* "Biosynthesis and Biodegradation of Cellulose" (C. H. Haigler and P. J. Weimer, Eds.), pp. 311–325. Marcel Dekker, Inc., New York.

Trueb, L. (1973). Bones, frogs, and evolution. *In* "Evolutionary Biology of the Anurans" (J. L. Vial, Ed.), pp. 65–132. Univ. Missouri Press, Columbia, MO.

Trueb, L., and Cannatella, D. C. (1986). Systematics, morphology, and phylogeny of genus *Pipa* (Anura: Pipidae). *Herpetologica* **42:** 412–449.

Trueb, L., and Cloutier, R. (1991a). Toward an understanding of the amphibians: Two centuries of systematic history. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 176–193. Comstock Publ. Assoc., Ithaca, NY.

Trueb, L., and Cloutier, R. (1991b). A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondylii). *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 223–313. Comstock Publ. Assoc., Ithaca, NY.

Tu, M.-C., Chu, C.-W., and Lue, K.-Y. (1999). Specific gravity and mechanisms for its control in tadpoles of three anuran species from different water strata. *Zool. Studies* **38:** 76–81.

Tuberville, T. D., Gibbons, J. W., and Greene, J. L. (1996). Invasion of new aquatic habitats by male freshwater turtles. *Copeia* **1996:** 713–715.

Turner, F. B. (1977). The dynamics of populations of squamates, crocodilians and rhynchocephalians. *In* "Biology of the Reptilia. Volume 7" (C. Gans and D. W. Tinkle, (Eds.), pp. 157–264. Academic Press, New York.

Turner, F. B., Medica, P. A., Lannom, J. R., Jr., and Hoddenbach, G. A. (1969). A demographic analysis of fenced populations of the whiptailed lizard, *Cnemidophorus tigris,* in southern Nevada. *Southw. Nat.* **14:** 189–202.

Tuttle, M. D., and Ryan, M. J. (1981). Bat predation and the evolution of frog vocalization in the neotropics. *Science* **214:** 677–678.

Twitty, V. C. (1966). "Of Scientists and Salamanders." W. H. Freeman & Co., San Francisco.

Tyler, M. J. (1985). Reproductive modes in Australian Amphibia. *In* "Biology of Australasian Frogs and Reptiles" (G. Grigg, R. Shine, and H. Ehmann, Eds.), pp. 265–267. Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Tyler, M. J. (1989). "Australian Frogs." Viking O'Neil, Ringwood, Australia.

Tyler, M. J. (1991a). *Kyarranus* Moore (Anura, Leptodactylidae) from the Tertiary of Queensland. *Proc. Roy. Soc. Victoria* **103:** 47–51.

Tyler, M. J. (1991b). Hylid frogs from the mid-Miocene Camfield Beds of northern Australia. *Beagle* **11:** 141–144.

Tyler, M. J. (1991c). Declining amphibian populations—A global phenomenon? An Australian perspective. *Alytes* **9:** 43–50.

Tyler, M. J., and Davies, M. (1978). Phylogenetic relationships of Australian hyline and neotropical phyllomedusine frogs of the family Hylidae. *Herpetologica* **34:** 219–224.

Tyler, M. J., and Davies, M. (1993). The Hylidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 58–63. Aust. Govern. Publ. Serv., Canberra.

Tyler, M. J., and Duellman, W. E. (1995). Superficial mandibular musculature and vocal sac structure in hemiphractine hylid frogs. *J. Morphol.* **224:** 65–71.

Uetz, P. (1999). The EMBL reptile database: www.embl-heidelberg.de/ uetz/LivingReptiles.html.

Ultsch, G. R., Bradford, D. F., and Freda, J. (1999). Physiology: Coping with the environment. *In* "Tadpoles: The Biology of Anuran Larvae" (R. W. McDiarmid and R. Altig, Eds.), pp. 189–214. Univ. of Chicago Press, Chicago.

Underwood, G. (1967). "A Contribution to the Classification of Snakes." British Mus. (Nat. Hist.), London.

Underwood, G. (1970). The eye. *In* "Biology of the Reptilia. Volume 2. Morphology B" (C. Gans and T. S. Parsons, Eds.), pp. 1–97. Academic Press, London.

Underwood, G., and Kochva, E. (1993). On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zool. J. Linn. Soc.* **107:** 3–64.

Underwood, G., and Stimson, A. F. (1990). A classification of pythons (Serpentes, Pythoninae). *J. Zool., London* **221:** 565–603.

Van Berkum, F. H., Huey, R. B., and Adams, B. A. (1986). Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* **59:** 464–472.

Van Beurden, E. K. (1984). Survival strategies of the Australian water-holding frog, *Cyclorana platycephalus. In* "Arid Australia" (H. G. Cogger and E. E. Cameron, Eds.), pp. 223–234. Australian Museum, Sydney.

Van Damme, R., Bauwens, D., Castilla, A. M., and Verheyen, R. F. (1989). Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia* **80:** 516–524.

Van Damme, R., Bauwens, D. Brana, F., and Verheyen, R. F. (1992). Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis. Herpetologica* **48:** 220–228.

Van den Elzen, P. (1975). Contribution a'connaissance de *Pelodytes punctatus* étudié en Camarque. *Bull. Soc. Zool. France* **100:** 691– 692.

Van Devender, R. W. (1982). Comparative demography of the lizard *Basiliscus basiliscus. Herpetologica* **38:** 189–208.

Van Dyke, J. H. (1997). Family Gerrhosauridae. *In* "Proceedings of the Fitzsimons Commemorative Symposium" (J. H. van Dyke, Ed.), pp. 44–51. Herpetol. Assoc. Africa, Matieland, South Africa.

