
ALLE ZEIT WACH
1842

Jean Chaline

Paleontology of Vertebrates

With 55 Figures

Translation
David le Vay

Springer-Verlag Berlin Heidelberg New York
London Paris Tokyo HongKong

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ISBN-13: 978-3-540-51755-9 e-ISBN-13: 978-3-642-75103-5
DOI: 10.1007/978-3-642-75103-5

Library of Congress Cataloging-in-Publication Data
Chaline, Jean. [Paléontologie des vertébrés. English] Paleontology of vertebrates / Jean Chaline. Translation of: Paléontologie des vertébrés. Includes bibliographical references.

1. Vertebrates, Fossil. I. Title.
QE841.C4513 1990, 90–9614
566–dc20, CIP

2131/3145-543210 – Printed on acid-free paper

Preface

Paleontology is a science which has played a great part in the history of ideas. We need only recall how up to and including the time of the Enlightenment, understanding the fossil nature of certain biological remains caused conflicts of ideas in which the greatest minds were not always the leading lights, often finding it easier to believe in "tricks of nature" that did not imply, for instance, that the sea once existed in places where there are now continents and mountain chains; or even, like Voltaire, preferring to believe that the fossil molluscs discovered in the Pyrenees had been lost there by pilgrims on their way to Santiago de Compostella, being the scallop-shells from their hats.

Later, at the end of the 18th century and during the whole of the 19th, the concept of evolution introduced new conflicts, paleontology being in the forefront with Lamarck and many others, notably Darwin, who, it is too often forgotten, was as much a geologist as a biologist. To read his account of the famous cruise of the *Beagle* will convince any doubters.

Finally, after barely a century, human paleontology emerged to torment consciences by placing Man in his historical setting, no longer the center of the living world, just as a few centuries before the astronomers had relocated the Earth in a universe of which it was also no longer the center.

It might therefore be imagined that paleontology has now become a mature, conservative discipline. Nothing could be less true. Like all the geosciences, it has undergone profound transformations due to new methods, predominantly quantitative in nature, and by being included in the evolution of the environment (paleoecology), related to other biological disciplines, and to the now global perspectives of the earth sciences (paleobiogeography).

In the course of this evolution, the paleontology of the vertebrates has played a special part by virtue of its rich resources, and also because it comes nearest to the natural history of man.

Jean Chaline was the obvious author for this work. His position in French and international research and his specialization in evolutionary paleontology, which he has studied profoundly, marked him out as particularly suited to write this compact and penetrating book, that will be useful to all present or past students of the subject, and, more simply, to all those stirred by curiosity as to our origins.

JEAN AUBOUIN

Introduction

To Marie-Claude
Emmanuel and Olivier

Paleontology is a *historical science* which studies the development of life on earth. It is thus at the junction of two complementary fields, the first, the earth sciences, treating the evolution of the planet and the universe, cannot be neglected without losing historical dimension and all the information as to the spatio-temporal environment of fossil organisms, gathered from stratigraphy, sedimentology, geochemistry, pedology, tectonics, etc; the second, the life sciences, studies the life of the past and research into the present outcome of evolution, the biosphere, and the mechanisms and processes that may explain this history.

While paleontology is a *fundamental discipline* with its own great research themes, it also provides *applications* that are indispensable to the earth sciences. Fossils are eminently suitable tools for *dating* and the success obtained by paleontology in this field has very nearly proved fatal to it, for the paleontologist has too often been relegated to the simple role of a supplier of information required to date territories for the geologist. As such dating is based on evolutionary phenomena, a knowledge of these is an indispensable preliminary to dating. Paleontology also contributes largely to the reconstruction of biosedimentary units and paleoenvironments by evaluating ecological data from biological communities. For the Quaternary, it even allows a precise reconstruction of the climatic conditions. Finally, evolutionary history, from a paleobiogeographic perspective, supplies key elements by which to test the validity of models of global tectonics.

Paleontology has improved its analytical methods by using performant statistical methods (factorial analysis of correspondences, discriminant functions, etc.) and informational theory. Cladistic analysis of characteristics has further allowed considerable progress in classification and has modified the majority of phylogenetic reconstructions. Paleontology has likewise questioned some concepts of the synthetic theory of evolution (the concept of stases, the respective roles of phyletic gradualism and allopatric speciation in morphological evolution). Finally, paleontology will in the future include developmental biology, which was missing from the synthetic theory of the 1940's, and thus progress from description to explanation and build a brigde to the life sciences.

This rejuvenation of the concepts and methods of paleontology has given it new vigor and fresh success and has widened even further the scope of its applications.

This volume will treat the paleontology of the vertebrates as a historic and dynamic evolutionary process in the paleogeographic framework of the history of the earth. Analysis of the principal groups of vertebrates is used to stress the characteristic problems of each group from the evolutionary viewpoint.

This study covers aspects of evolutionary theory and different fields of applied paleontology. This new orientation is essential not only to initiate training in research by means of research, but also to indicate the various paths of professionalization existing today in earth and biological sciences.

Unfortunately, paleontology is too little taught; yet it should form part of the cultural equipment, not only of naturalists, geologists and biologists, but also of those concerned with the history of the universe. Reasons of space have made it impossible to provide anatomical definitions. For these, readers can refer to the works of Grassé and Devillers (1965), Devillers and Clairambault (1976) or Beaumont and Cassier (1987).

I would like to express my thanks to Professor Jean Aubouin, Member of the Institute, for the confidence he showed in entrusting me to carry out this work. It is also a pleasure to thank Professors Jean Dercourt, Charles Devillers, Jacques Michaux and, more particularly, Philippe Janvier and Jean-Claude Rage, director of research at C.R.N.S., Dr. Pierre Mein and Dr. Olivier Rieppel for undertaking the onerous task of rereading this text, and for all the criticisms, corrections, and suggestions. Numerous colleagues have given me assistance by supplying often unpublished information: Eric Buffetaut, Jean-Yves Crochet, Christian de Muizon, Charles Devillers, Daniel Goujet, Jean-Jacques Jaeger, Philippe Janvier, Jean-Michel Mazin, Jacques Michaux, Jean-Claude Rage, Olivier Rieppel, Philippe Taquet. I am grateful to all of these.

For the sake of uniformity of illustration, I have redrawn the 55 plates, including 322 figures, and I express my sincere thanks to all those colleagues who have authorized me to make use of their original drawings. In this context Ms Annie Bussière and Didier Zani helped me construct several figures.

Dijon, 1990 JEAN CHALINE

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CHAPTER 1

Concepts, Methods, and Techniques

1.1 Fossils and Fossilization

1.1.1 Fossils

The *fossils* studied by paleontologists are the remains, fragmentary or complete, of organisms that have existed or the traces they have left in geological formations. Usually, fossils correspond to the hard parts of living creatures, in the vertebrates to parts of the skeleton and the teeth. Exceptionally, very fragile soft parts such as the skin, hair, membranes, feathers, and eggshells are preserved.

1.1.2 Fossilization

The primary condition for fossilization of an organism is its very rapid burial in sediments. Otherwise, in the course of nature, first the soft parts and then the skeletal elements are rapidly destroyed by predators (carnivores, ants, etc.), the bacteria of putrefaction and the resulting gases, climatic factors (frosts, wide ranges of temperature, rain, etc.), chemical, physical, and biological agents.

In most cases, once the soft parts have been destroyed, only the hard parts are preserved, rarely in their original connection, but usually dislocated and dispersed according to the type of deposit. Fossilization takes place on compaction and the diagenetic transformations of the surrounding ooze, mud, or sand. The organic components of the bones and teeth are replaced by inorganic constituents, changes which may more or less damage the initial structure of the skeletal elements. The quality of fossilization and the number and nature of the fossils is closely dependent on the type of deposit in which they are preserved.

1.1.3 Paleontological Deposits

According to their marine or continental origin, paleontological deposits can be grouped into eight categories.

1.1.3.1 Marine Deposits

When a marine vertebrate dies, its body does not immediately fall to the seafloor. It floats for some time before gently sinking to the bottom or being brought to shore. The gases released by putrefaction of the internal organs tend to disrupt the skeleton, which may be dispersed by local currents, although complete skeletons of fish or marine reptiles may exceptionally be found. These are generally very fine-grained deposits formed in sheltered bays or lagoons. These relatively undisturbed waters, without oxygen supply, constitute traps where organisms die of asphyxia. Examples are the famous sites of Holzmaden in Germany and Monte Bolca in Italy. The proliferation of a plankton very rich in diatoms may also cause the asphyxiation of fish in large numbers, as also the drying-up of isolated basins after withdrawal of the sea.

1.1.3.2 Marshy Continental Deposits

Marshes are favored sites for preservation, where vertebrates have perished by being bogged down or asphyxiated by methane emanations. Marshes rich in leaf deposits are very disintegrating and cause the destruction of vertebrate remains, for which reason there are few fossil vertebrates in carboniferous layers. On the other hand, they are abundant in marshes less rich in organic matter. One instance of this is the remains of the great deer *(Megaceros giganteus)* in the peat bogs of Ireland. Peat bogs have likewise allowed the perfect preservation of bodies buried several millennia ago, such as those of Tollund and Grauballe men.

Humic marls are unique deposits in the systematics of microvertebrates, especially micromammals.

1.1.3.3 Lacustrine Continental Deposits

Vertebrates fossilized in lakes derive either from animals brought down by the rivers emptying into them or from animals that came to drink and were engulfed on their shores. The remains of fish and aquatic vertebrates (crocodiles, turtles, hippopotami, rodents, etc.) are still to be found there (Messel, Germany). Drying-up of lakes has also produced hecatombs. One particular type of lake corresponds to natural accumulations of asphalt that are subsequently polymerized. This is responsible for the exceptional preservation of two woolly rhinoceroses in the ozocerite of Starunia in Galicia (URSS) and of over 3000 *Smilodon* in the Rancho La Brea tar pits in Los Angeles.

1.1.3.4 Fluviatile Continental Deposits

In the two preceding cases, the animals became fossilized at the site of their death, a state of autochthony. At sites of fluviatile deposits there has generally been transport, i.e., allochthony. This transport along the rivers may then favor the accumulation of cadavers in calmer zones. Flooding is mainly responsible for the destruction of animals, even of entire herds. Such phenomena can be observed today. In July 1985, herds of caribou (Cervidae) migrating 1500 km from east to west, from Labrador to Hudson's Bay, traversed the Caniapiscan and Koksoak rivers, 1500 km northeast of Montreal. The river flow that they traverse every year was too violent and caused some 10,000 caribou to drown, for, although excellent swimmers, they die of embolism within a few seconds of water entering their lungs. The bodies of these 10,000 caribou formed an almost continuous chain along the banks for some 50 km. Similar phenomena can occur in semi-desert countries where water can rise very rapidly in the wadis. Entire herds of Cervidae, Bovidae, and even fossil mastodons are sometimes found.

1.1.3.5 Desert Continental Deposits

In these environments of very reduced bacterial activity the cadavers mummify. However, major temperature ranges separate the bones and reduce them to dust. Mummified dinosaurs have been found showing skin with numerous ridges and tuberosities, paleotheria with hair, and bats with preserved alar membranes.

1.1.3.6 Periglacial Continental Deposits

In the periglacial zone bordering the great Quaternary glaciers (ice caps) of the northern hemisphere, a permanently frozen subsoil or permafrost has developed. During periods of thaw, mammoths and woolly rhinoceroses were bogged down in the upper part of the mollisol and caught in the ice, where they were completely preserved for several thousand years with flesh, skin, and hair.

1.1.3.7 Karstic Continental Deposits

Avens and caves constitute natural receptacles for the accumulation of sediments and fossils. Besides the animals that accidentally fall into the avens, the caves serve as lairs for numerous carnivorous predators (hyenas, lions, bears, etc.), and the remains of their prey accumulate. The accumulations of Tertiary phosphorites of bony remains in Quercy (France), for example, are abundant enough for commercial exploitation for the production of phosphates. To this should be added the remnants of hunts brought in by prehistoric man. The infills of caves and under-rock shelters are preferential deposits for micromammals, resulting from the accumulation of the pellets rejected by birds of prey, such as owls, which eat four to five small mammals a day. The flesh is digested in the predator's stomach, but the skeleton and residual hairs agglutinate into an ovoid mass or pellet which after several hours the raptor regurgitates at the foot of its nest eyrie. The accumulation of thousands, even millions, of rejection pellets can be noted, which, once the hairs are destroyed, constitute actual strata of micromammals. These deposits include rodents, insectivora, bats, small carnivores, small birds, batrachia, reptiles, and fish.

1.1.3.8 Deposits with Vertebrate Tracks

The vertebrates often left traces of their passage, the preservation of which implies particular conditions of sedimentation. To be preserved, an imprint must be impressed in a fine moist sediment and then be rapidly buried by another sediment of a different nature. These conditions have been met at the margins of seas, rivers, and lakes. Millions of tracks of amphibians and reptiles have been exhumed in Carboniferous, Permian, Triassic, Jurassic, and Cretaceous deposits. The study of these paleoichnology, allows the reconstruction of the mode of locomotion of the animals and their behavior and morphology. Comparison of the tracks with the fossils has led to their identification in many cases. Conditions favorable to preservation of tracks exist also in volcanic ash. One of the most extraordinary examples is at the site of Leatoli in Tanzania. After an eruption of ash by the Sandiman volcano and moistening of the deposit by rain, tracks of the entire local vertebrate fauna were recorded and covered by a new accumulation of ash dating back 3.6 million years (Ma). These include tracks of elephants, giraffes, guineafowl, rabbits and, above all, two parallel tracks of Hominidae attributed to the *Australopithecus* of the Afars. These tracks have confirmed in spectacular manner the findings of the skeleton of "Lucy", discovered in Ethiopia, proving by the shape of the pelvis that these Australopithecines had already acquired the bipedal state at this epoch (see Chap. 8).

1.1.3.9 The Abundance of Fossils

Allowing for the exceptional conditions which must combine for the preservation of fossil vertebrates, fossilization appears as a rare phenomenon. Moreover, even after fossilization, the fossils may undergo deformation or even disappear under the influence of processes of metamorphosis or agents of erosion. Yet, despite the exceptional nature of fossilization, fossils are in fact numerous in geological formations, where there is a very large store. It has been estimated that the deposits of the karoo in South Africa must include millions of skeletons of reptiles. Indeed, it is only the outcrops that yield fossils and the more exceptional doubtless still remain to be found.

1.1.4 Paleontological Techniques

Fossil discoveries are often fortuitous, made during geological investigations, the working of quarries or mines, or paleontological prospecting in theoretically favorable sites. The discovery of a skeletal remnant leads to a search over a large area to see if other elements have been preversed in the vicinity. After consolidation of the visible part of the bones in situ, the skeleton is freed with the block of sediment in which it is embedded. Sheathed in linen strips smeared with plaster, the fossil-bearing block is then stripped down in the laboratory. This is precision work, for which the specialist requires a whole outfit of chisels, needles, mallets, etc. Because of the fragility of the bones, consolidation with resins is often necessary as the stripping proceeds. Where micromammals are concerned, mobile sediments can be sifted under water, but consolidated sediments are stripped chemically using acetic, formic, or hydrofluoric acid.

The study of the skeletal remains is carried out by the classical methods of comparative anatomy. Very old fossils like those of the Agnatha and archaic fishes are often in such consolidated and compact nodules that only the external morphology is visible. However, the internal anatomy can be studied by use of the technique of serial sections. The fossil is abraded perpendicular to or parallel with the anteroposterior axis in a series of polished surfaces at intervals of approximately 25 microns. This very precise technique, analogous to that of the serial sections employed in zoology, allows reconstruction of the internal structure of the organisms: the skeleton and the paths of the nerves and blood vessels.

Study of fossil brains is possible thanks to the existence of the natural molding of the interior of the skull, now easily performed by making internal casts using rubberized materials which can be extracted via the occipital foramen. Other techniques for studying vertebral remains are the use of histologic sections and radiographs.

1.2 Species and Classification of Populations

1.2.1 The Concept of Species

During Antiquity and the Middle Ages, the concept of species remained in the realm of conjecture, subordinated to philosophic and religious concepts where the a priori method dictated and imposed solutions that replaced scientific observations. In 1758, Linne introduced the scientific method, but as a great systematician, he was more preoccupied with distinguishing species in terms of their similar characteristics than with analyzing their variability. The Linnaean classification is closely associated with the doctrine of the fixity of species which prevailed at that time. Concepts of the species are closely linked with systems of thought the cultural factors affecting research.

1.2.1.1 The Typological Concept of Species

In this concept the species is regarded as made up of individuals, all of which are identical and in which variability is no more than accidental. It follows that any individual which exhibits differences of the type described may itself be regarded as the type of a distinct species. It is clear that the discovery of isolated individuals has favored this tendency. The outcome of the strict application of this concept has been the multiplication of the units of classification (taxons) and a disintegration of species. The typological concept of the species corresponds to a static view of the world, considered as a system of perfectly defined and stable hierarchized structures. It is essentially a structuralist concept.

1.2.1.2 The Classification of Populations and the Biological Concept of Species

In the 1920's the field of population genetics developed, with the aid of the statisticians, who established mathematical models allowing a prediction of structural modifications in populations under the influence of small mutations. These models explain the extension of variability, the influence of natural selection and the modes of reproduction, and introduce the role of chance. The species is no longer considered as a structure, but as an assembly of individuals, all different, bound by a system of relationships (reproduction, genetic bond). This biological concept of species, where the individual is regarded as a morphologic variant in the midst of populations with geographic differentiations, has been defined by Mayr (1942) as follows: "The species is constituted of populations that are actually interfertile and isolated from the reproductive aspect from any other analogous group". This concept of the species applies to present-day species, and it is necessary to extend this definition if it is to include the temporal aspect.