Van Loben Sels, R. C., Congdon, J. D., and Austin, J. T. (1997). Life history and ecology of the Sonoran mud turtle (*Kinosternon sonoriense*) in southeastern Arizona: A preliminary report. *Chelonian Conserv. Biol.* **2:** 338–344.

Van Mieriop, L. H. S., and Barnard, S. M. (1978). Further observations on thermoregulation in the brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* **1978:** 615–621.

Vanzolini, P. E., Ramos-Costa, A. M. M., and Vitt, L. J. (1980). "Repteis das caatingas." Acad. Bras. Ciênc., Rio de Janeiro.

Vasudevan, K. (1996/1997). Reproductive ecology of *Aspideretes gangeticus* (Cuvier) in north India. *Int. Cong. Chelonian Conserv. 1995,* pp. 21–28.

Vaughn, L. K., Bernheim, H. A., and Kluger, M. J. (1974). Fever in the lizard *Dipsosaurus dorsalis. Nature* **252:** 473–474.

Vaz-Ferreira, R., and Gehrau, A. (1975). Epimeletic behavior of the South American common frog *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae). I. Brood care and related feeding and aggressive activities. *Physis Secc. B., Buenos Aires* **34:** 1–14.

Vaz-Ferreira, R., Covelo de Zolessi, L., and Achaval, F. (1970). Oviposicion y desarollo de ofidios y lacertilios en hormigueros de *Acromyrmex. Physis* **79:** 431–459.

Vences, M., Glaw, F., and Böhme, W. (1997/1998). Evolutionary correlates of microphagy in alkaloid-containing frogs (Amphibia: Anura). *Zool. Anz.* **236:** 217–230.

Verrell, P. A. (1982). The sexual behaviour of the red-spotted newt, *Notopthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Anim. Behav.* **30:** 1224–1236.

Verrell, P. A. (1983). The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia, Urodela: Salamandridae). *Behav. Ecol. Sociobiol.* **13:** 307–313.

Verrell, P. A. (1989). The sexual strategies of natural populations of newts and salamanders. *Herpetologica* **45:** 265–282.

Verrell, P. A., and Halliday, T. (1985). Reproductive dynamics of a population of smooth newts, *Triturus vulgaris*, in southern England. *Herpetologia* **41:** 386–395.

Vertucci, F. A., and Corn, P. S. (1996). Evaluation of episodic acidification and amphibian declines in the Rocky Mountains. *Ecol. Appl.* **6:** 449–457.

Vial, J. L. (1968). The ecology of the tropical salamander, *Bolitoglossa subpalmata,* in Costa Rica. *Rev. Biol. Trop.* **15:** 13–115.

Vial, J. L., Ed. (1973). "Evolutionary Biology of the Anurans." Univ. Missouri Press, Columbia.

Vial, J. L., Berger, T. J., and McWilliams, W. T. (1977). Quantitative demography of copperheads, *Agkistrodon controtrix. Res. Popul. Ecol.* **18:** 223–234.

Vidal, N., Lecointre, G., Vié, J. C., and Gasc, J. P. (1997). Molecular systematics of pitvipers: paraphyly of the *Bothrops* complex. *C. R. Acad. Paris, Sci. Vie, Ser. III* **320:** 95–101.

Viertel, B., and Richter, S. (1999) Anatomy: Viscera and endocrines. *In* "Tadpoles: The Biology of Anuran Larvae" (R. W. McDiarmid and R. Altig, Eds.), pp. 189–214. Univ. Chicago Press, Chicago.

Viets, B. E., Ewert, M. A., Talent, L. G., and Nelson, C. E. (1994). Sex-determining mechanisms in squamate reptiles. *J. Exp. Zool.* **270:** 45–56.

Villa, J. (1984). Biology of a neotropical glass frog, *Centrolenella fleischmanni* (Boettger), with special reference to its frogfly associates. *Milwaukee Publ. Mus. Contrib. Biol. Geol.* **55:** 1–60.

Villa, J. D., and Wilson, L. D. (1990). *Ungaliophis, U. continentalis, U. panamensis. Catalog. Am. Amphib. Rept.* **480:** 1–4.

Villiers, A. (1975). "Les Serpents de l'Ouest Africain," 3rd ed. Les Nouvelles Éditions Africaines, Dakar.

Vinegar, A., Hutchison, V., and Dowling, H. (1970). Metabolism, energetics, and thermoregulation during brooding of snakes of the genus *Python* (Reptilia. Boidae). *Zoologica* **55:** 19–48.

Vitt, L. J. (1981). Lizard reproduction: Habitat specificity and constraints on relative clutch mass. *Am. Nat.* **117:** 506–514.

Vitt, L. J. (1983). Ecology of an anuran-eating guild of terrestrial tropical snakes. *Herpetologica* **39:** 52–66.

Vitt, L. J. (1986). Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* **1986:** 773–786.

Vitt, L. J. (1991). Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. *Can. J. Zool.* **69:** 504–511.

Vitt, L. J. (1992a). Diversity of reproduction strategies among Brazilian lizards and snakes: The significance of lineage and adaptation. *In* "Reproductive Biology of South American Vertebrates" (W. C. Hamlett, Ed.), pp. 135–149. Springer-Verlag, New York.

Vitt, L. J. (1992b). Mimicry of millipedes and centipedes by elongate terrestrial vertebrates. *Nat. Geog. Res. Expl.* **8:** 76–95.

Vitt, L. J. (1993). Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. *Can. J. Zool.* **71:** 2370–2390.

Vitt, L. J., and Avila-Pires, T. C. S. (1998). Ecology of two sympatric species of *Neusticurus* (Sauria: Gymnophthalmidae) in the western Amazon of Brazil. *Copeia* **1998:** 570–582.

Vitt, L. J., and Breitenbach, G. L. (1993). Life histories and reproductive tactics among lizards in the genus *Cnemidophorus* (Sauria: Teiidae). *In* "Biology of the Whiptail Lizard (Genus *Cnemidophorus*)" (J. W. Wright and L. J. Vitt, Eds.), pp. 211–243. Oklahoma Mus. Nat. Hist., Norman, OK.

Vitt, L. J., and Colli, G. R. (1994). Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Can. J. Zool.* **72:** 1986–2008.

Vitt, L. J., and Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards. Resolution of a paradox. *Am. Nat.* **112:** 595–608.

Vitt, L. J., and Cooper, W. E., Jr. (1985). The evolution of sexual dimorphism in the skink *Eumeces laticeps*:: An example of sexual selection. *Can. J. Zool.* **63:** 995–1002.

Vitt, L. J., and Cooper, W. E., Jr. (1986a). Foraging and diet of a diurnal predator (*Eumeces laticeps*) feeding on hidden prey. *J. Herpetol.* **20:** 408–415.

Vitt, L. J., and Cooper, W. E., Jr. (1986b). Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): Age-specific differences in costs and benefits. *Can. J. Zool.* **64:** 583–592.

Vitt, L. J., and Cooper, W. E., Jr. (1988). Feeding responses of broad-headed skinks (*Eumeces laticeps*) to velvet ants (*Dasymutilla occidentalis*). *J. Herpetol.* **22:** 485–488.

Vitt, L. J., and Goldberg, S. R. (1983). Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia* **1983:** 131–141.

Vitt, L. J., and Lacher, T. E., Jr. (1981). Behavior, habitat, diet, and reproduction of the iguanid lizard *Polychrus acutirostris* in the caatinga of northeastern Brazil. *Herpetologica* **37:** 53–63.

Vitt, L. J., and Price, H. J. (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* **38:** 237–255.

Vitt, L. J., and Zani, P. A. (1996a). Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Can. J. Zool.* **74:** 1313–1335.

Vitt, L. J., and Zani, P. A. (1996b). Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *J. Trop. Ecol.* **12:** 81–101.

Vitt, L. J., and Zani, P. A. (1996c). Ecology of the lizard *Ameiva festiva* (Teiidae) in southeastern Nicaragua. *J. Herpetol.* **30:** 110–117.

Vitt, L. J., and Zani, P. A. (1996d). Ecology of the elusive tropical lizard *Tropidurus* [=*Uracentron*] *flaviceps* (Tropiduridae) in lowland rain forest of Ecuador. *Herpetologica* **52:** 121–132.

Vitt, L. J., and Zani, P. A. (1997). Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon region. *Herpetologica* **53:** 165–179.

Vitt, L. J., Congdon, J. D., and Dickson, N. A. (1977). Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* **58:** 326–337.

Vitt, L. J., Zani, P. A., Caldwell, J. P., and Carrillo, E. O. (1995a). Ecology of the lizard *Kentropyx pelviceps* (Sauria: Teiidae) in lowland forest of Ecuador. *Can. J. Zool.* **73:** 691–703.

Vitt, L. J., Zani, P. A., and Durtsche, R. D. (1995b). Ecology of the lizard *Norops oxylophus* (Polychrotidae) in lowland forest of southeastern Nicaragua. *Can. J. Zool.* **73:** 1918–1927.

Vitt, L. J., Avila-Pires, T. C. S., and Zani, P. A. (1996a). Observations on the ecology of the rare Amazaonian lizard, *Enyalius leechii* (Polychrotidae). *Herpetol. Nat. Hist.* **4:** 77–82.

Vitt, L. J., Zani, P. A., and Caldwell, J. P. (1996b). Behavioural ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *J. Trop. Ecol.* **12:** 81–101.

Vitt, L. J., Zani, P. A., and Avila-Pires, T. C. S. (1997a). Ecology of the arboreal lizard *Tropidurus* (=*Plica*) *umbra* in the Amazonian region. *Can. J. Zool.* **75:** 1876–1882.

Vitt, L. J., Zani, P. A., and Barros, A. A. M. (1997b). Ecological variation among populations of the gekkonid lizard *Gonatodes humeralis* in the Amazon Basin. *Copeia* **1997:** 32–43.

Vitt, L. J., Avila-Pires, T. C. S., Caldwell, J. P., and Oliveira, V. R. L. (1998a). The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. *Conserv. Biol.* **12:** 654–664.

Vitt, L. J., Sartorius, S. S., Avila-Pires, T. C. S., and Espósito, M. C. (1998b). Use of time, space, and food by the gymnophthalmid lizard *Prionodactylus eigenmanni* from the western Amazon of Brazil. *Can. J. Zool.* **76:** 1681–1688.

Vitt, L. J., Zani, P. A., and Esposito, M. C. (1999). Historical ecology of Amazonian lizards: Implications for community ecology. *Oikos* **87:** 286–294.

Vogt, R. C., and Guzman, S. (1988). Food partitioning in a Neotropical freshwater turtle community. *Copeia* **1988:** 37–47.

Vogt, R. C., and Villela, O. F. (1992). Effects of incubation temperature on sex determination in a community of Neotropical freshwater turtles in southern Mexico. *Herpetologica* **48:** 265–270.

Volsøe, H. (1944). Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spoila Zool. Mus. Huan.* **5:** 1–157.

Voris, H. K. (1985). Population size estimates for a marine snake (*Enhydrina schistosa*) in Malaysia. *Copeia* **1985:** 955–961.

Voris, H. K., and Karns, D. R. (1996). Habitat utilization, movements, and activity patterns of *Enhydris plumbea* (Serpentes: Homalopsinae) in a rice paddy wetland in Borneo. *Herpetol. Nat. Hist.* **4:** 111–126.