1.2.1.3 The Spatiotemporal Concept of Species

Present-day species constitute the arrangement of nature corresponding to the most advanced stage of biologic evolution across all its phyla. Mayr's biological concept of species has a spatial dimension and applies at any given moment, but it does not allow for the temporal dimension of descent, which is the subject of paleontological research. It is useful therefore to extend the definition of the species to a spatiotemporal dimension which takes account of both biological and paleontological approaches. Such a definition could read as follows: the species corresponds to a continuum in time and space between groups of natural populations, which interbreed and are isolated in the reproductive aspect from all other analogous groups, at each instant of the temporal continuum (Chaline 1972, 1987). This species, or specific spatiotemporal continuum, corresponds to a chronospecies (Cain, 1954) or to what Bonde (1977) calls a temporal biospecies. The spatiotemporal species begins with reproductive isolation resulting from the changes induced by the processes of speciation, and is completed either with the extinction of the species, or with the initiation of a new speciation by means of a new reproductive isolation (see Chap. 9).

This concept, which is the opposite of a static and structured vision, is that of a historical development of the universe whose complexity can be explained only on the basis of spatiotemporal systems of relationships.

1.2.2 Paleontological and Biological Species

While zoologists and biologists are able to analyze species in their biological reality and at all the organizational levels of the living organism: molecular, genic, biochemical, chromosomal, cytologic, physiologic, ontogenetic, anatomic, ecologic, and ethologic, paleontologists are at a marked disadvantage. They work only with available fossilized remains, mainly bones and teeth, i.e., only one part of the anatomical elements of a morphospecies. These remains represent only one part of the individuals and not necessarily the most important. Thus the paleontologist works like a detective to reconstruct the characteristics of a species with the aid of circumstantial evidence, in this case fossils, bones, and tracks. As far as he can, the paleontologist seeks to approach the biological species, i.e., to discover the system of relationships reflecting the underlying criterion of interfertility within the paleospecies or morphospecies. In the case where the zoological group, genera, and species still exist, the paleontologist can compare fossil data with those of present-day species. This comparison will be made in certain rodents, the voles. The nordic vole *(Microtus oeconomus)* and the grey lemming of the steppes *(Lagurus lagurus)* have an identical external morphology: the same coat, the same length of tail, the same size of eyes and ears, the same overall size. The only way to identify them is to open their mouths and inspect the shape of the teeth, which are very different in the two species. Now, in the fossil state the paleospecies are essentially represented by populations of teeth (morphospecies). This comparison shows that two existing biological species can be distinguished only by using the criteria of the morphospecies. Other comparisons between the fossil and existing voles prove that the paleospecies represented by morphospecies have real validity as biological species. However, this conclusion must be hedged by indicating the limit of paleontological investigation. A certain number of morphologically similar species exist, identified by biochemical, chromosomal, ecologic, or ethologic criteria, characteristics which do not fossilize. These so-called sister or cryptic species evade the wisdom of paleontologists. In other words, paleospecies or morphospecies may be good biological species, whereas others resemble several biological species indistinguishable on grounds of morphology alone. These last may be regarded as collections of biological species; but the paleontologist also has at his disposal for approaching biological species the special tool of biometry.

1.2.3 Biometrical Analyses

The paleontologist has an indirect means of testing the validity of paleospecies by analyzing the distribution of morphological characteristics and their variability by means of biometry. In a population where the individuals are interfertile, the distribution of the frequencies of morphological characteristics takes place along a normal Gaussian curve. The biometric study of morphology is conducted with the aid of more or less complex morphometry. The data can then be treated by univariate, bivariate, or multivariate statistical methods in current usage. These statistical tools, which utilize the possibilities of the computer, provide the paleontologist with grounds for his judgment.

1.3 Analysis of Characteristics and Classifications

1.3.1 Classical Systematics

The notion of classifying animal forms goes back to Aristotle, but modern zoological nomenclature was elaborated only in 1758 by the Swedish naturalist Linne in his work *Systema Naturae.* Framed in a fixed concept of the species, classification founded on resemblance was aimed at describing the natural order and was considered as immutable. It was conceived as a hierarchical system of increasingly higher levels from species to phylum, by way of genera, families, orders, and classes. The development of transformist ideas and the elaboration of the theory of evolution by descent with modifications by Darwin (1859) brought about a reconsideration of this classification. The characteristics of resemblance or difference could then be considered as the outcome of the evolutionary phenomenon, of the history of life, which Haeckel (1856) called *phylogeny.* Classification may be entirely independent of phylogeny but the ideal is for classification to reflect phylogeny.

1.3.2 Evolutionary Systematics

The elaboration, in the 1940's, of the synthetic theory of evolution by the conjunction of research in genetics, biology, and paleontology, did not neglect systematics, which is the science of classification of the living. Simpson (1945) has studied the principles, rules, and laws of classification of what is called *taxinomy* (or *taxonomy).* In evolutionary systematics, phylogeny is reconstructed on the basis of the fossil record and supported by the direct relationships of ancestors to descendants. This has been termed the *stratophenetic* method by Gingerich (1979). The characteristics of a very old fossil are regarded as primitive, those of a recent fossil as evolved. Thus the age of the fossil bearing a characteristic serves to define its degree of evolution. This approach, considered as eclectic, follows no strict rules and is more akin to an "art" specific to each specialist, in which logic cedes to arbitrary judgment.

1.3.3 Phylogenetic Systematics or Cladism

Hennig (1950) is to be credited with the elaboration of a rigorous method of systematics. His work, published in English under the title of *Phylogenetic Systematics* unleashed a considerable renovatory movement, cladism.

1.3.3.1 The Principles of Phylogenetic Systematics

This method, based on the postulate of biological evolution by descent with modification, consists of investigating the degrees of kinship between species and the antiquity of their common ascendancy. As in evolutionary systematics, the cladistic method is based on the analysis and distribution of the characteristics of species. But while the relationship of similarity reflect those of phylogeny, they may have a very different significance that is not always taken into account by evolutionary systematics. Depending on whether the similar morphological characteristics are primitive (*plesiomorphous*) or derived (*apomorphous*), they have very different phylogenetical significance. Three types of patterns may be observed.

In the first type, the morphological resemblance may be due to possession of the same apomorphous characteristics inherited from a common species strain. When several apomorphous characteristics are shared by one group, the term *synapomorphy* is used, and organisms possessing a synapomorphy constitute with their ancestor a so-called *monophyletic* group. Synapomorphies, which must be homologous characteristics, i.e., having one and the same origin, are the sole indices of close relationship. For example, the birds constitute a monophyletic group, since they possess as synapomorphies wings, feathers, and other features. Morphological resemblance may also result from the possession of plesiomorphous characteristics or a primitive nature. These archaic characteristics appeared a very long time ago and have been shared at the whim of evolutionary diversification by a very large number of groups derived from this common ancestor. At the epoch when the new characteristic made its appearance it corresponded to an apomorphy, but with the unfolding of the history of life it became plesiomorphous. The possession of several plesiomorphous characteristics, or *symplesiomorphy*, characterizes the so-called *paraphyletic* groups. Symplesiomorphies indicate bonds of remote, ancestral relationships. As an example, the four feet of the tetrapoda constitued an apomorphy when the character first appeared, but is regarded as a plesiomorphy within the mammals.

Resemblance may result from a phenomena of convergent adaptation. For example, one could not think of grouping together the marsupial mouse *Antechi-*

nomys, Elephantulus (Macroscelidae), *Dipodomys* (Heteromyidae), *Dipus* (Dipodidae) and *Argyrolagus* (South American marsupial), which have the same external appearance of a kangaroo-mouse but belong to different groups. The group formed by these five types is called *polyphyletic* including descendants of more than one ancestor.

1.3.3.2 The Cladistic Approach

Phylogenetic systematics investigates the monophyletic groups which have a specific history, and adopts a retrospective approach since it is the descendants which provide indications as to their ancestors. If we consider two taxons, A and B, having the same direct common ancestor, we can label them *sister-groups*. With their ancestor, they form a monophyletic group. If this group is compared to a third external taxon C, taxon C may be regarded as the sister-group of the collectivity AB since they have the same direct ancestor. The collective ABC is also a monophyletic group. Taxons A and B (Fig. 1.1) share a synapomorphy (a) that does not exist in taxon C, and therefore have a closer relationship between themselves than with taxon C. Taxons B and C possess a symplesiomorphy (b) which gives us hardly any information as to the degree of phylogenetic relationship between these two taxons. Phylogenetic systematics employs the hypothetico-deductive method. It analyzes the distribution of characteristics among living forms and fossils in an attempt to demonstrate the greatest possible number of synapomorphies. This yields a hypothesis of phyletic relationships which uses the *principle of parsimony* consisting or employment of the simplest hypothesis, a hypothesis capable of being refuted by the production of other data. The degrees of phylogenetic relationship are expressed in a *cladogram* (Fig. 1.1), setting out the distribution of the synapomorphies. The nodes define the limits of the monophyletic groups. The cladogram is a basic hypothesis making it possible to establish a systematic *hierarchical classification* founded on phylogenetic relationships. In such a classification the sister-groups have the same taxonomic rank, independent of their evolutionary diversification. In principle, there are as many taxonomic ranks as dichotomies in the cladogram, which constitutes a major difficulty with

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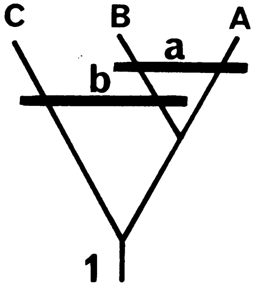
Fig. 1.1. Cladograms and phenogram. **1.** Cladogram of three species, *A, B, C:* the taxons *A* and *B* share a derived character *a* (apomorph) while taxons *B* and *C* resemble each other by the primitive character *b* (plesiomorph). Taxons *A* and *B* are more closely related among themselves (sister-group) than either of them with taxon *C* (after Goujet 1980); **2** to **7** possible phylogenetic trees for cladogram **1**; **8** scenario of the phylogenetic tree **7** replaced in its stratigraphic framework (stages 1 and 2) and biogeographic framework (zones 1 and 2), (**2** to **8** after Janvier 1984); **9** cladogram of 16 populations of five species (*M, P, B, A, E.*) of fish of the genus *Menidia*; **10** phenogram of the same analysis using all the characters without regard for their apomorphous or plesiomorphous aspect and considering the absence of a character as a character (**9** and **10** after Mickevich and Johnson 1976, modified by Janvier 1984)



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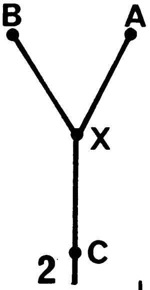

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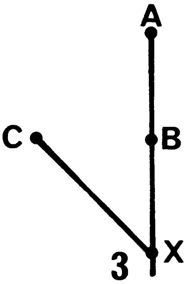

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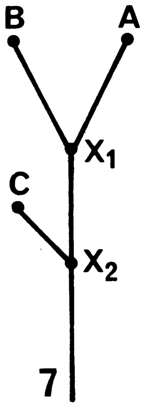

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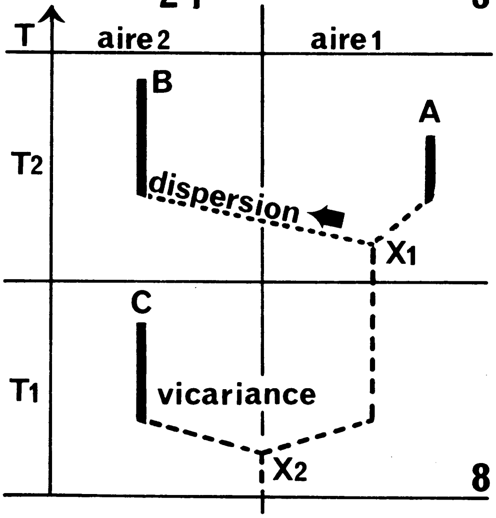

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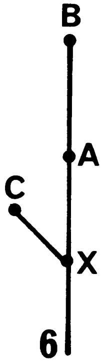

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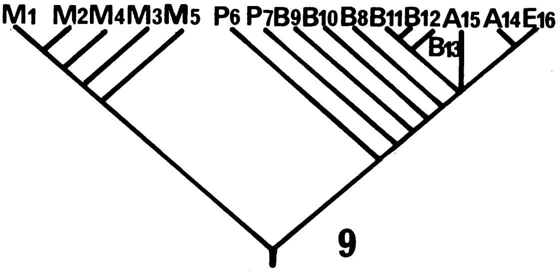

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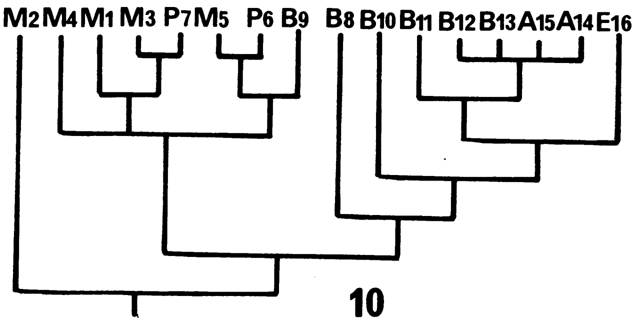

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fossil forms. To avoid the creation of categories among fossils, Patterson and Rosen (1977) have proposed the concept of *plesion*. A plesion corresponds to every monophyletic fossil group, sister-group of the larger existing monophyletic group.

There are three possible cladograms (Fig. 1.1), for three related taxa. Since synapomorphies can unite sister-groups with each other as well as ancestors with their descendants, cladograms reveal nothing about speciation or evolutionary rates. The distribution of synapomorphies can be used to test and choose among all possible cladograms for any monophyletic group. Based on cladograms, one can elaborate a *phylogenetic tree* constructed on nodes of divergence. Since cladograms reflect only certain degrees of relationships, phylogenetic tree try to reconstruct ancestor-descendant relationships (Platnick 1977). For any cladogram of three taxa there are six possible phylogenetic trees (Fig. 1.1 : 2 to 7).

Beyond that, one can go on to a *scenario* which corresponds to a tree set in its stratigraphical, biogeographical, and ecological framework. These criteria indicate that a given tree may be probable or improbable. Platnick (1977) claimed that "phylogenetic trees are not testable by character distributions and thus that scientific phylogeny reconstruction is *not* possible at the level of phylogenetic trees and must be restricted to the level of cladograms". He concluded with Cracraft (1974) that "the goal of a phylogeny reconstructed at the level of trees is irrelevant to and inappropriate for systematics, since a hierarchical classification can store information only on degrees of relationships and not on ancestry". This view is challenged by evolutionary systematists and paleontologists, who argue that phylogeny reconstructions are possible even at the phylogenetic tree level. The distinction between these three levels of approach to phylogeny is extremely important.

1.3.3.3 Problems of Phylogenetic Systematics

One of the key problems of phylogenetic systematics consists of the distinction between plesiomorphies and apomorphies. In fact, there is no absolute criterion. The major argument corresponds to what is called "out-group comparison". The characteristics of the members of the hypothetical monophyletic group considered are compared with their homologs in the sister-group. If they are unique for the group, or absent in the sister-group, they are catalogued as apomorphous; on the other hand, if they are present in the sister-group and other groups they are plesiomorphs for the monophyletic group. It is essential to recognize the direction of evolution and the possible reversions of characteristics. The state of a character may be determined by paleontological arguments and the geologic order of appearance of characters. In general, the primitive characters appear first. The paleontological criterion, sharply criticized by certain cladists, can be employed only in the rare groups where the evolutionary history is very well documented and the chronomorphoclines are undeniable. The biogeographical data may also be informative as to the state of characteristics. For example, the formation of two species by fragmentation (plate tectonics) of the area of distribution of the common ancestor, called *vicariance* (Fig. 1.1:8) allows assessment of the degrees of relationship in the secondary taxons in the two new distribution zones. The polarity of states of characters is often revealed by the morphoclines observed in existing species. Finally, the ontogenetical criterion considered by some as essential is based on the law of recapitulation, and postulates that the most general and most primitive characteristics appear in the course of individual development before the more specialized. This criterion must be discussed as heterochronies may inverse the polarity of characters changes (McNamara 1988; see Chap 4.4).

While cladistic analysis may be regarded as a tool theoretically intended to introduce more rigor into the elaboration of phylogeny and systematics, the methods just sketched of the cladistic approach show that the determination of plesiomorphous-apomorphous states is not without ambiguities. A certain number of criticisms may be formulated with regard to the cladistic methodology.

For example, in a phylogenetic tree derived from a cladogram the strain species is considered to disappear and give birth to two distinct species; yet this theoretic case seems rare in the processes of speciation. Aware of this problem, Bonde (1981) recognizes that if a species (before and after speciation) has different phylogenetic relationships with the rest of the system, the part before speciation is ancestral to a line of which the part after speciation becomes a sister-group! In principle, these two segments of species should be given different names, even if the strain species is maintained in unchanged morphologic stasis!

Systematics and evolutionary theory are independent of each other. The hierarchy of groups, common plan and homology indicate a biological order, or pattern, as identified by systematics. Systematics constitute an initial study, independent of a theory of mechanisms providing a reasonable explanation of these patterns, as Darwin suggested. This view has been defended by Nelson and Platnick (1981), Patterson (1982) and Brady (1984), who claimed that the theory of descent with modification according to Hennig, is not neccesary for the construction of a phylogeny by analysis of the distribution of characters and for systematics. These writers were accused by Beatty (1982) of being "pattern cladist". However, Mayr (1982) argued that we can establish a meaningful classification of organisms only when historical processes are reconstructed, taking into account the fossil record, weighing the characters in order to arrive at a "classification of organisms that is based on the theory that the relationships of organisms is due to common descent". Mayr also claimed that a classification founded only on characters would lack "biological meaning", remaining very similar to a classification of inanimate objects (Brady 1984). "Pattern" cladists, have radicalized the method and modified the terminology. A plesiomorphous character becomes *general* and an apomorphous characteristic *particular* or *special*. Synapomorphy becomes the equivalent of homology, since non-homologous characters are left aside. It follows that the only way to assess the hierarchy or polarity of homologies is by ontogeny and the concordance (or congruence) of the characteristics invoked.