Voris, H. K., and Voris, H. H. (1983). Feeding strategies in marine snakes: An analysis of evolutionary, morphological, behavioral and ecological relationships. *Am. Zool.* **23:** 411–425.

Voris, H. K., and Voris, H. H. (1995). Commuting on the tropical tides: The life of the yellow-lipped sea krait. *Ocean Realm* April: 57–61.

Vorobyeva, E. I., Ed. (1994). "The Siberian Newt (*Salamandrella keyserlingii* Dybowski, 1870). Zoogeography, Systematics, Morphology." Nauka, Moscow. [In Russian]

Vorobyeva, E. I., Ed. (1995). "The Siberian Newt (*Salamandrella keyserlingii* Dybowski, 1870). Ecology, Behavior, Conservation." Nauka, Moscow. [In Russian]

Vorobyeva, E., and Schultze, H.-P. (1991). Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 68–109. Comstock Publ. Assoc., Ithaca, NY.

Vrijenhoek, R. C., Dawley, R. M., Cole, C. J., and Bogart, J. P. (1989). A list of the known unisexual vertebrates. *In* "Evolution and Ecology of Unisexual Vertebrates" (R. M. Dawley and J. P. Bogart, Eds.), pp. 19–23. New York State Museum, Albany, NY.

Wager, V. A. (1986). "Frogs of South Africa. Their Fascinating Life Stories," 2nd ed. Delta Books, Craighall, South Africa.

Wainwright, P. C., and Bennett, A. F. (1992a). The mechanism of tongue projection in chameleons. II. Electromyographic tests of functional hypotheses. *J. Exp. Biol.* **168:** 1–21.

Wainwright, P. C., and Bennett, A. F. (1992b). The mechanism of tongue projection in chameleons. II. Role of shape change in muscular hydrostat. *J. Exp. Biol.* **168:** 23–40.

Wainwright, P. C., Kraklau, D. M., and Bennett, A. F. (1991). Kinematics of tongue projection in *Chamaeleo oustaleti. J. Exp. Biol.* **159:** 109–133.

Wake, D. B., and Dresner, I. G. (1967). Functional morphology and evolution of tail autotomy in salamanders. *J. Morphol.* **122:** 265–306.

Wake, D. B., and Hanken, J. (1996). Direct development in the lungless salamanders: What are the consequences for developmental biology, evolution and phylogenesis? *Int. J. Develop. Biol.* **40:** 859–869.

Wake, D. B., and Özeti, N. (1969). Evolutionary relationships in the family Salamandridae. *Copeia* **1969:** 124–137.

Wake, M. H. (1977). The reproductive biology of caecilians: An evolutionary perspective. *In* "Reproductive Biology of Amphibians" (D. H. Taylor and S. I. Guttman, Eds.), pp. 73–101. Plenum Press, New York.

Wake, M. H. (1978). The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *J. Herpetol.* **12:** 121–133.

Wake, M. H. (1980). Reproduction, growth, and population structure of the Central American caecilian *Dermophis mexicanus. Herpetologica* **36:** 244–256.

Wake, M. H. (1982). Diversity within a framework of constraints: Reproductive modes in the Amphibia. *In* "Environmental Adaptation and Evolution, a Theoretical and Empirical Approach" (D. Mossakowski and G. Roth, Eds.), pp. 87–106. Gustav Fischer Verlag, Stuttgart.

Wake, M. H. (1986). A perspective on the systematics and morphology of the Gymnophiona (Amphibia). *Mém. Soc. Zool. France* **43:** 21–38.

Wake, M. H. (1992a). Reproduction in caecilians. *In* "Reproductive Biology of South American Vertebrates." (W. C. Hamlett, Ed.), pp. 112–120. Springer-Verlag, New York.

Wake, M. H. (1992b). Biogeography of Mesoamerican caecilians (Amphibia: Gymnophiona). *Tulane Stud. Zool. Bot., Suppl. Publ.* **1:** 321–325.

Wake, M. H. (1993a). Non-traditional characters in the assessment of caecilian phylogenetic relationships. *Herpetol. Monog.* **7:** 42–55.

Wake, M. H. (1993b). Evolution of oviductal gestation in amphibians. *J. Exp. Zool.* **266:** 394–413.

Wake, M. H. (1998). Cartilage in the cloaca: Phallodeal spicules in caecilians (Amphibia: Gymnophiona). *J. Morphol.* **237:** 177–186.

Wallach, V. (1993). Presence of a left lung in the Typhlopidae (Reptilia: Serpentes). *J. Herpetol. Assoc. Afr.* **42:** 32–33.

Wallach, V. (1998). The lungs of snakes. *In* "Biology of the Reptilia. Volume 19, Morphology G" (C. Gans and A. S. Gaunt, Eds.), pp. 93–295. Soc. Study Amphibians and Reptiles, Ithaca, NY.

Wallach, V., and Günther, R. (1998). Visceral anatomy of the Malaysian snake genus *Xenophidion,* including a cladistic analysis and allocation of a new family (Serpentes: Xenophidiidae). *Amphibia-Reptilia* **19:** 385–404.

Warburg, M. R., Lewinson, D., and Rosenberg, M. (1994). Structure and function of *Salamandra* skin and gills. *Mertensiella* **4:** 423–452.

Wassarman, P. M. (1987). The biology and chemistry of fertilization. *Science* **235:** 553–560.

Wassersug, R. J. (1971). On the comparative palatability of some dry-season tadpoles from Costa Rica. *Am. Midl. Nat.* **86:** 101–109.

Wassersug, R. J. (1972). The mechanism of ultraplanktonic entrapment in anuran larvae. *J. Morphol.* **137:** 279–288.

Wassersug, R. J. (1973). Aspects of social behavior in anuran larvae. *In* "Evolutionary Ecology of the Anurans" (J. L. Vial, Ed.), pp. 273–297. Univ. Missouri Press, Columbia.

Wassersug, R. J. (1974). Evolution of anuran life cycles. *Science* **185:** 377–378.

Wassersug, R. J. (1976). Internal oral features in *Hyla regilla* (Anura: Hylidae) larvae An ontogenetic study. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* **49:** 1–24.

Wassersug, R. J. (1980). Internal oral features of larvae from eight anuran families: Functional, systematic, ecolutionary and ecological considerations. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **68:** 1–146.

Wassersug, R. (1996). The biology of *Xenopus* tadpoles. *In* "The Biology of *Xenopus*" (R. C. Tinsley and H. R. Kobel, Eds.), pp. 195–211. Zool. Soc. London, London.

Wassersug, R. J., and Pyburn, W. F. (1987). The biology of the pe-ret' toad, *Otophryne robusta* (Microhylidae), with special consideration of its fossorial larva and systematic relationships. *Zool. J. Linn. Soc.* **91:** 137–169.

Wassersug, R. J., Lum, A. M., and Patel, M. J. (1981). An analysis of school structure for tadpoles (Anura: Amphibia). *Behav. Ecol. Sociobiol.* **9:** 15–22.

Watkins, J. F., Gehlbach, F. R., and Kroll, J. C. (1969). Attractant-repellant secretions in blind snakes (*Leptotyphlops dulcis*) and army ants (*Neivamyrex nigrescens*). *Ecology* **50:** 1098–1102.

Watling, D. (1986). "Mai Veikau. Tales of Fijian Wildlife." Privately printed, Suva, Fiji.

Watrous, L. E., and Wheeler, Q. D. (1981). The outgroup comparison method of character analysis. *Syst. Zool.* **30:** 1–11.

Webb, C., and Joss, J. (1997). Does predation by the fish *Gambusia holbrooki* (Atheriniformes: Poeciliidae) contribute to declining frog populations? *Aust. Zool.* **30:** 316–324.

Webb, G. J. W. (1977). The natural history of *Crocodylus porosus*. *In* "Australian Animals and Their Environments" (H. Messel and S. Butler, Eds.), pp. 239–312. Shakespeare Head Press, Sydney.

Webb, G. J. W., and Manolis, S. C. (1989). "Crocodiles of Australia." Reed, Chatswood, N.S.W.

Webb, G., and Manolis, C. (1993) "Crocodiles of Australia," Rev. ed. Reed, Chatswood, N.S.W.

Webb, G. J. W., and Vernon, B. (1992). Crocodiles management in the People's Republic of China-A review with recommendations. *In* "Crocodile Conservation Action" (Croc. Specialist Group, SSC), pp. 1–27. IUCN, Glands.

Webb, G. J. W., Messel, H., and Magnusson, W. (1977). The nesting of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* **1977:** 238–249.

Webb, G. J. W., Buckworth, R., and Manolis S. C. (1983). *Crocodylus johnstoni* in the McKinlay River, N. T. VI. Nesting biology. *Aust. Wildl. Res.* **10:** 607–637.

Webb, G. J. W., Choquenot, D., and Whitehead, P. J. (1986). Nests, eggs, and embryonic development of *Carettochelys insculpta* (Chelonia: Carettochelidae [sic]) from northern Australia. *J. Zool., London B* **1:** 521–550.

Webb, G. J. W., Manolis, S. C., and Whitehead, P. J. (1987). "Wildlife Management: Crocodiles and Alligators." Surrey Beatty & Sons Pty Ltd., Chipping Norton, N.S.W.

Webb, J. K., and Shine, R. (1997). A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides. Biol. Conserv.* **82:** 203–217.

Webb, J. K., and Shine, R. (1998). Ecological characteristics of a threatened snake species, *Hoplocephalus bungaroides* (Serpentes, Elapidae). *Anim. Conserv.* **1:** 185–193.

Weekes, H. C. (1935). A review of placentation among reptiles with particular regard to the function and evolution of the placenta. *Proc. Zool. Soc. London* **3:** 625–645.

Weldon, P. J. (1990). Responses by vertebrates to chemicals from predators. *In* "Chemical Signals in Vertebrates 5" (D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, Eds.), pp. 500–521. Oxford Univ. Press, Oxford.

Wells, K. D. (1977). The social behaviour of anuran amphibians. *Anim. Behav.* **15:** 666–693.

Wells, K. D. (1980). Social behavior and communication of a dendrobatid frog (*Colostethus trinitatis*). *Herpetologica* **36:** 189–199.

Wells, K. D. (1981). Parental behavior of male and female frogs. *In* "Natural Selection and Social Behavior" (R. D. Alexander and D. W. Tinkle, Eds.), pp. 184–197. Chiron Press, New York.

Wells, K. D. (1988). The effect of social interactions on anuran vocal behavior. *In* "The Evolution of the Amphibian Auditory System" (B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington, and W. Walkowiak, Eds.), pp. 433–454. Wiley, New York.

Wells, K. D., and Bard, K. M. (1988). Parental behavior of an aquatic-breeding tropical frog, *Leptodactylus bolivanus. J. Herpetol.* **22:** 361–364.

Wells, K. D., and Wells, R. A. (1976). Patterns of movement in a population of the slimy salamander, *Plethodon glutinosus,* with observations on aggregations. *Herpetologica* **32:** 156–162.

Welsch, H. H., Jr., and Lind, A. J. (1996). Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern California. *J. Herpetol.* **30:** 385–398.

Werner, D. I., Baker, E. M., Gonzales, E. C., and Sosa, I. R. (1987). Kinship recognition and grouping in hatchling green iguanas. *Behav. Ecol. Sociobiol.* **21:** 83–89.