The "pattern cladists" relay on the convergence of a majority of homologies to support phylogenetic relationships, and arrive from this at the *principle of* *scores*. The example of the relations between birds and mammals gives some idea of this. The birds constitute a monophyletic group, its sister-group classically being that of the crocodiles. Gardiner comparing birds and mammals, found a greater number of apparent synapomorphies between birds and mammals (17) than between birds and crocodiles. These synapomorphies relate to the anatomy of the soft parts and to physiology, not observable in fossils, where all the data contradict this hypothesis. For Gardiner the principle of parsimony supports the bird-mammal relationship and the only possible refutation is to demonstrate the existence of at least 18 synapomorphies between birds and crocodiles. This quite aberrant result shows the importance of definition of characteristics, so as to know if they are correlated or not, and what weight they have in relation to each other.

1.3.4 Phenetic Taxonomy

Sokal and Sneath (1963) have proposed a system of classification without phylogenetic implications. Using the greatest possible number of characters regarded as equally significant among themselves, they have initiated data-processing programs for the establishment of phenograms (Fig. 1.1:10) and the cladograms used by cladists (Wagner trees). Without any regard for the state of the characters (apomorphous or plesiomorphous), they consider the absence of a character just as if it were a character. It is a matter of establishing a classification which explains the greatest number of characters without taking account of proper balance, correlated characters or convergences. Phenetic taxonomy does not offer very much of interest to evolutionists.

1.3.5 The Choice of a Phylogenetic Systematics and Evolutionary Mechanisms Analysis

It is clear that from a methodological point of view, systematics must be independent of theories of processes. O'Hara (1988), while studying systematics and evolutionary biology from the perspective of the philosophy of history, suggests that cladograms may be considered as *evolutionary chronicles* very different from *narrative evolutionary history* (interpretative or explanatory writing), and that systematics is the discipline which estimates the evolutionary chronicles.

For this reason, phylogenetic systematics, the cladistic approach, will be introduced first. This method has yielded enormous progress in groups where fossils are few and where the detailed evolutionary history cannot be reconstructed.

Secondly, the stratigraphical and biogeographical indications will be taken into consideration to arrive at phylogenetic trees and spatio-temporal scenarios. In these investigations of narrative evolution, comparative biology will be continuously coordinated with the findings of general biology indicative of processes.

A unique problem, which has caused many specialists to reject the cladistic approach, should be clarified : gradual series. As will be shown in Chapter 7, phyletic gradualism sequences have been conventionally divided into successive paleospecies by paleontologists. In fact, these paleospecies, considered from a spatio-temporal point of view, belong to only one species lineage and represent diverse evolutionary degrees of changes, as will be shown in Chapter 9. The controversy between evolutionists and cladists over these gradual lineages originated from the fact that the cladists were misinformed about the spatio-temporal concept. They considered each paleospecies of the continuum of the lineage as having as many divergences, even though only the species concept was considered, despite morphological changes over time. With this in mind, contradictions of cladograms, phylogenetic trees and historical scenarios are evident as the debate over the synthetic theory of evolution continues.

The purpose of this book is not only to provide the most recent classification using cladistics, but also to reconstitute the evolutionary diversifications, modalities, and rhythms of evolution using the vertebrate organizational plan in order to understand the mechanism. The fundamental role of morphological innovations and internal chronological developments, called heterochronies, will be analyzed in detail. They provide a mechanism that partly explains the morphological changes and discontinuities, without intermediates evident in the fossil record.

1.4 The Search for a Mechanism of Evolutionary Change: Heterochrony

"Heterochrony, the change through time in the appearance, cessation or rate of development (of ancestral characters) encompasses a series of patterns and processes of morphological evolution that can be recognized in fossils" (McNamara 1988).

According to shape, size and time dissociation there are six major heterochronic processes (neoteny, progenesis, post-displacement, acceleration, hypermorphosis and pre-displacement) and two global morphological expression: paedomorphosis and peramorphosis.

In *paedomorphosis*, the ancestral juvenile characters are retained in the adult descendant. It is produced either by progenesis, neoteny or post-displacement (Figs. 1.2; 1.3).

Progenesis is seen by premature appearance of sexual maturation (in the descendant) which curtails the development of the later ontogenetic stage. The result is a descendant of small body size which has the shape of the juvenile of the ancestral form. Progenesis affects the whole organism.

Neoteny corresponds to a reduction in the rate of morphological development affecting either the whole organism or a specific structure. The descendant has the same body size as the ancestor but the shape of a juvenile ancestor.

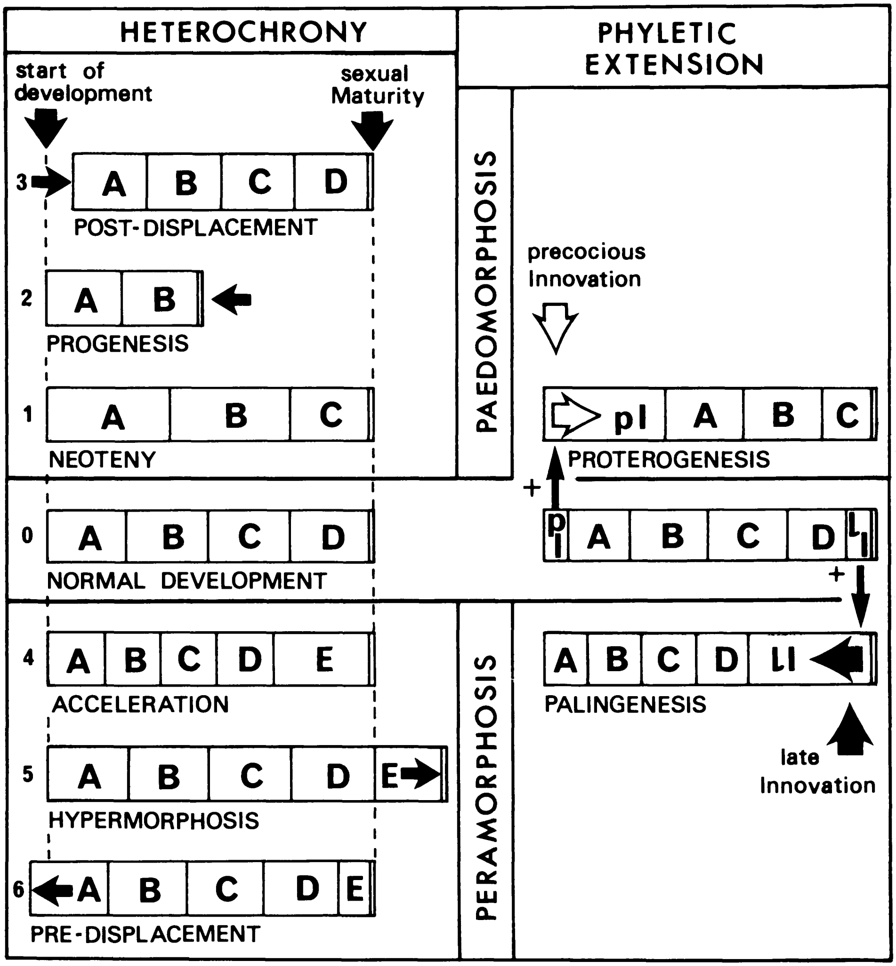


Fig. 1.2. Developmental heterochronies and innovations. The normal development of the individual is schematized at the *left center* (0) by a box (proportional to adult size) divided into four successive stages *A, B, C, D* (from fetus to adult) and may be altered by six types of heterochronie: **1** Neoteny (Kollman 1885). Reduction of rates of morphologic development affecting entire organism and producing a »retarded« adult whose characters remain juvenile. **2** Progenesis (Giard 1887). From a precocious appearance of sexual maturity there arises a small-sized adult possessing juvenile characters due to the truncation of development. **3** Post-displacement (Alberch et al. 1979). Delay in the start of development of certain structures in relation to global development results in the formation of a »retarded« adult with more juvenile characters than those of the ancestor with normal development. **4** Acceleration (Cope 1887). An increase in rates of morphologic development affecting the whole organism or only certain structures prolongs development until a more advanced morphologic stage (*E*) than that of the ancestral adult. **5** Hypermorphosis (de Beer 1930). Delayed appearance of sexual maturity permitting longer development of the individual, resulting in a hyperadult morphology (*E*) and greater size. **6** Predisplacement (Alberch et al. 1979). The start of ontogenetic development of an organ is advanced compared with that of the normal development of the organism. The arrow *»start of development«*

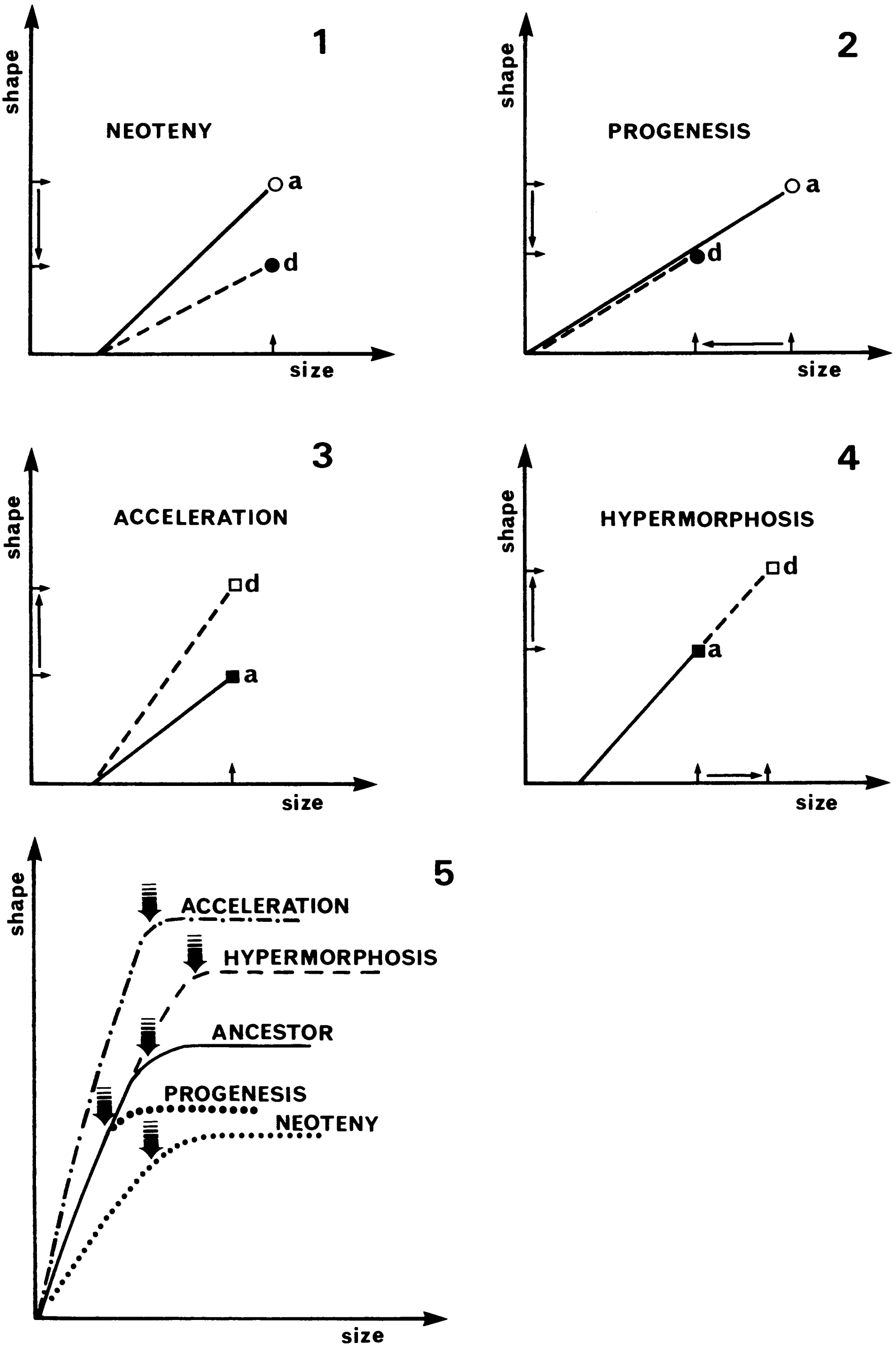
Post-displacement affects only a particular structure by late onset of its growth. Thus the descendant has the same size and shape as the ancestor except for the post-displaced structure which is less advanced and looks like the juvenile of the ancestor.

Peramorphosis, characterized by the earliest appearance of adult ancestral characters in descendant juveniles, may occur either by hypermorphosis, acceleration, or pre-displacement.

Hypermorphosis results by extending the juvenile growth period by a delayed onset of sexual maturation. Since it affects the whole organism, the descendant would have a larger size and a hyper-adult shape of the ancestor.

Acceleration, is the opposite of neoteny. The acceleration of morphological development increases the degree of allometry and the rate of production of hyper-adult structures, the size being stable. It affects either the whole organism or only a single structure.

indicates the commencement of development of a chain of characters. Extension in geologic time (phyletic) of the first three types of heterochronies (*1* to *3*) results in paedomorphosis, that of the last three types (*4* to *6*) to peramorphosis. Normal development may also be altered by innovations, precocious (*pI*) or late (*lI*). If a precocious innovation appears in a paedomorphic line, it leads to a proterogenesis, while a late innovation in a peramorphic line leads to a palingenesis. (Table based on Dommergues *et al.* 1986; McNamara 1986)


1
NEOTENY
shape
size
a
d
2
PROGENESIS
shape
size
a
d
3
ACCELERATION
shape
size
d
a
4
HYPERMORPHOSIS
shape
size
d
a
5
shape
size
ACCELERATION
HYPERMORPHOSIS
ANCESTOR
PROGENESIS
NEOTENY

Pre-displacement is characterized by the earlier onset of a particular structure, the whole organism maintaining a normal development rate. The descendant is the same as the ancestor except for the particular structure which is larger and more advanced than the equivalent in the ancestor.

Heterochrony seems to have played a major role in evolution, in generating speciation and in morphological trends, as well as large morphological discontinuities without missing links. It may explain also changes of ecological zones by alteration of developmental processes, when ancestral juvenile and adult living in water and on earth, respectively, in the descendants, are restricted to only one biotope (see Chap 4).

Fig. 1.3. Chronological shifts in development (heterochronies). As in the preceding figure, these five sketches illustrate changes in the ontogenetic development. Here the curves (or paths) of development of the ancestor (*a* in sketches 1–4) serve as reference for showing the results of the respective changes: **1)** Neoteny: retardation of development without modification of the appearance of the sexually mature stage, resulting in an adult descendant of same size as the ancestor, but with a morphology ressembling that of a juvenile form of the ancestor. **2)** Progenesis: the set-in of early sexual maturity blocked or terminated by development, resulting in a smaller adult descendant with the morphology of a juvenile form of the ancestor. **3)** Acceleration: accelerated development results in an adult individual of the same size as the ancestor, but with a new morphology »beyond« that of the ancestor. **4)** Hypermorphosis: slowing down the appearance of sexual maturity allows the individual to continue its growth for a long time, leading to a larger adult with a morphology »beyond« that of the ancestor. **5)** Comparative scheme of deviations from the development path vs. normal ancestral development, illustrating the shift of sexual maturity (vertical black arrow) and differences in size and morphology of the adult descendants. (1–4: after P. Alberch, S.J. Gould, G. Oster, and D.B. Wake; 5: modified after K.J. McNamara).

CHAPTER 2

The Vertebrates

2.1 The Vertebrate Organization Plan

The vertebrates are multicellular animals, *Metazoa*, whose body is surrounded by a protective envelope enclosing internal systems allowing nutrition, respiration, the elimination of excreta and reproduction (Grassé and Devillers, 1965; Grassé, 1979; Beaumont and Cassier, 1987). They are animals with *bilateral symmetry* which derive their name from the presence of a *dorsal notochord* around which there is formed a metamerized skeletal axis, the *vertebral column*. The dorsal notochord is a flexible strand which exists in every vertebrate embryo, but while it persists in the adults of the lover vertebrates (Cyclostomes), it rapidly disappears in the higher vertebrates. There it regresses progressively under the influence of the development of the cartilaginous or bony vertebral column that surrounds it.

Above the dorsal notochord is situated the nervous system, consisting of an *encephalon* or brain in front and extending backwards as the *spinal notochord*. Ten to 12 pairs of cranial nerves and the spinal nerves emerge from these two nerve centers respectively. The brain is surrounded by a periencephalic skeleton, or *cranium* (skull).

The body of a vertebrate consists of three successive parts: the *head, trunk,* and *tail*.

Below the dorsal notochord there develop the *digestive tube* and the *circulatory system*.

The *integuments* consist of a multilayered epidermis lined with a dermis.

In the chambered *eyes*, the retina is derived directly from the encephalon. *Auditory organs* complement these visual organs in the Tetrapoda.

These characteristics are more or less useful in the field of paleontology as governed by the conditions of fossilization of the skeleton. Other vertebrate characters such as the structure of the liver, the presence of differentiated endocrine glands, a muscular heart, hemoglobin, kidneys, genital organs, and striated muscles, are not accessible to paleontologists. However, they will be taken into account in the cladistic analysis of the phylogenetic relationships of groups on the basis of existing forms.

The division of the body into three regions is one of the most important characteristics of vertebrates for paleontologists, whose researches are necessarily usually limited to the skeleton.

The bony tissue characteristic of vertebrates can develop either from or on a cartilaginous matrix (endochondral mode) in the origin of the endoskeleton, or from connective tissue (dermal type) leading to the exoskeleton. The trunk is bounded in front by the articulation of the cranium with the vertebral column, and behind at the cloaca. The trunk carries paired appendages (fins or limbs) and unpaired appendages (fins). The two pairs of paired appendages are supported by an appendicular skeleton and connected by the pectoral girdle. In the Tetrapoda the pelvic girdle marks the boundary between the trunk and tail. In the mammals, the trunk is divided into a thoracic region supported by the ribs in an anterior position and an abdominal region, separated by the diaphragm. In the vertebral column, this division is into thoracic and lumbar regions.