Werner, E. E. (1986). Amphibian metamorphosis: growth rate, predator risk, and the optimal size at transformation. *Am. Nat.* **128:** 319–341.

Werner, Y. (1997). Observations and comments on active foraging in geckos. *Russ. J. Herpetol.* **4:** 34–39.

Werner, Y. L., Okada, S., Ota, H., Perry, G., and Tokunaga, S. (1997). Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetol. Rev.* **7:** 153–165.

West, N. H., and Van Vliet, B. N. (1983). Open-loop analysis of the pulmocutaneous baroreflex in the toad *Bufo marinus. Respir. Physiol.* **245:** 642–650.

Wever, E. G. (1978). "The Reptile Ear. Its Structure and Function." Princeton Univ. Press, Princeton.

Wever, E. G. (1985). "The Amphibian Ear." Princeton Univ. Press, Princeton.

Wevers, E. (1988). Enige Opmerkingen over de Pijlgifkikker *Dendrobates parvulus. Lacerta* **46:** 51–53.

Weygoldt, P. (1976). Beobachtungen zur Biologie und Ethologie von *Pipa* (*Hemipipa*) *carvalhoi* Mir. RiB. 1937 (Anura, Pipidae). *Z. Tierpsychol.* **40:** 80–99.

Weygoldt, P. (1991). Zur Biologie und zum Verhalten von *Phyllomedusa marginata* Izeckshohn & Da Cruz, 1976 im Terrarium. *Salamandra* **27:** 83–96.

Weygoldt, P., and de Carvalho e Silva, S. P. (1991). Observations on mating, oviposition, egg sac formation and development in the egg-brooding frog, *Fritziana goeldii. Amphibia-Reptilia* **12:** 67–80.

Whimster, I. W. (1990). Neural induction of epidermal sensory organs in gecko skin. *In* "The Skin of Vertebrates" (R. I. C. Spearman and P. A. Riley, Eds.), pp. 161–167. Linn. Soc. London, London.

Whitaker, A. H. (1968). The lizards of the Poor Knights Islands, New Zealand. *N. Z. J. Sci.* **11**: 623–651.

Whitaker, A. H. (1973). Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). *Proc. NZ Ecol. Soc.* **20:** 121–130.

Whitaker, R., and Basu, D. (1983). The gharial (*Gavialis gangeticus*) A review. *J. Bombay Nat. Hist. Soc.* **79:** 531–548.

Whitear, M. (1977). A functional comparison between the epidermis of fish and of amphibians. *Symp. Zool. Soc. London* **39:** 291–313.

Whitford, W. G. (1973). The effects of temperature on respiration in the Amphibia. *Am. Zool.* **13:** 505–512.

Whitford, W. G., and Bryant, M. (1979). Behavior of a predator and its prey: The horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). *Ecology* **60:** 686–694.

Whiting, M. J., Dixon, J. R., and Murray, R. C. (1993). Spatial distribution of a population of Texas horned lizards (*Phrynosoma cornutum:* Phrynosomatidae) relative to habitat and prey. *Southw. Nat.* **38:** 150–154.

Whittier, J. M., and Crews, D. (1987). Seasonal reproduction: patterns and control. *In* "Hormones and Reproduction in Fishes, Amphibians, and Reptiles" (D. O. Norris and R. E. Jones, Eds.), pp. 385–409. Plenum Press, New York.

Wibbels, T., Bull, J. J., and Crews, D. (1994). Temperature dependent sex determination A mechanistic approach. *J. Exp. Zool.* **270:** 71–78.

Wiens, J. J., and Reeder, T. W. (1997). Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetol. Monog.* **11:** 1–101.

Wiens, J. J., and Titus, T. A. (1991). A phylogenetic analysis of *Spea* (Anura: Pelobatidae). *Herpetologica* **47:** 21–28.

Wiewandt, T. A. (1982). Evolution of nesting patterns in iguanine lizards. *In* "Iguanas of the World: Their Behavior, Ecology, and Conservation" (G. M. Burghardt and A. S. Rand, Eds.), pp. 117–149. Noyes Publ., Park Ridge, NJ.

Wilbur, H. M. (1972). Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* **53:** 3–21.

Wilbur, H. M. (1975a). A growth model for the turtle *Chrysemys picta*. *Copeia* **1975:** 337–343.

Wilbur, H. M. (1975b). The evolutionary and mathematical demography of the turtle *Chrysemys picta*. *Ecology* **56:** 64–77.

Wilbur, H. M. (1980). Complex life cycles. *Ann. Rev. Ecol. Syst.* **11:** 67–93.

Wilbur, H. M. (1987). Regulation of structure in complex systems: Experimental temporary pond communities. *Ecology* **68:** 1437–1452.

Wilbur, H. M. (1997). Experimental ecology of food webs: Complex systems in temporary ponds. *Ecology* **78:** 2279–2302.

Wilbur, H. M., and Collins, J. P. (1973). Ecological aspects of amphibian metamorphosis. *Science* **182:** 1305–1314.

Wilbur, H. M., and Fauth, J. E. (1990). Experimental aquatic food webs: Interactions between two predators and two prey. *Am. Nat.* **135:** 176–204.

Wild, E. R. (1995). New genus and species of Amazonian microhylid frog with a phylogenetic analysis of New World genera. *Copeia* **1995:** 837–849.

Wiley, E. O. (1981). "Phylogenetics. The Theory and Practice of Phylogenetic Systematics." John Wiley & Sons, New York.

Wiley, E. O., Siegel-Causey, D., Brooks, D. R., and Funk, V. A. (1991). The Compleat Cladist. A Primer of Phylogenetic Procedures. *Univ. Kansas Mus. Nat. Hist., Spec. Publ.* **19:** 1–158.

Wilhoft, D. C. (1963). Reproduction in the tropical Australian skink, *Leiolopisma rhomboidalis*. *Am. Midl. Nat.* **70:** 442–461.

Wilkinson, M. (1989). On the status of *Nectocaecilia fasciata* Taylor, with a discussion of the phylogeny of the Typhlonectidae (Amphibia: Gymniophona). *Herpetologica* **45:** 23–36.

Wilkinson, M. (1992a). The phylogenetic position of the Rhinatrematidae (Amphibia: Gymnophiona): Evidence from the larval lateral line system. *Amphibia-Reptilia* **13:** 74–79.

Wilkinson, M. (1992b). On the life history of the caecilian genus *Uraeotyphlus* (Amphibia). *Herpetol. J.* **2:** 121–124.

Wilkinson, M. (1996). Resolution of the taxonomic status of *Nectocaecilia hyadee* (Roze) and a revised key to the genera of the Typhlonectidae. *J. Herpetol.* **30:** 413–415.

Wilkinson, M. (1997). Characters, congruence and quality A study of neuroanatomical and traditional data in caecilian phylogeny. *Biol. Rev.* **72:** 423–470.

Wilkinson, M., and Nussbaum, R. A. (1996). On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona). *Copeia* **1996:** 550–562.

Wilkinson, M., and Nussbaum, R. A. (1997). Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). *Biol. J. Linn. Soc.* **62:** 39–109.

Wilkinson, M., Sebben, A., Schwartz, E. N. F., and Schwartz, C. A. (1998). The largest lungless tetrapod: Report on a second specimen of *Atreochoana eiselti* (Amphibia: Gymnophiona: Typhlonectidae) from Brazil. *J. Nat. Hist.* **32:** 617–627.

Williams, E. E. (1950). Variation and selection in the cervical central articulations of living turtles. *Bull. Am. Mus. Nat. Hist.* **94:** 505–561.

Williams, E. E. (1969). The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* **44:** 345–389.

Williams, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. *Evol. Biol.* **6:** 47–89.

Williams, E. E. (1983). Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. *In* "Lizard Ecology: Studies of a Model Organism" (R. B. Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 326–370. Harvard Univ. Press, Cambridge, MA.

Williams, E. E. (1988). A new look at the Iguania. *In* "Proceedings of a Workshop on Neotropical Distribution Patterns" (W. R. Heyer and P. E. Vanzolini, Eds.), pp. 429–486. Acad. Brasileira Ciên., Rio de Janeiro.

Williams, G. C. (1966). "Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought." Princeton Univ. Press, Princeton, NJ.

Willis, P. M. A. (1997). Review of fossil crocodilians from Australasia. *Aust. Zool.* **30:** 287–298.

Wilson, D. S. (1998). Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* **79:** 1884–1892.

Wilson, E. O., and Bossert, W. H. (1971). "A Primer of Population Biology." Sinauer Assoc., Inc., Stamford CT.

Wilson, L. D., and Porras, L. (1983). "The Ecological Impact of Man on the South Florida Herpetofauna." Univ. Kansas Mus. Nat. Hist. Spec. Publ. 7, Lawrence, KS.

Winemiller, K. O., and Pianka, E. R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monog.* **60:** 27–55.

Winter, D. A., Zawada, W. M., and Johnson, A. A. (1986). Comparison of the symbiotic fauna of the family Plethodontidae in the Ouachita Mountains of western Arkansas. *Proc. Arkansas Acad. Sci.* **40:** 82–85.

Wirot, N. (1979). "The Turtles of Thailand." Bankok, SIAM-FARM Zool. Gard.

Withers, P. C. (1992). "Comparative Animal Physiology." Saunders College Publishing, New York.

Withers, P. C., and Richards, S. J. (1995). Cocoon formation by the treefrog *Litoria alboguttata* (Amphibia: Hylidae) A 'waterproof' taxonomic tool? *J. Roy. Soc. W. Aust.* **78:** 103–106.

Withers, P. C., Hillman, S. S, Drewes, R. C., and Sokol, O. M. (1982). Water loss and nitrogen excretion in sharp-nosed reed frogs (*Hyperolius nasutus:* Anura, Hyperoliidae). *J. Exp. Biol.* **97:** 335–343.

Whitford, W. G. (1973). The effects of temperature on respiration in the Amphibia. *Am. Zool.* **13:** 505–512.

Witmer, L. M. (1991). Perspectives on avian origins. *In* "Origins of the Higher Groups of Tetrapods. Controversy and Consensus" (H.-P. Schultze and L. Trueb, Eds.), pp. 427–466. Comstock Publ. Assoc., Ithaca, NY.

Witt, W. (1999). Report on the status of populations of *Plethodon shenadoah.* Personal communication.

Witten, G. J. (1993). Family Agamidae. *In* "Fauna of Australia. Volume 2A. Amphibia & Reptilia" (C. J. Gasby, G. J. B. Ross, and P. L. Beesley, Eds.), pp. 240–252. Aust. Govern. Publ. Serv., Canberra.

Woinarski, J. C. Z. (1989). The vertebrate fauna of broombush *Melaleuca unicinata* vegetation in northwestern Victoria. *Aust. Wildl. Res.* **16:** 217–238.

Woolbright, L. L. (1983). Sexual selection and size dimorphism in anuran Amphibia. *Am. Nat.* 121, 110–119.

Woolbright, L. L. (1991). The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica* **23:** 462–467.

Woolbright, L. L. (1997). Local extinctions of anuran amphibians in the Luquillo Experimental Forest of northeastern Puerto Rico. *J. Herpetol.* **31:** 572–576.

Worthy, T. H., (1987). Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil *Leiopelma* species. *J. Roy. Soc. NZ* **17:** 201–251.