The tail is supported by the vertebral column. In the lower vertebrates, the respiratory system consists of gills fixed on branchial arches; the other vertebrates have lungs. Further anatomical details can be found in summaries of the zoology of vertebrates (Grassé and Devillers 1965; Grassé, 1979; Beaumont and Cassier 1987). The osteologic data will be dealt with during the description of the different groups.

2.2 Origin of Vertebrates

2.2.1 The Chordata

The origin of the vertebrates is a much-discussed problem which is not yet entirely resolved. The vertebrates constitute a sub-kingdom of the chordates with the urochordates (tunicates) and the cephalochordates (lancelots). In the embryonic state they share in common a postanal tail, a notochord, a hollow neural axis dorsal in relation to the notochord and a ventral digestive tube expanded in front into a pharynx pierced with openings. The structure of the pharynx is associated with microphagous feeding by filtration of water as observed in the tunicates, lancelots, and the larvae of lampreys. The origin of the vertebrates is poorly documented since the forms ancestral to those provided with a skeleton were soft and not fossilized. A hypothesis put forward by Jefferies (1968) took the view that the vertebrates were derived from a particular group of echinoderms, the calcichordates of the Ordovician, a theory rejected as founded on erroneous anatomic observations. The current approach to this problem is based on comparative anatomy and embryology. The presence in embryos of characters such as the notochord or pharyngeal pouches, which may disappear in the adults, makes it possible to assess phylogenetic relationships. In particular, resemblances have been noted between the larvae of the Holothuria (echinoderms) and those of *Balanoglossus*, a hemichordate. It has been suggested that the vertebrates may have resulted from a heterochrony of development, in particular a neoteny or a progenesis. This would mean that the adult vertebrates have preserved the intensified larval morphology of the ancestral forms (Devillers, 1981).

The origin of the chordates is another problem. With the hemichordates (Enteropneustes, Pterobranchs, Graptoliths) and the echinoderms, the chordates constitute a larger group, of those animals where the mouth is formed at the emplacement of the blastopore, or else may be a new formation. The Chordata have been linked with the Hemichordata by zoologists because of the presence of branchial orifices.

2.2.2 Scenario and Phyletic Relationships Among the Chordata

It may be imagined that, about 500 Ma ago, a primitive chordate began to swim by undulation of its trunk. The posterior trunk then lost its original role, which was to allow creeping on the sea floor. Fixation by the trunk in the juvenile stage was abandoned and the trunk became a real tail. The skeleton was lightened by the loss of calcite. The tunicates were derived from a form of this type, adopting a sedentary life. The lancelots (*Amphioxus*) specialized in a burrowing existence. Others continued to swim and became more symmetrical and their nervous system more complex. Finally acquiring a phosphated bony skeleton, these swimmers became the first vertebrates. Whereas until quite recently the lancelets were still considered as more skin to the vertebrates than the tunicates, the type of innervation of the muscles seems to prove the contrary. In *Amphioxus*, the nerves are connected to the muscles by a strip of muscle tissue as in the echinoderms, whereas

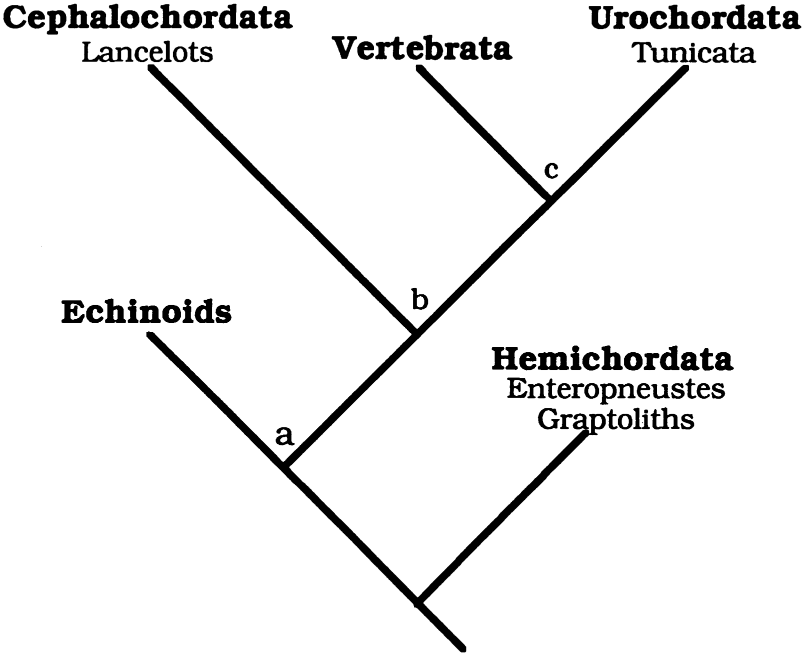


Fig. 2.1. Phylenogenetic relations of the Chordata. Appearances of characters: *a* calcareous skeleton; *b* straight gill slits; *c* lateral line. (After Jefferies 1981)

the tunicates and vertebrates have the nerves directly connected to the muscles. Thus the vertebrates would have closer affinities with the tunicates than with the lancelots. Figures 2.1 is a cladogram expressing the phyletic relationships between the chordates after the data of Jefferies (1981).

2.3 Diversity of Vertebrates

The diversification of living species on earth is altogether extraordinary, to the extent that evaluation of the number of species varies from one author to another. In general terms, there is agreement on the existence of over a million animal species and half a million plant species. Some specialists estimate that there are at least a further million living species to be discovered. While more than 300,000 fossil species have been identified, some authors assess at more than one or two billions the number of species that have lived during the 4000 million years of the history of the earth.

These figures express the succes of biologic evolution. What do the vertebrates represent within this gigantic biomass? The number of living vertebrates is assessed at more than 40,000 species, while at least 16,000 fossil species have been described. There is an ambiguity in the listing of living species due to the fact that specialists are not always agreed on the status to be applied to a form, whether species or subspecies. As for the fossils, many of the names of species established in a typological concept of the species must be regarded as synonyms. This is therefore an order of magnitude to be taken with reserve. Their ancestors being marine, the vertebrates originated in a marine environment but very rapidly conquered the freshwater and then the different biotopes of the continental environments. The diversification of the vertebrates results from an essentially contingent evolution in which circumstances have played a fundamental part. This diversification has been carried out in the shifting framework of the formation and displacement of the continents under the influence of plate tectonics. Temporal and spatial distribution and the evolutionary history of groups have been conditioned, at least in part, by the history of the oceans and continents.

2.4 Temporal Distribution of Vertebrates

The oldest certain remains of vertebrates known date from the upper Cambrian and lower Ordovician. They are fragments of dermal skeleton attributed to the group of the Heterostraci, of the Agnatha. It was at the same epoch that there appeared the thelodonts and other jawless vertebrates, the pteraspidomorphs. But the main development of jawless vertebrates is found in the Silurian, where the Osteostraci and the Anaspidae (cephalaspidomorphs) appear. The first Gnathostomes are represented by the Acanthodia. The placoderms and Actinopterygii were differentiated at the end of the Silurian.

The Devonian is an important epoch in the history of the vertebrates. Apart from the presence of the jawless vertebrates, which disappeared for the most part at the end of this stage, and the abundance of the Actinopterygii, the individualization of the Sarcopterygii is to be noted. The development of the old red sandstone strata seems to have played a major part in the conquest of the terrestrial environment, the osteolepiforms having given rise to the first Tetrapoda at the end of the Devonian. It was also during the Devonian that the Chondrichthyes (elasmobranchs and Holocephali) became individualized. In the Carboniferous there appeared the first Amniota, truly independent of the aquatic environment (cotylosaurs). The Permian was a period of expansion for the Amphibia, the Amniota and the ancestral lines of the mammals (pelycosaurs and Therapsidae). A thecodont of the ancestor group of the two great divisions of dinosaurs is known in the upper Permian.

The Triassic was a great epoch for vertebrate radiation. It was then that the plesiosaurs and ichthyosaurs appeared in the marine environment, and the turtles, lizards, crocodiles, pterosaurs and the two great groups of dinosaurs. Finally there appeared the primitive mammals, triconodonts and symmetrodonts.

In the Jurassic and Cretaceous, the terrestrial environment was dominated by the dinosaurs; there was also an unobtrusive development of the multituberculate mammals and the Pantotheria. The pterosaurs shared the aerial environment with the first birds.

The end of the Cretaceous was marked by the disappearance of a large number of groups: plesiosaurs, ichthyosaurs, pterosaurs, and dinosaurs.

The Tertiary was characterized in the terrestrial environment by the radiations of the mammals, some of which, such as the bats, were to conquer the aerial environment. Alongside certain groups of mammals which colonized the marine environment there should be noted the great radiations of teleost fish. Finally, in the Quaternary, the human line, properly so-called, emerged from the primates. Thus the history of the vertebrates covers a period of about 480 Ma, in which successive groups had increasingly complex structures. This briefly related history did not unfold regularly; periods of crisis can be distinguished, with extinctions, and periods favorable to radiations. This history is explained by that of the terrestrial continents and oceans that have partly conditioned it.

2.5 Spatial Distribution of Vertebrates

The spatial distribution of the vertebrates forms the subject of *paleobiogeographic* studies and provides an understanding of the often complex history of the groups. The geographic distribution of existing groups often differs from the one they had during more ancient geologic periods. For example, in the Eocene the lemuriforms had a wide distribution which covered Europe and North America, whereas they are now restricted to Africa, notably to Madagascar and southern India. Present-day marsupials are confined to Australia, Tasmania, New Guinea, and South America, but in the Tertiary they had a vast distribution in South and North

America, which also extended to Europe, Asia, and even North Africa, where they have been discovered quite recently. Their history, like that of many other groups, cannot be understood without a knowledge of the paleobiogeography at different epochs and the demonstrations of immigrations. Conversely, the distribution of vertebrate remains throughout the world proves to be an excellent test for the hypotheses of plate tectonics. The present distribution of the continents results from displacement of the two great continental masses which existed in the middle of the Jurassic: *Laurasia* in the north and the territory of Gondwana in the south, separated by the *sea of Tethys*. In the Triassic, these two vast continents were joined in a single continental mass, the *Pangaea*. The Pangaea resulted from the collision of a vast southern continent and three isolated northern continental masses in the Carboniferous.

In each continental mass, the climates at the different epochs were sufficiently different to play a part in the distribution of species. The present situation is only a momentary phase, transient in the history of the earth. The existing distribution of biogeographic zones is that of the interglacial phase in which we currently exist. It differs from that which existed at the maximum of the last glaciation 20,000 years BP (Before Present). This paleobiogeographic history has conditioned the development of the different groups, their distribution and their adaptations.

2.6 An Attempt at Vertebrate Classification

As discussed in Chapter 1.3, a classification must include only strictly monophyletic taxa. Hennig (1950) pointed out that all members of a given taxonomic group descend from a single ancestor, the ancestor itself being included in the taxon.

The classification adopted is a modified synthesis of Schoch (1984), including also reviews of Janvier (1986) for Agnatha and Sarcopterygii, of Patterson (1982) for Actinopterygii, of Panchen (1985) for Amphibia, of Gaffney (1975) for Eureptilia (Diapsida and Synapsida), of Benton (1985) for the classification of Diapsida, of Gauthier and Padian (1984) for Archosauria, as well as personal ideas from O. Rieppel for Euryapsida (Sauropterygia and Placodontia). This classification has attempted to reflect the phylogeny. In order to avoid a complex nomenclature of categorical ranks, a numerical code system is used from lower numbers to higher, more inclusive ranks, as suggested by McKenna (1975).

Chordata
1-Urochordata (= Tunicata)
2-Ascidiacea-ascidians, sea squirts
2-Thaliacea-salps and doliolids
2-Larvacea-appendicularians
1-Cephalochordata-Acrania, amphioxus, lancelots
1-Craniata
2-Myxinoidea-Cyclostoma, in part-extant hagfishes, slime hags

2-Vertebrata
3-Pteraspidomorphi-Agnatha, in part-primitive jawless fishes
4-Heterostraci
4-Thelodonti
3-Myopterygii
4-Cephalaspidomorphi-Agnatha, in part
5-Petromyzonida-Cyclostoma, in part-lampreys
5-Osteostraci (= Cephalaspida)-armored jawless fishes
5-Anaspida-armored jawless fishes
5-Galeaspidida
4-Gnathostomata-jawed vertebrates
5-Elasmobranchiomorphi
6-Placodermi
7-Arthrodira
7-Ptyctodontida
7-Petalichthyida
7-Rhenanida
7-Antiarchi
7-Acanthothoraci
6-Chrondrichthyes-cartilaginous, jawed fishes
7-Elasmobranchii-sharks, rays, sawfishes
7-Holocephali-chimaeras
5-Teleostomi
6-Acanthodii-spiny sharks
6-Osteichthyes-bony fishes and tetrapods
7-Actinopterygii
8-Cladistia (*Polypterus*)
8-Actinopteri
9-Chondrostei
9-Neopterygii
10.Ginglymodi (*Lepisosteus*)
10-Halecostomi
11-Halecomorphi (*Amia*)
11-Teleostei
7-Sarcopterygii
8-Onychodontiforme
8-Actinistia (=Coelacantiformes)
8-Porolepiformes
8-Osteolepiformes (*Eusthenopteron*)
8-Dipnoi-lungfishes
8-Tetrapoda
9-Ichthyostegalia (paraphyletic)
9-Temnospondyli (paraphyletic, questionably assigned here)
10-Palaeostegalia (*Crassigyrinus*)
10-Loxommatoidea

10-Lepospondyli (paraphyletic)
11-Nectridea
11-Aistopoda
11-Microsauria
10-Lissamphibia
11-Anura-frogs and toads
11-Urodela-salamanders
11-Apoda-Gymnophiona-Cecilians
10-Anthracosauria (questionably assigned here)
11-Herpetospondyli
11-Embolomeri
11-Gephyrostegoidea
11-Seymouriamorpha (*Seymouria*)
11-Diadectomorpha ?
10-Amniota
11-Anapsida (paraphyletic group questionably assigned here), Captorhinomorpha
11-Chelonia-turtles
11-Eureptilia
12-Diapsida
13-? Ichthyosauria
13-Euryapsida
14-Sauropterygia
14-Placodontia
13-Lepidosauromorpha
14-Younginiformes
14-Lepidosauria
15-Sphenodontia (*Sphenodon*)
15-Squamata
16-Sauria-lizards
16-Serpentes-snakes
13-Archosauromorpha
14-Pterosauria-flying "reptiles"
14-Rhynchosauria (*Scaphonyx*)
14-Archosauria
15-Crocodilia
15-Dinosauria-dinosaurs, in part
16-Saurischia
16-Ornithischia
16-Aves-birds
12-Synapsida
13-Pelycosauria
13-Therapsida
13-Mammalia-mammals
14-Prototheria-Multituberculata, Monotremata
14-Theria

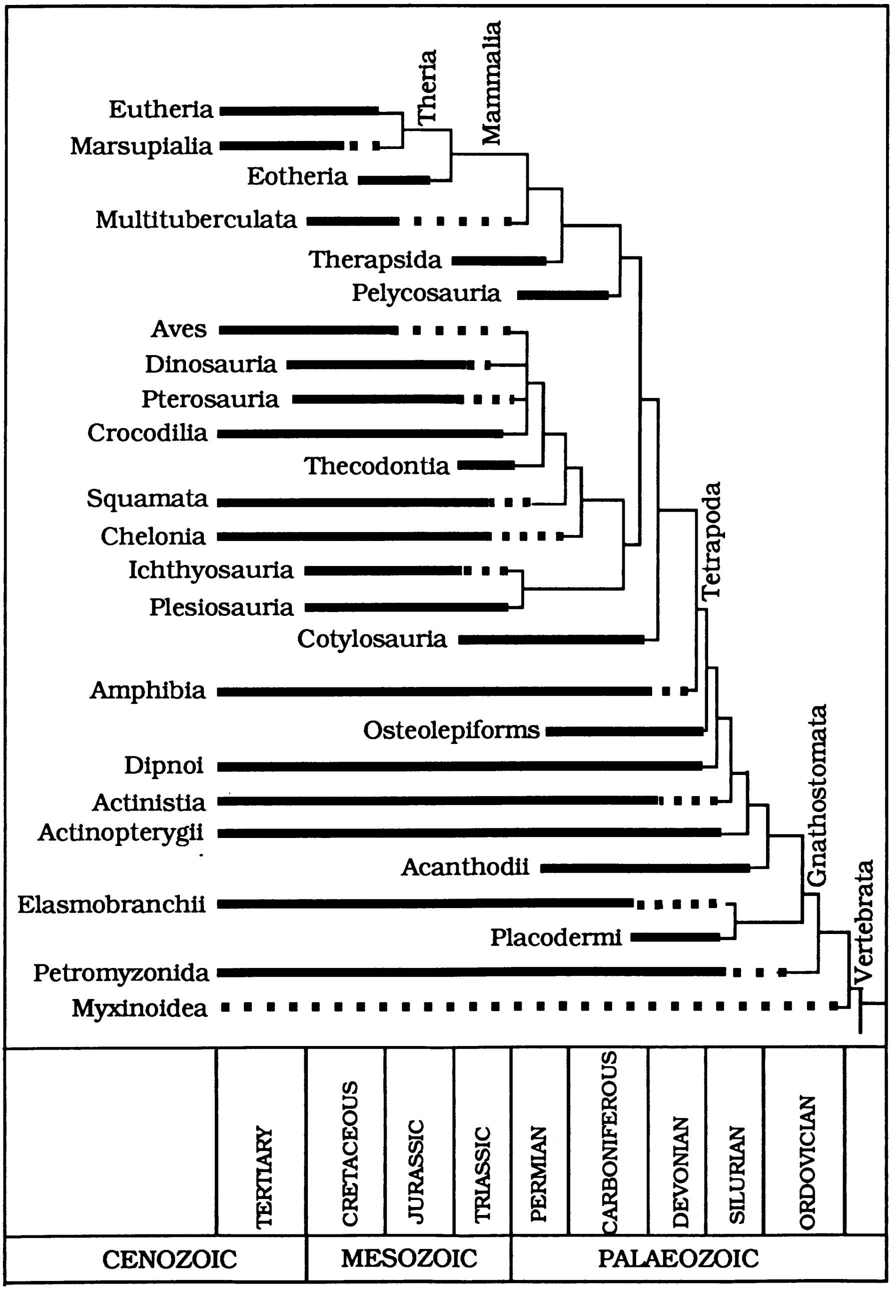


Fig. 2.2. Phylogenetic relationships of the principal groups of vertebrates in their chronologic framework. (After Forey 1980)

15-Marsupialia (=Metatheria)-marsupials
15-Eutheria-placental mammals

This attempt at classification relating phylogenetic relationships of the principle groups of vertebrates is presented in Fig. 2.2. Since many relationships are very uncertain and controversial, alternative classifications are possible. A certain number of exclusively fossil groups such as Temnospondyli, Anthracosauria, Anapsida, still appear as entirely heterogeneous (paraphyletic) "wastebasket" groupings, i.e., groups for gathering together genera and species of ill-defined relationships.