Wright, J. W. (1993). Evolution of whiptail lizards (*Cnemidophorus*). *In* "Biology of the Whiptail Lizard (Genus *Cnemidophorus*)" (J. W. Wright and L. J. Vitt, Eds.), pp. 27–81. Oklahoma Mus. Nat. Hist., Norman, OK.

Wright, J. W., and Vitt, L. J., Eds. (1993). "Biology of Whiptail Lizards (Genus *Cnemidophorus*)." Oklahoma Mus. Nat. Hist., Norman, OK.

Wu, X.-C., Brinkman, D. B., and Russell, A. R. (1996a). A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. *Palaeonotology* **39:** 351–375.

Wu, X.-C., Sues, H.-D., and Dong, Z.-M. (1996b). *Sichuanosuchus shuhanensis,* a new Early Cretaceous protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. *J. Vert. Paleontol.* **17:** 89–103.

Wu, X.-C., Brinkman, D. B., and Russell, A. R. (1997a). *Sineoamphisbaena hexatabularis,* an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. *Can. J. Earth Sci.* **33:** 541–577.

Wu, X.-C., Russell, A. R., and Brinkman, D. B. (1997b). Phylogenetic relationships of *Sineoamphisbaena hexatabularis:* Further considerations. *Can. J. Earth Sci.* **34:** 883–885.

Wynn, A. H., Cole, C. J., and Gardner, A. L. (1987). Apparent triploidy in the unisexual brahminy blind snake, *Ramphotyphlops braminus. Am. Mus. Novitates* **2868:** 1–7.

Xavier, F. (1986). La reproduction des *Nectophrynoides. In* "Traité de Zoologie. Vol XIV, fasc. I-B. Amphibiens" (P. P. Grasse and M. Delsol, Eds.), pp. 497–513. Massons, Paris.

Yeomans, S. R. (1995). Water-finding in adult turtles: Random search or oriented behavior? *Anim. Behav.* **49:** 977–987.

Young, B. A. (1988). The cephalic vascular anatomy of three species of sea snakes. *J. Morphol.* **196:** 195–204.

Young, B. A. (1997). On the absence of taste buds in monitor lizards (*Varanus*) and snakes. *J. Herpetol.* **31:** 130–137.

Zaher, H. (1994a). Les Tropidopheoidea (Serpentes; Alethinophidia) son-ils réellement monophylétiques? Arguments en faveur de leur polyphylétisme. *C. R. Acad. Sci. Paris, Sci. Vie Evol.* **317:** 471–478.

Zaher, H. (1994b). Comments on the evolution of the jaw adductor musculature of snakes. *Zool. J. Linn. Soc.* **111:** 339–384.

Zaher, H. (1998). The phylogenetic position of *Pachyrhachis* within snakes (Squamata, Lepidosauria). *J. Vert. Paleontol.* **18:** 1–3.

Zaher, H. (1999). Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bull. Am. Mus. Nat. Hist.* **240:** 1–168.

Zamudio, K. R., and Greene, H. W. (1997). Phylogeography of the bushmaster (*Lachesis muta:* Viperidae): Implications for Neotropical biogeography, systematics, and conservation. *Biol. J. Linn. Soc.* **62:** 421–442.

Zardoya, R., and Meyer, A. (1998). Complete mitochondrial genome suggests diapsid affinities of turtles. *Proc. Natl. Acad. Sci. USA* **95:** 14226–14231.

Zhao, E., and Adler, K. (1993). "Herpetology of China." Soc. Study Amphibians and Reptiles, Ithaca, NY.

Zhao, E., Hu, Q., Jiang, Y., and Yang, Y. (1988). "Studies on Chinese Salamanders." Soc. Study Amphibians and Reptiles, Oxford, OH.

Ziegler, T., and Böhme, W. (1997). Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. *Mertensiella* **8:** 1–207.

Zimmerman, K., and Heatwole, H. (1990). Cutaneous photoreception: A new sensory mechanism for reptiles. *Copeia* **1990:** 860–862.

Zug, G. R. (1991). The lizards of Fiji: Natural history and systematics. *Bishop Mus. Bull. Zool.* **2:** 1–136.

Zug, G. R., and Mitchell, J. C. (1995). Amphibians and reptiles of the Royal Chitwan National Park, Nepal. *Asiatic J. Herpetol.* **6:** 172–180.

Zug, G. R., and Parham, J. F. (1996). Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): A skeletochronological analysis. *Chelonian Conserv. Biol.* **2:** 244–249.

Zug, G. R., and Zug, P. B. (1979). The marine toad, *Bufo marinus:* A natural history resumé of native populations. *Smith. Contrib. Zool.* **284:** 1–58.

Zweifel, R. G. (1972). Results of the Archbold Expeditions. No.97. A revision of the frogs of the subfamily Asterophryinae family Microhylidae. *Bull. Am. Mus. Nat. Hist.* **148:** 411–546.

Zweifel, R. G. (1985). Australian frogs of the family Microhylidae. *Bull. Am. Mus. Nat. Hist.* **182:** 265–388.

Zweifel, R. G. (1986). A new genus and species of microhylid frog from the Cerro de la Neblina region of Venezuela and a discussion of relationships among New World microhylid genera. *Am. Mus. Novitates* **2863:** 1–24.

Zweifel, R. G. (1989). Long-term ecological studies on a population of painted turtles, *Chrysemys picta,* on Long Island, New York. *Am. Mus. Novitates* **2952:** 1–55.

Zweifel, R. G., and Lowe, C. H. (1966). The ecology of a population of *Xantusia vigilis,* the desert night lizard. *Am. Mus. Novitates* **2247:** 1–57.

Taxonomic Index

Author Index

Italic numerals indicate authors cited in the Bibliography

Subject Index