Some groups of unknown relationships, such as Anthracosauria, Lepospondyli, Ichthyosauria, Plesiosauria, Placodontia and Crocodilia are assigned to their proposed group place with a certain degree of doubt.

This classification differs considerably from the traditional classification of fish, amphibia, reptiles, birds, and mammals and *should not be regarded as definitive*. Since there are no reptilian characteristics, there is no longer any justification for the class of reptiles and it is replaced by the collection of groups that it used to include.

CHAPTER 3

The Conquest of the Aquatic Environment

3.1 The First Vertebrates

The vertebrates discovered in the upper Cambrian and lower Ordovician are animals without jaws (Agnatha), the first vertebrates with jaws (Gnathostomes) not being identified until the lower Silurian, that is at least 50 Ma later. These two groups have anatomically different structures (Fig. 3.1) corresponding to two modes of nutrition: microphagous for the Agnatha, macrophagous for the Gnathostomes. The first Gnathostomes were the fishes. It should be specified here that the popular sense of the term "fish" applies to free aquatic vertebrates with "cold blood" (the tunnies are warm-blooded as an exception in the group, since only the mammals, birds, and possibly the dinosaurs have acquired this characteristic), gills, and fins, a description applying to both the Agnatha and the fishes. The term "fish" has some validity in systematics, but it designates a group which cannot be characterized by the presence of a specific character, a paraphyletic group. The presence of a rigid exoskeleton led to the first vertrebrates being qualified as armored Cyclostomes or Ostracoderms. This term groups together the Heterostraci, the Osteostraci, and even the Anaspidae.

This difference in appearance between Agnatha and Gnathostomes in the fossil record led specialists to consider the agnathous condition as primitive in relation to that of the Gnathostomes. In fact, the arguments advanced have been refuted and it is often believed that the Agnatha and the Gnathostomes constitute two divergent specializations emerging from a common ancestor. The proof is given by the position of the gills, which develop on the internal border of the branchial arches in the Agnatha and towards the exterior in the Gnathostomes. This differentiation between the two positions of the gills comes to us from Goette (1901), amplified by Severtzov (1916) and elevated to a quasi-dogma by Stensiö (1927) and Jarvik (1960). In the lampreys there exist pigment cells on the gills, indicating a contribution from the neural crest (ectodermal), but it should be borne in mind that the ectodermal origin of the gills in the Gnathostomes is reliable only in the Osteichthyes. In the Chondrichthyes the gillslits open before the formation of the gills, thus facilitating exchanges between endoderm and ectoderm. Thus, it is impossible to determine the tissue origin of the gills with any certainty (Fig. 3.1). In any case, these relations are still very disputed. Lövtrup (1977), Janvier (1981), Mallatt (1984) etc. consider that the Agnatha are paraphyletic, but the contrary opinion can also be defended.

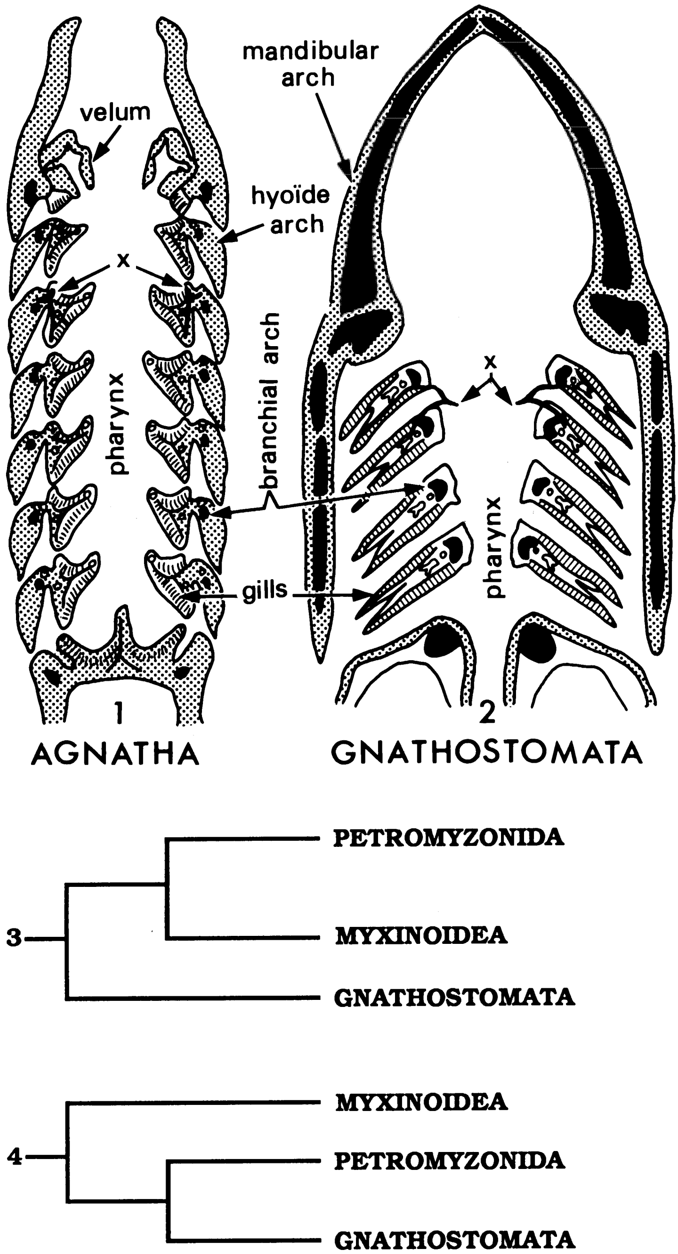


Fig. 3.1. Frontal sections of the branchial regions of an agnath (*1*) and of a gnathostome (*2*) showing the different positions of the gills. x: first visceral trunk of the vagus nerve, which innervates the preceding gill in the gnathostomes. *Below* the two most plausible phylogenies of existing Craniata, the cyclostomes being either monophyletic (*3*) or paraphyletic (*4*). *1–2* after Jarvik (1960); *3–4* after Janvier (1986)

3.2 Relationships of Agnatha

The Agnatha are a group without much documentation from the paleontological aspect because of the rarity of deposits favorable to their preservation. Therefore it remains impossible to reconstruct their history. The introduction of the cladistic approach has made it possible to specify relationships of the main groups. The cladogram in Fig. 3.2 illustrates the concepts of Moy-Thomas and Miles (1971), while those of Figs. 1.2. and 3.1: 4 express the concept of Janvier (1981), according to which the Agnatha are paraphyletic. Whereas in the traditional classifications the myxines and lampreys, sole survivors of the Agnatha, were grouped together and opposed to the Gnathostomes, it was noted that the lampreys (Petromyzontidae) shared with the Gnathostomes around 50 synapomorphies unknown in the myxines: muscles attached to the rays of the fins, a divided hypophysis, cardiac innervation, a pineal eye and, especially, vertebral elements. It follows that the myxines constitute a group apart, of which the other Agnatha and the Gnathostomes would be the sister group. The cladogram of Janvier (1981), by placing the Heterostraci in the position of a second-rank sister group to the rest of the Agnatha-Gnathostomes, renders obsolete the old group of Cyclostomes, which, including the myxines, henceforth appears as a paraphyletic group. Moreover, the position of the Heterostraci is still very uncertain.

The conodonts are attached to the Agnatha by some specialists and may be placed between the myxines and the Heterostraci. The Osteostraci, possessing paired fins like those of the more archaic Gnathostomes, are regarded as the third-rank sister group of the Gnathostomes, but close to the lampreys, with whom they share some derived characteristics.

3.3 Myxines

These are the most primitive existing vertebrates. *Gilpichthys*, an enigmatic vertebrate of the Middle Carboniferous from Illinois, has been interpreted as a fossil myxine by Janvier (1981), but an undeniable myxine has been discovered in the same deposit by Bardack (1985). There has been an attempt to join them with the Pteraspidomorpha by virtue of the analogous position of the hypophyseal opening; but, given the absence in the myxines of any rudiment of the vertebral elements present in the lampreys and homologous with those of the Gnathostomes, Janvier (1981) suggests restricting the taxon of the vertebrates to the lampreys and Gnathostomes only, leaving the myxines as no more than the sister group of the vertebrates within the Craniata.

3.4 Conodonts

The conodonts are known from the Cambrian to the Triassic and their diversity makes them very useful in biostratigraphy, but their affinities remain obscure.

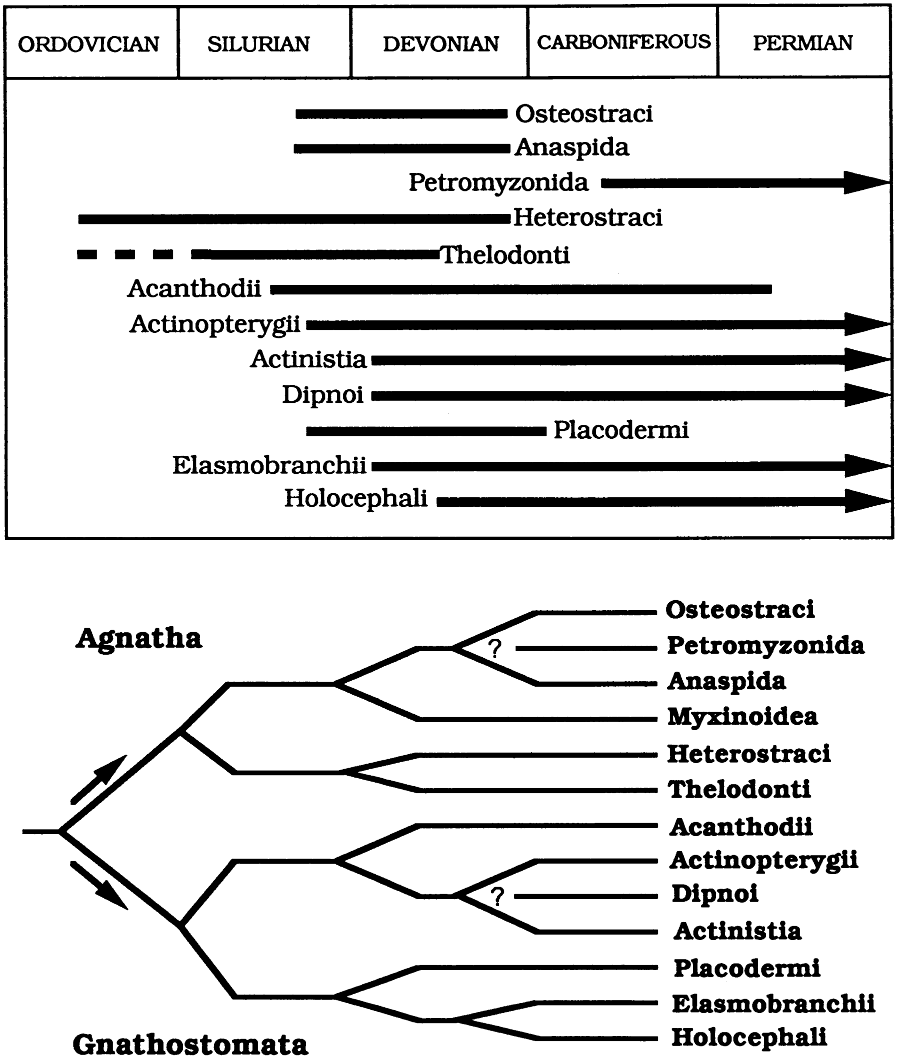


Fig. 3.2. Stratigraphic distribution of the principal groups of fish during the Paleozoic (*above*) and their phyletic relationships (*below*). (After Moy-Thomas and Miles 1971).

The discovery of four specimens preserving the soft parts in the Carboniferous at Granton (Edinburgh, Scotland) has enabled Aldridge et al. (1986), Derek et al. (1987) to show that by their V-shaped somites, the transversely operating nutrient apparatus, and the presence of fins in the caudal region, the conodonts would have more affinities with the agnathous Craniata than with the Cephalochordata (*Amphioxus*). These affinities with the chordates have been challenged by Tillier and Cuif (1986), for whom the conodontes represent the mouth pieces of the aplacophore molluscs. On this very uncertain affinity with the chordates, the conodonts could be considered as a separate group from the Agnatha, whose relations with the Myxinoidae and Heterostraci remain uncertain.

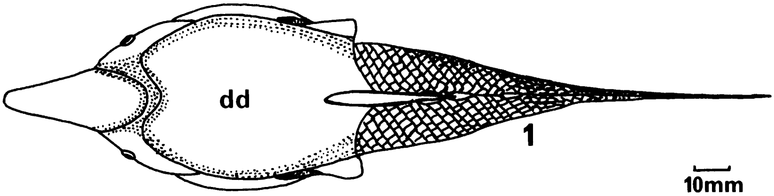
3.5 Pteraspidomorpha

3.5.1 Characteristics

These are Agnatha which seem to have a pair of orifices and nasal sacs like the Gnathostomes. No dorsal hypophyseal duct can be seen. It should open in the roof of the buccal cavity between it and the rostrum in a position identical to that of the myxines. The rostral region is formed by the anterior part of the head. The absence of an ossified endocranium denies us any knowledge of their internal anatomy. On the other hand, they are covered by an exoskeleton composed of large plates and scales in the Heterostraci and of superficial denticules in the Thelodonti. As a rule, the Heterostraci possess only one pair of branchial openings, whereas there are several in the thelodonts.

3.5.2 Heterostraci

The oldest vertebrate remains known are attributed to the Heterostraci. There have been ascribed to them isolated fragments of plates derived from the greensand of Estonia (lower Ordovician): *Palaeodus* and *Archodus*, but these doubtful remains could have derived from a "pollution" by material of the upper Devonian outcropping into the quarry. The most convincing vestiges are *Arandaspis* of the Ordovician of Australia, *Eriptychius* and *Astraspis* of the middle Ordovician of the United States and, especially, *Sacabambaspis* of the lower Ordovician of Bolivia, known from absolutely complete specimens (Gagnier et al. 1986). They developed in the Silurian and died out in the upper Devonian. Their average size was 30 cm but some attained 1.5 m. The head and anterior part of the trunk were flattened dorso-ventrally, giving the body the appearance of a ray. A shield formed by a variable number of bony plates surrounded the head and the front of the trunk (Fig. 3.3). The exoskeleton was prolonged in front by a rostrum overhanging the anteriorly and ventrally placed buccal orifice. The lateral eyes were small and well separated. The pineal orifice was dorsal. The gills opened to the exterior by



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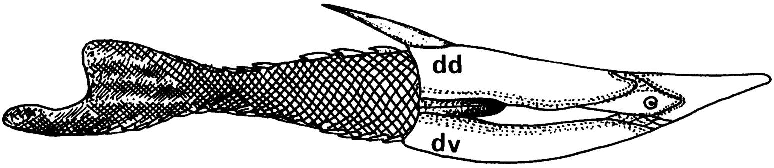

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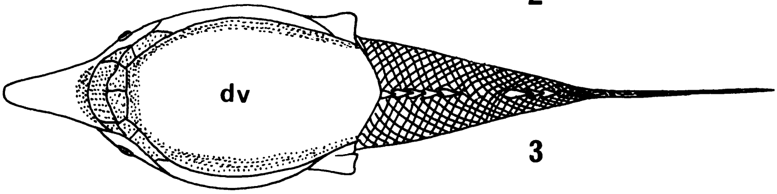

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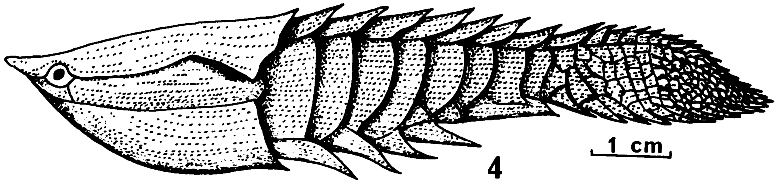

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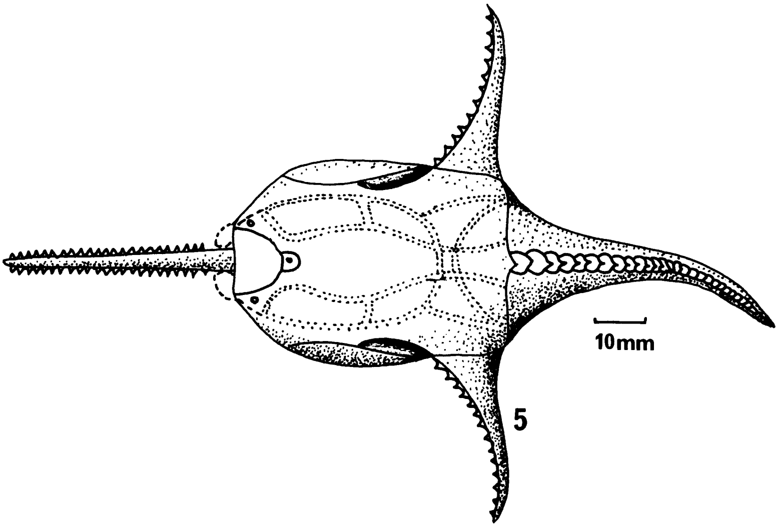

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a single branchial orifice. The endoskeleton is not known, but certain structures can be reconstructed from the impressions left on the internal parts of the dorsal and ventral cephalic shields. The system of the lateral line consisted of two pairs of canals, dorsal and ventral, opening externally by pores. Unlike the dorso-ventrally flattened anterior part, the posterior part was compressed laterally. The tail was almost homocercal. There were neither dorsal, anal, nor paired fins.

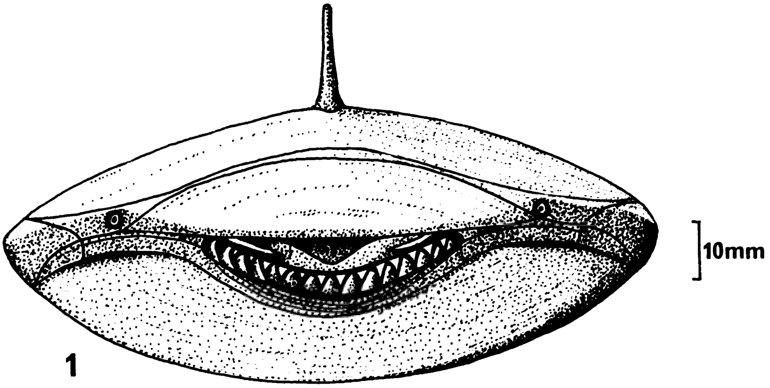
The oldest forms, like *Astraspis* and *Eriptychius*, had shields composed of separate plates, but the more recent Heterostraci had a shield formed of two independent parts. A large dorsal spine was supported on the posterior part of the dorsal shield (*Errivaspis waynensis* = *Pteraspis rostrata*). The Heterostraci include quite a large variety of forms (Fig. 3.3). *Doryaspis*, with mouth open dorsally, possessed a denticulated pseudorostrum emerging from the anterior edge of the ventral shield. The dorsal shield was prolonged laterally by a pair of long horns. Certain Pteraspidae, like *Drepanaspis gemuendenensis*, had a shield composed of several large plates connected by a mosaic of scales. Other Heterostraci of the lower Devonian and middle Devonian of the URSS had a pointed shield with the eyes close together (*Hibernaspis macrolepis*) or a very rounded shield (*Gabreyaspis tarda*, *Zascinaspis obtusirostrata*).

3.5.3 Thelodontia

These are Agnatha whose body is covered with denticules of placoid appearance found in the Ordovician and middle Devonian. Varying from 10 to 40 cm in size, and flattened dorso-ventrally, the thelodonts had well-spaced small lateral eyes (Fig. 3.4). The ventral mouth was placed far forward. The gills doubtless opened by a single lateral orifice. They had a lateral sensory line. The tail was hypocercal, its lower lobe being the larger. *Phlebolepis* had unpaired dorsal and anal fins, while *Thelodus* had only a dorsal fin. These animals also had a pectoral natatory apparatus comparable to but certainly not homologous with the brachial plates or the shield-horns of the Heterostraci, for the cornual plates of the Heterostraci appear only in the remotely derived pteraspidomorphs.

The thelodonts constitute a heterogeneous group, as shown by the diversity of histologic structure of their scales. They are a paraphyletic group whose various taxons can be related either to the Heterostraci (which is why they are described subsequently to these) or to the Anaspidae, Galeaspidae, Osteostraci, even the Gnathostomes (Janvier 1981). They lived in a littoral and freshwater environment on the bottom, searching in the mud for the small organisms that were their food.

Fig. 3.3. Heterostraci. **1, 2, 3** *Errivaspis waynensis* (= *Pteraspis rostrata*) in dorsal (**1**), lateral (**2**) and dorsal (**3**) view; *dd* dorsal disc; *dv* ventral disc; **4** *Anglaspis heintzi* lateral view; **5** *Doryaspis* sp. reconstruction in dorsal view (**1, 2, 3** after White 1935; **4** after Kiaer 1928; **5** after Heintz 1960)



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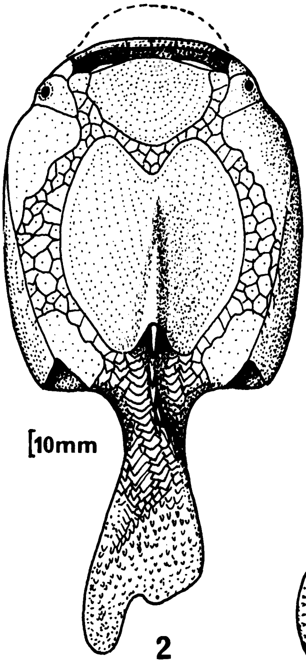

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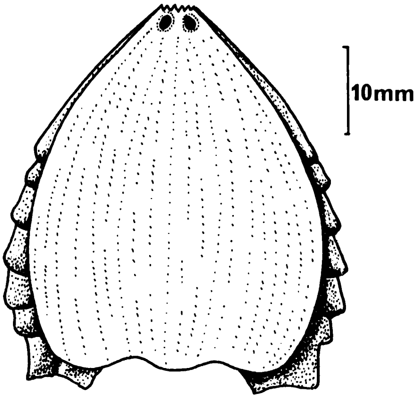

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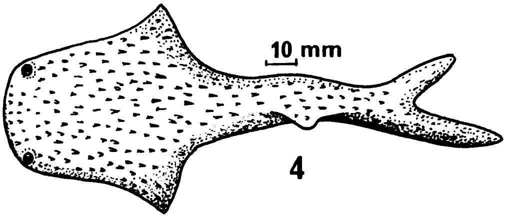

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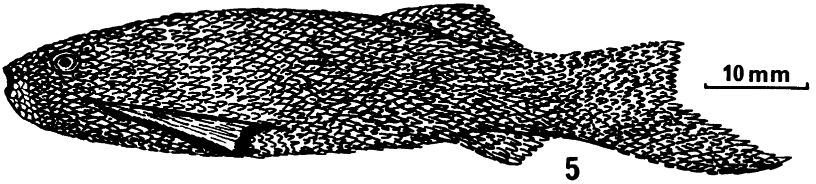

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3.6 Lampreys (Petromyzontidae) and Cephalaspidomorpha

3.6.1 Characteristics

The Cephalaspidomorpha are characterized by a single dorsal nasal and hypophyseal opening, the presence of numerous gills and a considerable number of external branchial clefts, reaching as many as 15. The embryologic development of existing forms seems to indicate that the presence of a single nasal opening is secondary and derived from a structure with paired openings and nasal sacs. Some forms possessed a rigid thick bony skeleton, the cephalic shield protecting the head and the anterior part of the trunk. On the ventral aspect the cephalic shield was pierced by an orobranchial fenestra closed by a membrane during life. The internal anatomy of these animals is quite accurately known, since the perichondral bone molded the brain and the cranial nerves and vessels, whose pathways have been established by the serial section method.

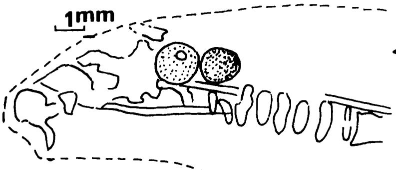
3.6.2 Lampreys

The existing lampreys or Petromyzontidae (*Petromyzon marinus*, *Lampetra fluviatilis*) have an eel-like body and a rounded mouth furnished with a sucker. In the adult state they are ectoparasites of fish, feeding by means of their rasping tongue. Their larva is microphagous and the passage to the adult state is associated with migration in the marine forms, though this is not the case for the exclusively freshwater *Lampetra planeri*. The first fossil lamprey known was discovered in the upper Carboniferous of Illinois (Fig. 3.5): *Mayomyzon pieckoensis* closely resembles *Lampetra*. *Hardistiella*, discovered subsequently in the lower Carboniferous of Montana (Janvier and Lund, 1983), preserved an anal fin that disappeared in *Mayomyzon* and existing lampreys.

3.6.3 Osteostraci

Distributed in the fossil record from the upper Silurian to the upper Devonian, the Osteostraci are the best-known group of fossil Agnatha. Their average size did not exceed 30 cm, with the exception of the middle Devonian form *Cephalaspis magnifica*, which reached 60 cm. The Osteostraci had a wide head, flattened

Fig. 3.4. Heterostraci and thelodonts. **1** *Zascinaspis obtusirostrata*, frontal view; **2** *Drepanaspis gemuendenensis*, dorsal view; **3** *Hibernaspis macrolepis*, shield in dorsal view; **4** *Longania scotica*, reconstruction in dorsal view; **5** *Phlebolepis elegans*, reconstruction in lateral view (**1**, **2** after Stensiö 1964; **3** after Obrutschev 1967; **4** after Traquair 1899; **5** after Ritchie 1968)



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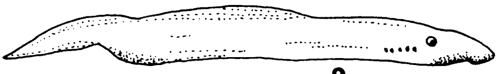

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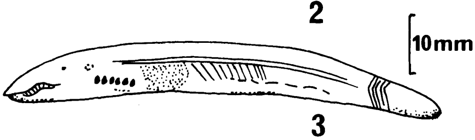

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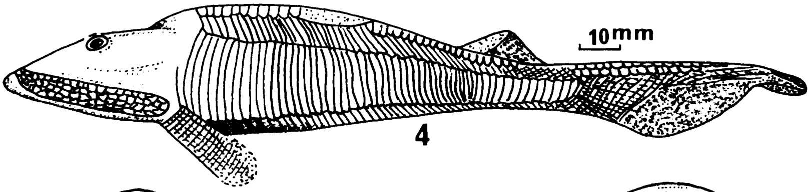

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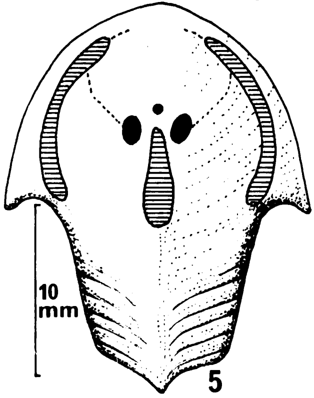

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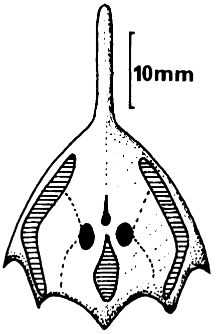

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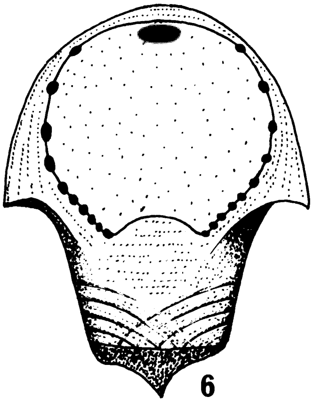

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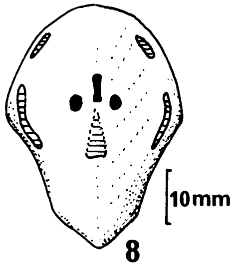

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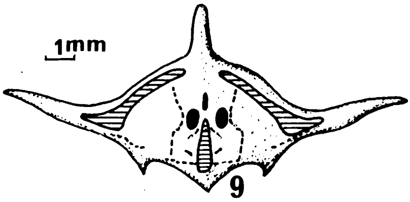

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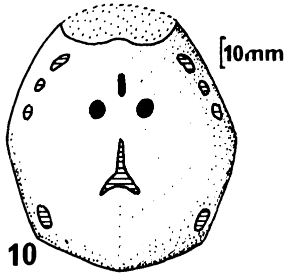

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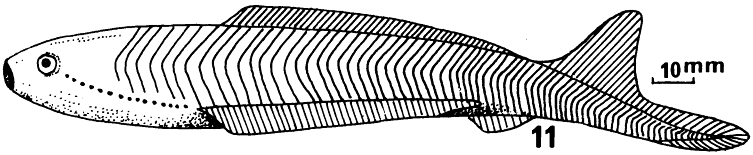

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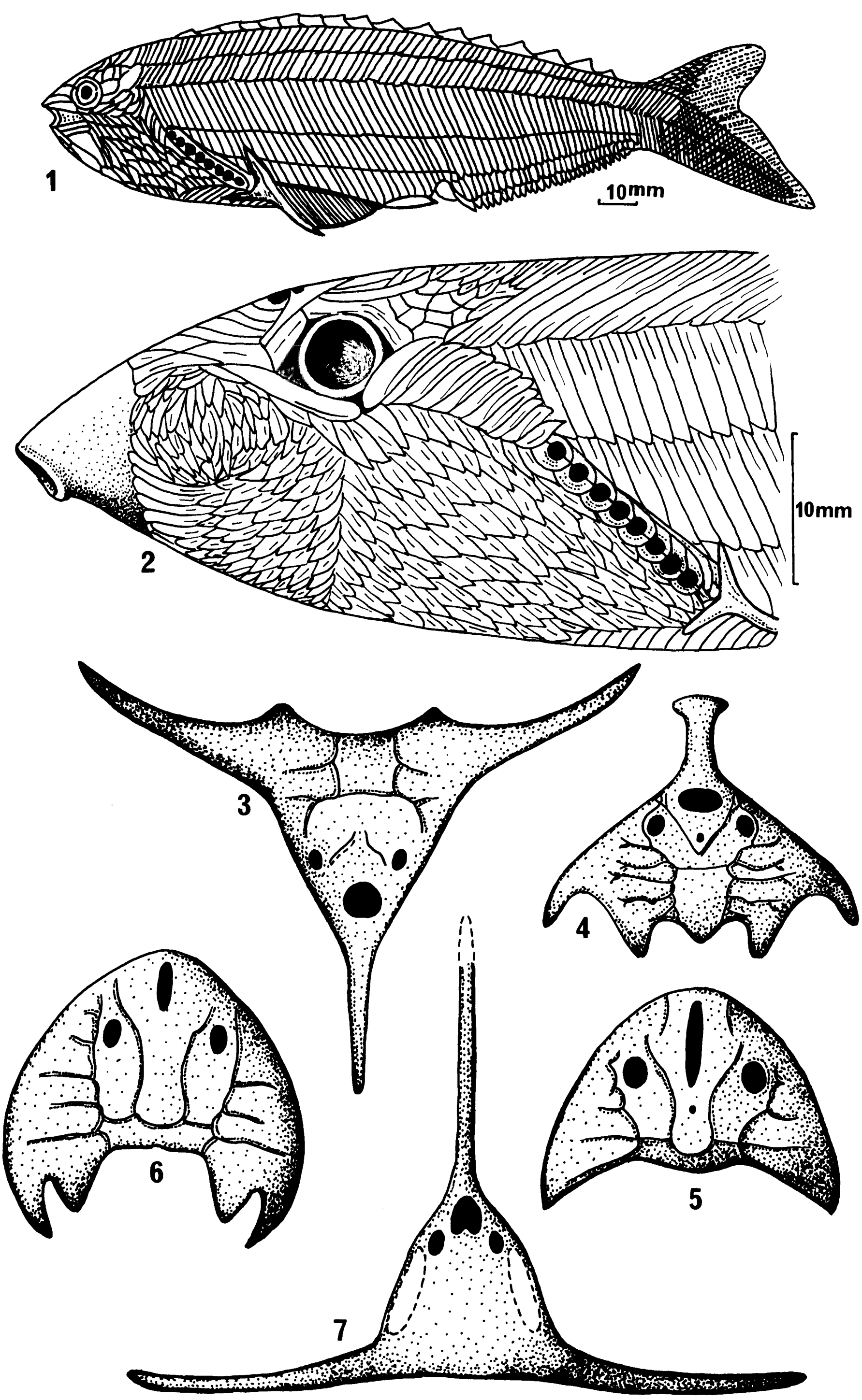
dorso-ventrally, with the eyes close together on the dorsal surface (Fig. 3.5). The mouth and gill clefts opened on the ventral aspect. According to Janvier (1985), the branchial system can be interpreted from a model very similar to that of larval lampreys, which suggests processes of neoteny. The head and the anterior part of the trunk were enclosed in the cephalic shield, whereas the abdominal region was covered with scales or plates with spines in the later forms. A dorsal crest extended as far as the caudal fin. The tail was long and heterocercal, with a slender ventral lobe. The number of dorsal fins varied from one to two (*Ateleaspis*). Two paired pectoral fins were sometimes supported on the posterior horns of the cephalic shield. It is though that the Osteostraci must have had an unarmored larva and that, as in some of the lampreys, the passage to the adult state was associated with migration. The possibility of migration from the sea into lagoons or freshwater has been suggested. The different groups of the Osteostraci show an evolutionary tendency in the shape of the cephalic shields, from those devoid of sinuses and horns to those with well-marked sinuses and long horns. This would indicate increased power in swimming. The elongation of the prepineal part of the shield as in *Boreaspis costata* (Fig. 3.5) is interpreted as associated with feeding. One of the classical series is that of the shields of the Kiaeraspididae from the lower Devonian of Spitzbergen (Fig. 3.5). The oldest forms like *Kieraspis auchenaspidoides* have a long shield with two small horns, but then the horns disappear and the shield is proportionately reduced with enlargement of the pectoral fins (*Axinaspis whitei*, *Acrotomaspis instabilis*). Finally, in *Nectaspis peltata*, the cephalic shield is greatly reduced. Allowing for the fact that the most primitive forms (*Ateleaspis*) and the most evolved forms (*Tremataspis*) existed simultaneously from the lower Silurian, it may be deduced that the radiation of the group is probably before the Silurian and contemporary with the Ordovician.

3.6.4 Anaspidae

These are small Cephalaspidomorphs, less than 15 cm long, known from the lower Silurian by individual scales and from the upper Silurian to the upper Devonian. Fusiform and somewhat compressed laterally, with large lateral eyes, the Anaspidae had bodies covered either with large plates (*Birkenia, Pterygolepis*) or scales (Fig. 3.6). The terminal mouth was oval. On the dorsal aspect a single naso-

Fig. 3.5. Lampreys, Osteostraci, and Anaspidae. **1** *Mayomyzon pieckoensis*, petromyzontid of the upper Carboniferous; **2** *Hardistiella montanensis*, lower Carboniferous; **3** *Gilpichthys greenei*, myxinoid of middle Carboniferous; **4** *Hemicyclaspis murchisoni*, lateral view; **5** *Kieraspis auchenaspidoides*, cephalic shield in dorsal view; **6** same, ventral view showing branchial orifices; **7** *Boreaspis robusta*, cephalic shield in dorsal view; **8** *Axinaspis whitei*, cephalic shield in dorsal view; **9** *Acrotomaspis trinodis*, cephalic shield in dorsal view; **10** *Hoelaspis angulata*, cephalic shield in dorsal view; **11** *Jamoytius kerwoodi*, lateral view (**1** after Bardack and Richardson 1977; **4** after Heintz 1939; **5, 6, 7, 8, 9** after Wängsjö 1952; **11** after Ritchie 1968)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scales (Fig. 3.6). The terminal mouth was oval. On the dorsal aspect a single naso-hypophyseal orifice lay in front of a small pineal foramen. The branchial orifices were small, varying in number from 6 to 15, and were arranged laterally in an oblique row. Some sclerotic ossifications around the eye constituted the reduced bony endoskeleton, the major part being cartilaginous. Because of this, very little is known of their internal anatomy. In *Euphanerops* of the upper Devonian there existed a branchial skeleton resembling that of the lampreys, but composed of at least 30 branchial arches. The Anaspidae possessed in common a series of large ridged scales acting as a dorsal fin. The tail was hypocercal with a large lower lobe. In most cases a small anal fin was reinforced by a spine. A natatory fold supported by a strong pectoral spine extended in a long crest from the branchial orifices to the anal region.

The oldest anaspid known is *Jamoytius kerwoodi* of the lower Silurian in Scotland. This is an animal exhibiting many primitive or, on the contrary, very evolved characteristics, approximating to the lampreys. The structure of its branchial sacs had led it to be compared with the larva of *Amphioxus*. It is, in fact, an anaspid with a poorly ossified skeleton and a round subterminal mouth (Fig. 3.5). *Birkenia* and *Lasanius* also derive from the Silurian of Scotland, *Pharyngolepis*, *Rhyncholepis* and *Pterygolepis* (Fig. 3.6) from the Dowtonian of Norway, and *Endeiolepis aneri* from the Devonian of Canada.

3.6.5 Galeaspidae

Recorded from the Silurian and Devonian of China and Viet-Nam, the Galeaspidae, like the Osteostraci, possessed a massive endo- and exoskeletal shield (Fig. 3.6). They had a ventral mouth and a large median orifice on the dorsal aspect of the shield communicating ventrally with the orobranchial cavity. They possessed branchial orifices whose number varied from 10 pairs in primitive forms (*Hanyangaspis*) to 24 pairs in evolved forms (*Paraduynaspis*).

3.6.6 Modes of Life

The groups of Cephalaspidomorphs described have very different appearances corresponding to different modes of life. The Osteostraci were benthonic animals which shovelled and aspirated the mud to extract invertebrates and organic matter.

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Fig. 3.6. Anaspidae and Galeaspidae. **1** *Rhyncholepis parvulus*, lateral view; **2** *Birkenia elegans*, reconstruction of head in lateral view; **3** *Szechuanaspis*, dorsal shield; **4** *Sanchaspis*, dorsal shield; **5** *Eugaleaspis changi*, dorsal shield; **6** *Yunanogaleaspis*, dorsal shield; **7** *Lungmenshanaspis*, dorsal shield (**1** after Ritchie 1980; **2** after Heintz 1958, modified by Stensiö 1964; **3** to **7** after Liu 1975, P'an and Wang 1978, 1980, P'an et al. 1975 in Janvier 1984)

Although the Anaspidae were less committed to the botton, they must have had an identical manner of feeding, though it is not impossible that some of them may have possessed a rasping tongue like the Petromyzontidae. This structure, with its suggestion of an ectoparasitic existence, was actually already acquired in *Mayomyzon* in the Carboniferous.

3.7 Gnathostomata

3.7.1 Jaws and Fins

With the elasmobranchs, and later with the teleosts, we approach the study of the gnathostome vertebrates, that is, of animals provided with jaws. Jaws, derived from the second visceral skeletal arch, allowed the capture of larger prey and this acquisition was accompanied by the development of paired fins. Fins are essential elements in the diffusion of stability and mobility. The movement of a modern fish is effected by rhythmic alternating muscular waves traveling along the body and transmitted to the tail. These pulsations push a column of water backwards and propel the fish forwards. The dorsal fins act as a keel and prevent the animal from rolling. The anal fin acts as a ventral stabilizer. Finally, the paired pectoral and pelvic fins allow the fish to rise, descend, turn right or left, and slow down. They also enable the animal to move backwards. The development of paired fins was to give these fish better mobility than that of the Agnatha and to enable them to supplant them.

3.7.2 Diversity and Phylogenetic Relationships of the First Gnathostomata

The gnathostome fish discussed here are classed into two groups: the elasmobranchiomorphs and the teleosts. While the elasmobranchiomorphs, which include the placoderms (Rhenanidae and Ptychodontidae) and Chondrichthyes (Elasmobranchs and Holocephali), constitute a homogeneous group, this is not the case for the aggregate of teleosts. These comprise the Acanthodia, the Osteichthyes including the Actinopterygii and the Sarcopterygii (Actinistia or Coelacanths, Dipnoi, Onychodontiforms, Porolepiforms, Osteolepiforms, and Tetrapoda), whose relationships, far from being clearly defined, will be discussed later. The best arguments supporting the idea that the placoderms are related to existing elasmobranchs (sharks) and Holocephali (chimera) consist in the structure of the nasal openings of the snout in the Arthrodira (placoderms), identical with that of the elasmobranchs, and in the presence of an "ocular peduncle" connecting the eye to the neurocranium. Further, the presence of pelvic claspers in the Ptychodontidae suggests that the placoderms had the same reproductive biology as the elasmobranchs and the Holocephali. Preferential relationships between placoderms (Ptyctodontes) and Holocephali have been envisaged on the basis of the presence of a pair of rostral processes supporting the fleshy nose, of large labial cartilages, a palato-quadrate attached to the neurocranium under the orbit, large dental plates and an elongated body traversed by a dorsal fin. In fact, these are characters acquired in parallel and resulting from the same benthonic mode of life. The same applies to the suggested characters of relationship between the Rhenanidae and the rays. These relationships are therefore far from being clearly established and three hypotheses have been advanced to specify the position of the placoderms in relation to the other gnathostomes. According to Moy-Thomas and Miles (1971) and Goujet (1984), the placoderms are closely related to the Chondrichthyes, the most seriously based view and one upheld here, but Schaeffer and Williams (1977) regard the placoderms as the sister group of all the other gnathostomes, while Forey (1981) considers them the sister group of the teleosts alone. On the other hand, the relationship between elasmobranchs and Holocephali is well supported by the presence of an internal cartilaginous skeleton with the prismatic calcifications of a dentition in which the teeth, barely modified scales, are replaced successively. These features, which are not shared by the placoderms, justify grouping the elasmobranchs and the Holocephali in the Chondrichthyes.

3.7.3 Placoderms

Included under this heading are groups of essentially Devonian fishes: Arthrodira, Ptyctodontidae, Phyllolepididae, Petalichtyidae, Rhenanidae and Antiarchi. Possessing a well-developed lower jaw, they have the front part of the body covered with a strong armor made of two parts, a head shield articulated with armor for the trunk. Thus the head retains some degree of mobility in relation to the trunk. This armor is made up of bony plates. The tail is generally heterocercal (Fig. 3.7).

3.7.3.1 Arthrodira

These appeared in the lower Devonian and persisted until the lower Carboniferous. The eyes were surrounded by sclerotic plates. The upper and lower jaws were differentiated into more or less numerous denticulations with the external appearance of sharp-pointed teeth. In fact, teeth of selachian or teleost type do not exist in the placoderms. A fenestra situated behind the spinal plate served for articulation of the pectoral fins with the scapulo-coracoid, included in the shield. Behind the armor there developed pelvic fins and a dorsal fin.

The evolution of the Arthrodira is characterized by a certain number of tendencies (Fig. 3.7). The primitive forms with a long thorax (dolichothoracic) gave rise to forms with a short thorax (brachythoracic). The former had large spinal plates and small pectoral fenestrae on the trunk armor, small eyes on the

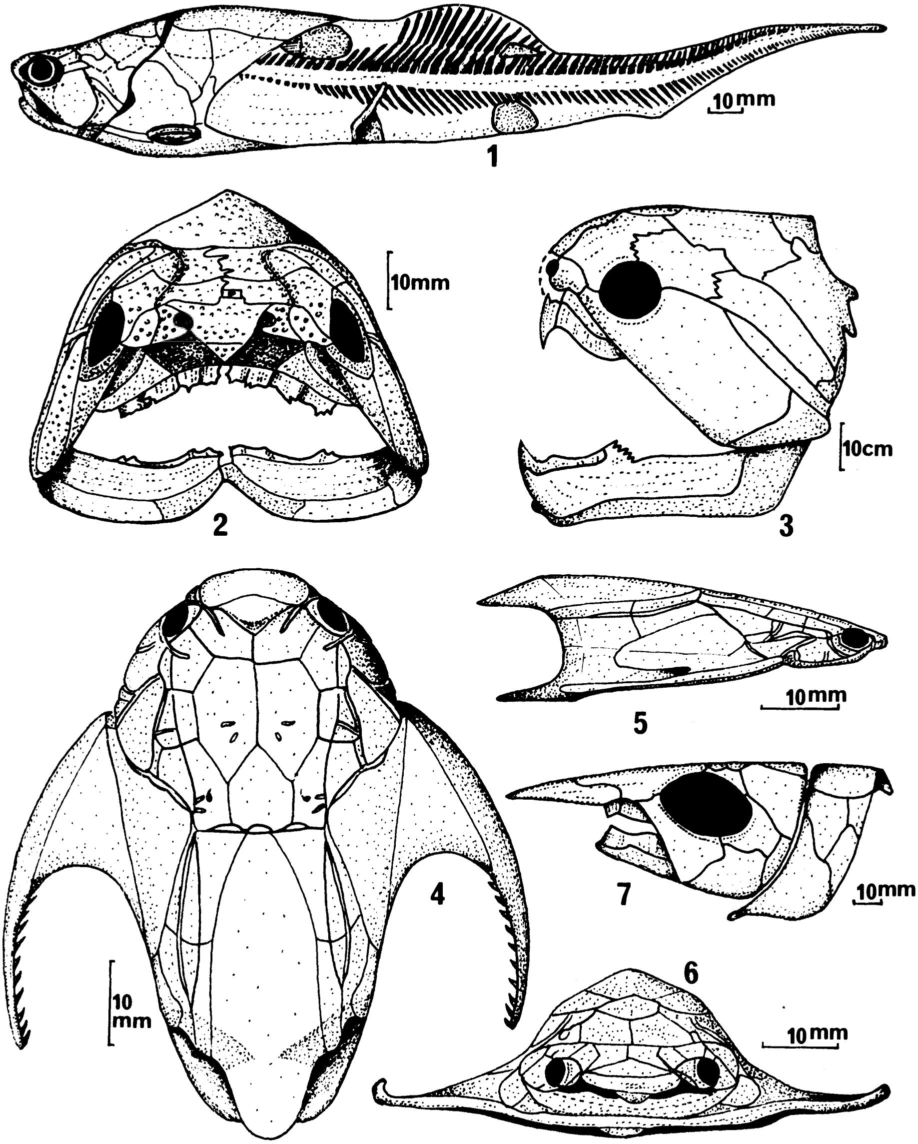

Fig. 3.7. Placoderms: Arthrodira. **1** *Coccosteus cuspidatus*, reconstruction in lateral view; **2** same, cranium in anterior view; **3** *Dunkleosteus terreli*, reconstruction of cephalic shield in lateral view; **4** *Dicksonosteus arcticus*, reconstruction of precaudal dermal skeleton in dorsal view; **5** same in lateral view; **6** same in anterior view; **7** *Oxyosteus rostratus*, reconstruction of cephalic and trunk shields in lateral view. (**1**, **2** after Miles and Westoll 1968; **3**, **7** after Miles 1967; **4**, **5**, **6** after Goujet 1984b)

cephalic shield and mandibular denticulations on the anterior part of the lower jaw (*Dicksonosteus*). The derived forms (*Coccosteus*) had a reduced trunk armor with enlarged pectoral fenestrae, the mandibular denticulations were differentiated and the spinal plate reduced. All these tendencies correspond to a better adaptation to the swimming accompanying an increase in size. This changed from less than 10 cm in the archaic forms to more than 2 m (*Dinichthys*, *Dunkleosteus*, *Titanichthys*) in the evolved forms. These giant Arthrodira were redoutable predators.

3.7.3.2 Ptyctodontidae

These are characterized by a reduction of the armor and do not exceed 20 cm in length. They were once thought to be related to the Holocephali (chimeras), but this hypothesis has now been abandoned.

3.7.3.3 Petalichthyidae

The Petalichthyidae (lower to upper Devonian), not more than 50 cm in length, exhibit dorso-ventral flattening and long spinal plates as shown in *Lunaspis broilii* (Fig. 3.8).

3.7.3.4 Rhenanidae

The special feacture of these small fish (50 cm) was the existence of a mosaic of small bones between the large plates of the cephalic shield. *Gemuendina stuertzi* (Fig. 3.8) was flattened dorso-ventrally and had very large rounded pectoral fins giving it a ray-like appearance. The body was covered with denticulate scales and the tail was diphycercal.

3.7.3.5 Antiarchi

These are known from the lower Devonian to the lower Carboniferous and were small animals in whom the head and fore-part of the trunk were covered with overlapping plates, the rear with scales. The cephalic shield of *Bothriolepis canadensis*, shorter than that of the trunk (Fig. 3.8), carried articulated pectoral appendages homologous with pectoral fins and covered with small bony plates reminiscent of the limbs of crustaceans. The closely set median eyes were surrounded by sclerotic plates. The median dorsal plate formed a protuberance (*Bothriolepis*) or a large spine (*Byssacanthus*). Mention may also be made of *Yunnanolepis* of the lower Devonian in China, a very primitive form whose pectoral appendages did not yet exhibit the complex articulations seen in the other Antiarchi.

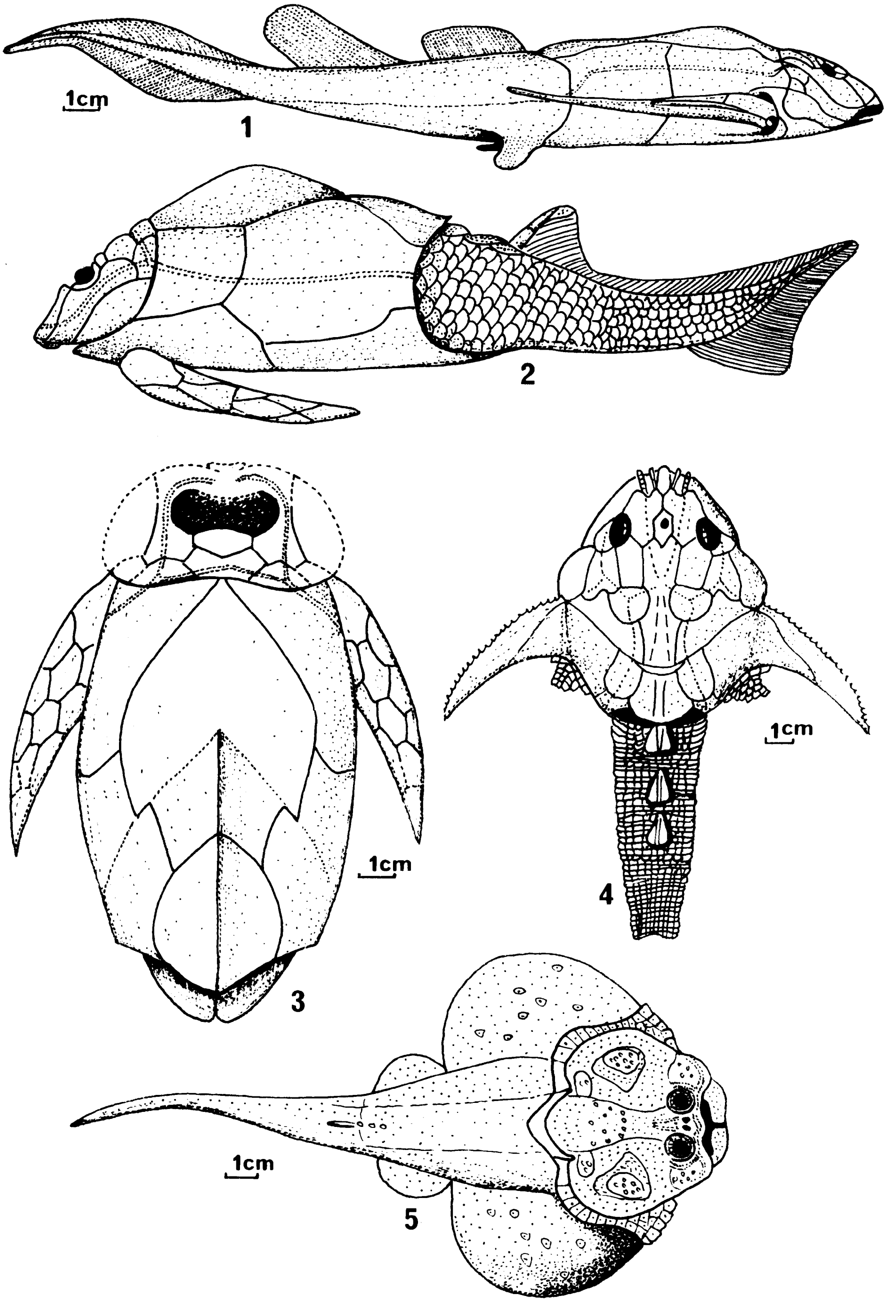

Fig. 3.8. Placoderms: Antiarchi, Petalichthyidae, Rhenanidae. **1** *Bothriolepis canadensis*, lateral view; **2** *Perichthyodes*, lateral view; **3** *Remigolepis* sp., reconstruction of cephalic and trunk shields in dorsal view; **4** *Lunaspis broilii*, dorsal view; **5** *Gemuendina stuertzi*, dorsal view. (**1, 3** after Stensiö, 1969; **2** after Traquair 1894–1914; **4, 5** after Gross 1961, 1963)

3.7.3.6 Mode of Life

Most of the placoderms were benthonic animals exploiting the various available ecologic niches. The primitive arthrodira sought their food in the mud, while the more evolved forms were doubtless predators staying settled near the bottom. The ptyctodonts seem to have had the same adaptations as present-day chimeras, while the Rhenanidae, like the rays, were able to use their pectoral fins to cover their bodies with a layer of mud, the better to surprise their prey while lurking on the bottom. As for the Antiarchi, whose eyes and nasal openings were dorsal as in the Rhenanidae, their pectoral appendages allowed them to move about by lifting themselves up. They were nourished by organic matter contained in the mud.

3.7.3.7 Evolution of Placoderms

Besides the evolution of the shields in the Arthrodira (Fig. 3.7) as mentioned above, allowing better adaptation to swimming and a major increase in size, the placoderms are also notable for the diversification of the pectoral fins. There are two tendencies to be noted. In the Arthrodira the pectoral appendages became more mobile and powerful, linked with a better adaptation to swimming. As against this, the pectoral appendages in the Antiarchi assumed the specialized function of stilts. The stability of the mandibular structure and the absence of true teeth led to this group, which dominated the seas and the fresh water during the Devonian, being supplanted by the Chrondrichthyes, which were better adapted from the beginning of the Carboniferous.

3.7.4 Chondrichthyes

3.7.4.1 Characteristics

These appear in the fossil record at the end of the lower Devonian, fade away in the Carboniferous and persist at the present time as the sharks, rays, and chimeras (about 3% of all fish). These fish, with an essentially cartilaginous skeleton, were considered even quite recently to be devoid of bone, in contrast with the Osteichthyes, whose ossified skeleton was composed of perichondral and endochondral bone. The discovery of perichondral bone in the vertebral column of the spotted dogfish confirmed in surmise that the cartilaginous skeleton plus the prismatic calcified cartilage were all derived, at least in the gnathostomes (Peignoux-Deville and Janvier 1984). The cartilaginous skeleton, often covered with a prismatic calcified layer, constitutes the principal synapomorphy (autapomorphy) in the chondrichthyes. The exoskeleton was formed of placoid scales. They had five to seven gill slits opening directly to the exterior, but covered with an operculum in the chimeras (Holocephali). They had large olfactory capsules in the cartilaginous snout, jutting out in front of the ventral mouth. The teeth were not fused to the jaw and were replaced successively one after the other.

Because of the cartilaginous nature of the skeleton, the Chondrichthyes left only rare fossils and are often known only by their teeth and spines. They became diversified into two great groups: the Elasmobranchs and the Holocephali.

3.7.4.2 *Cladoselache* and the Elasmobranchs

The studies of Maisey (1984) led to general agreement that *Cladoselache* was the most primitive of all known Chondrichthyes. Thus, *Cladoselache* would be the sister group of the grouped elasmobranchs and Holocephali. The principal reason for this is that the paired fins of *Cladoselache* have unsegmented endoskeletal rays attached directly to the scapulo-coracoid girdle without basal elements. *Cladoselache fyleri* (Fig. 3.9) of the upper Devonian, about 2 m long and fusiform, had two dorsal fins preceded by a short spine. The apparent symmetry of the spine actually concealed its heterocercal structure. The paired pectoral and pelvic fins gave the appearance of a triangular flap identical with those of shark embryos. The vertebral column was devoid of centra, allowing persistence of the notochord. The so-called "cladodont" teeth were formed of a central cusp surrounded by a variable number of small tubercles.

Starting from this or other related types, there developed the Selachia. Among these, the Ctenacanthidae (*Ctenacanthus*) and the Hybodontidae constitute the most important groups of the Paleozoic. Another group, that of the Xenacanthidae, distributed from the Devonian to the Triassic, exhibited interesting pelvic fins of biseriate archipterygian type (convergence with the Sarcopterygii) with a segmented axis bearing a row of preaxial and postaxial radial elements (Fig. 3.9). *Xenacanthus sessilis* was further characterized by a cephalic spine, a long dorsal fin, a dyphycercal tail, and a double anal fin.

The Ctenacanthidae were particularly abundant in the Carboniferous and replaced by the Hybodontidae dominant during the Triassic and Jurassic. The modern selachia with very mobile jaws appeared in the Mesozoic (Liassic), but there has been a recent report of scales and teeth of selachian type from the Carboniferous. They diversified into the sharks and rays. The sharks are pelagic and frequent littoral waters and the open sea; the rays are benthonic. From the Carboniferous to the Triassic there lived strange elasmobranchs sometimes compared with the Holocephali, the Edestidae, which developed a gigantic slicing dental spiral on the mandibular symphysis. In the Carboniferous and the Permian

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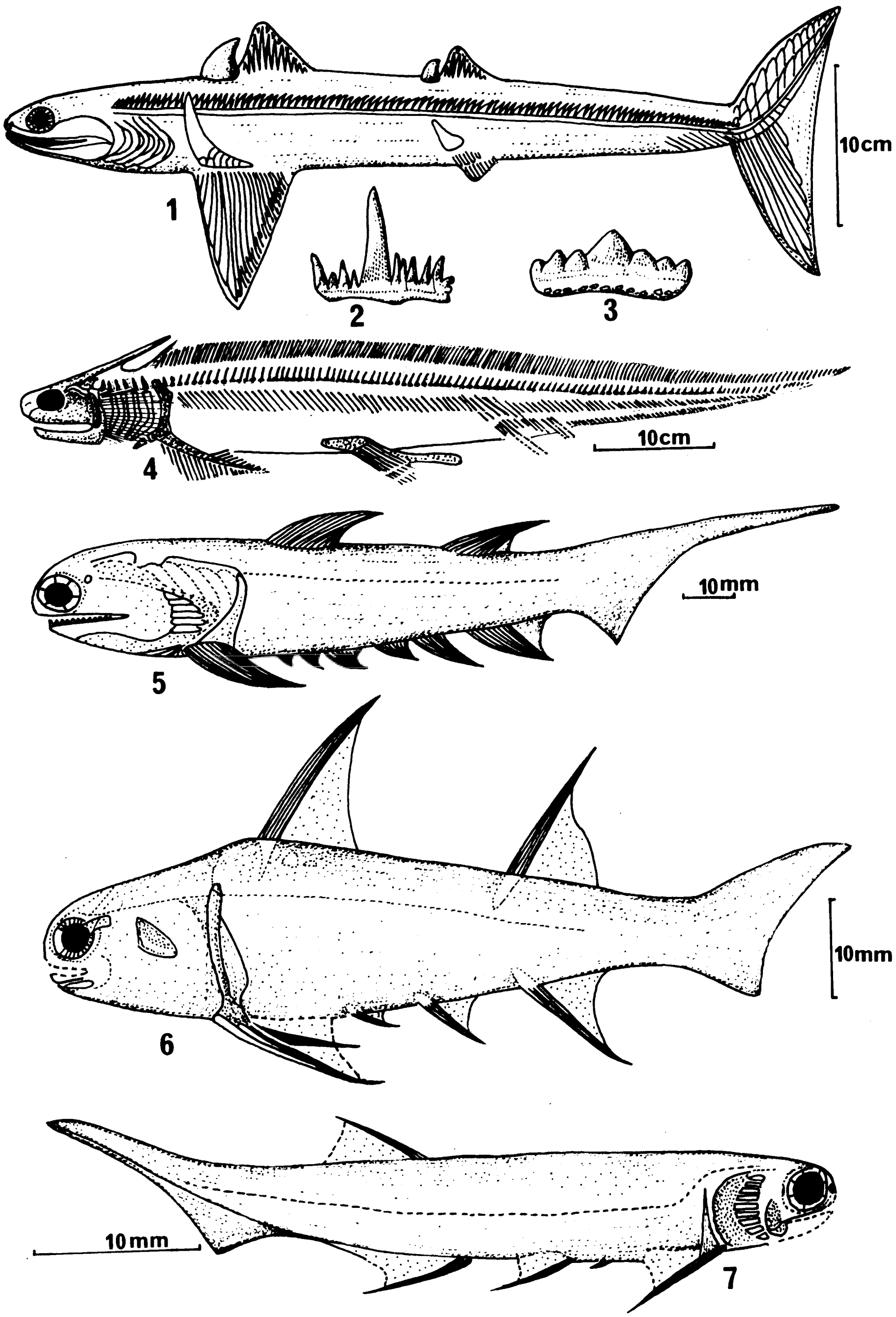
Fig. 3.9. Elasmobranchs, Acanthodia. **1** *Cladoselache fyleri*, lateral view; **2** *Cladodus* sp., tooth; **3** *Xenacanthus* sp., tooth; **4** *Xenacanthus sessilis*, lateral view; **5** *Climatius reticulatus*, lateral view; **6** *Diplacanthus striatus*, lateral view; **7** *Triazeugacanthus affinis*, lateral view. (**1, 2, 3** after Schaeffer 1967; **4,** after Taeckel 1906; **5, 6** after Watson 1937; **7** after Miles 1966)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another group, the Petalodontidae, were represented by stout squat elasmobranchs whose appearance resembled that of present-day scorpion fish and the shape of whose teeth was like that of a flower petal.

3.7.4.3 Holocephali

These are distinguished from the preceding by their mandibular articulation (upper jaw fused to the cranium), the structure of their teeth and the presence of an operculum covering the gill slits. Apart from some old forms with successively replaced teeth of selachian type, the chimeras were characterized by the development of dental plates resulting from fusion of several teeth. The Bradyodonti, so called because of their slow dental replacement, form a possibly monophyletic group that lived from the Devonian to the Permian. They are related to the Holocephali or the present-day chimeras, whose teeth are composed of vertical parallel tubules of dentine. *Helodus simplex* of the Carboniferous was 1 m long and flattened dorso-ventrally and resembled an existing chimera by having dorsal fins of which the anterior bore a spine.

3.7.4.4 Mode of Life

The Holocephali, which attained their greatest expansion in the Carboniferous, were benthonic animals with a durophagous regime, as evidenced by the remains of brachiopod valves discovered in their stomachs. At this period they partly filled the ecologic niches previously held by the placoderms, sharing them with the elasmobranchs and the actinopterygia. The chimeras survive today in deep waters.

3.8 Teleostomi

3.8.1 Characteristics and Phylogenetic Relationships

Grouped together in the teleosts are the Acanthodia, an exclusively fossil group, the Actinopterygii, the Actinistia (or coelacanths), Dipnoi, onychodontiforms, porolepiforms, osteolepiforms and the Tetrapoda. Besides the presence of dermal rays in the fins, composed of lepidotrichae (modified scales), they had an ossified endoskeleton and a swim-bladder acting either as a hydrostatic organ or as a lung. Their bodies were covered with scales. The relationships between these groups are still very debatable, notably those of the Dipnoi, variously regarded as the sister group of the other Osteichthyes, the Actinopterygii, the other Sarcopterygii or the Tetrapoda, and based on the presence of a large number of anatomical and biochemical synapomorphies. Further, the characteristics shared by certain Rhipidistia and the Tetrapoda are interpreted by some as synapomorphy, but by others as symplesiomorphy of Osteichthyes. In fact, while the Dipnoi are probably among the closest relatives of the Tetrapoda in nature today, there exist certain Rhipidistia like *Panderichthys* which are even still closer. The relationships are not definitively resolved. We refer for hypotheses to the general cladograms of Fig. 2.1 by Jefferies (1981), 3.2 by Moy-Thomas and Miles (1971), and 3.12 by Janvier (1986).

3.8.2 Acanthodia

These are the first gnathostomes encountered in the fossil record from the lower Silurian on. The principal synapomorphies shared by the Acanthodia and the Osteichthyes are opercular dermal plates and otoliths composed of vaterite. The Acanthodia were fusiform fish with an average length of 20 cm, sometimes reaching 2 m, whose bodies were covered with small adjacent lozenge-shaped scales. The dorsal, anal, pectoral and pelvic fins were supported by powerful spines, which earn them the inappropriate name of spiny sharks. They possessed between the pectoral and pelvic fins a series of pairs of intermediate spines, possibly as many as six, doubtless derived from the ventro-lateral folds of the body. In *Climatius reticulatus*, shown in Fig. 3.9, other characteristics appeared; a large eye surrounded by bony plates situated very far forward and a heterocercal tail.

The first Acanthodia had short bodies, thick scales, and broad spines (Climatiidae), but the derived forms (Diplacanthidae) had longer and narrower spines and were devoid of teeth (Fig. 3.9). During the evolution of the group there can be noted a tendency to reduction of the dermal skeleton, compensated by thickening of the endoskeleton. There was also a diminution of the number of intermediate spines. Apart from the Ischnacanthidae (upper Silurian to Carboniferous), with teeth and long bodies, the Acanthodidae (lower Devonian to lower Permian) are the only fish without teeth. *Triazeugacanthus affinis* (Fig. 3.9) shows a reduced number of intermediate spines.

The Acanthodia, marine and freshwater animals, lived at the surface and moderate depths and, apart from some benthonic species, did not compete with the Agnatha. With the exception of the predatory Ischnacanthidae, the other Acanthodidae followed a microphagous (plankton) regime.

3.8.3 Osteichthyes

Although these appear at least in the upper Silurian, they are not properly known until the lower Devonian. With a bony skeleton showing endochondral bone, a very ossified cranium, a branchial region covered by a single bone, the operculum, the upper border of the mouth formed by the premaxillary and maxillary and the teeth fused to the bones, the Osteichthyes resemble the Actinopterygii (fish with radiating fins) and the Sarcopterygii (fish with fleshy fins) (former Crossopterygii, Dipnoi and Tetrapoda).

3.8.3.1 Actinopterygii

Known from the upper Silurian by isolated scales, these are better documented in the lower Devonian. They are characterized by the structure of their paired fins devoid of axes of symmetry and by a membrane supported by a radiating pattern of lepidotrichae. These were fish covered with ganoid scales of rhombohedral shape arranged in diagonal rows. They also possessed a special dental tissue made of acrodine and a pelvic girdle in which the metapterygium supporting the fin was composed of separate juvenile cartilages which fused in the adult (Rosen et al. 1981). The ossified vertebrae carried spines. The pectoral fins articulated with the cranium via the cleithrum (dermal bone). There was a single dorsal fin in all the primitive forms. The second dorsal fin in certain teleosts is a neoformation by subdivision of the single dorsal fin. The large eyes often played a more important part than the sense of smell. In the archaic forms the swimbladder functioned as a lung, in the evolved species as a hydrostatic air pocket. They constitute the largest group of present-day vertebrates (around 23,000 species), having colonized the aquatic environment from the oceanic trenches (- 11,000 m) to mountain torrents (+ 4500 m) and from cold waters (- 1.8^{0}C) to warm waters (43^{0}C). They include the smallest vertebrate known, whose adult size is 7.5 mm. The relationships between the very numerous groups of Actinopterygii have been clarified thanks to the cladistic approach of Lauder and Liem (1983), a study available for reference for a detailed synthesis of the Actinopterygii. These appeared in the marine waters of the middle Devonian. Their structure was very diverse, as can be seen in part from the examples of the Paleoniscidae, *Aeduella blainvillei*, or *Cheirolepis canadensis* (Fig. 3.10).

They were fusiform fish with large eyes, a long snout and a heterocercal tail with a large upper lobe, covered with rhomboidal scales. Possessors of a single dorsal fin and a heterocercal caudal fin with the notochord and vertebrae located in its dorsal lobe, their size varied from 10 cm to 1 m. The Paleoniscidae were predators needing a body capable of speed. The Platysomoidae formed a group with laterally flattened bodies like *Chirodus granulosus*. The archaic Actinopterygii were to diversify into numerous lines and reached their greatest expansion in the upper Carboniferous and the Permian. In the Triassic, progressive forms exhibit a reduction of the upper lobe of the heterocercal tail and a shortening of the jaws (*Redfeldius*). Survivors of the archaic Actinopterygii exist: the Polypteridae (*Polypterus*) and the sturgeons (*Acipenser*), known since the upper Cretaceous. *Moythomasia* is a form from the upper Devonian which is placed between the Polypteridae and the sturgeons. The Actinopterygii further evolved (halecomorphs and teleosts) acquired a mode of suction feeding, a negative pressure in the buccal cavity drawing prey with a current of water into the open mouth. Among the group of the halecomorphs, known since the Jurassic and culminating in the start of the Cretaceous and diversified into rounded (*Microdon radiatus*) or elongated (*Aspidorhynchus*) forms, there still exist the genera *Amia* and *Lepisosteus* (Fig. 3.10). But the most important group of these fish is that of the teleosts (20,000 existing species), which appeared in the middle Triassic (*Lepto-*

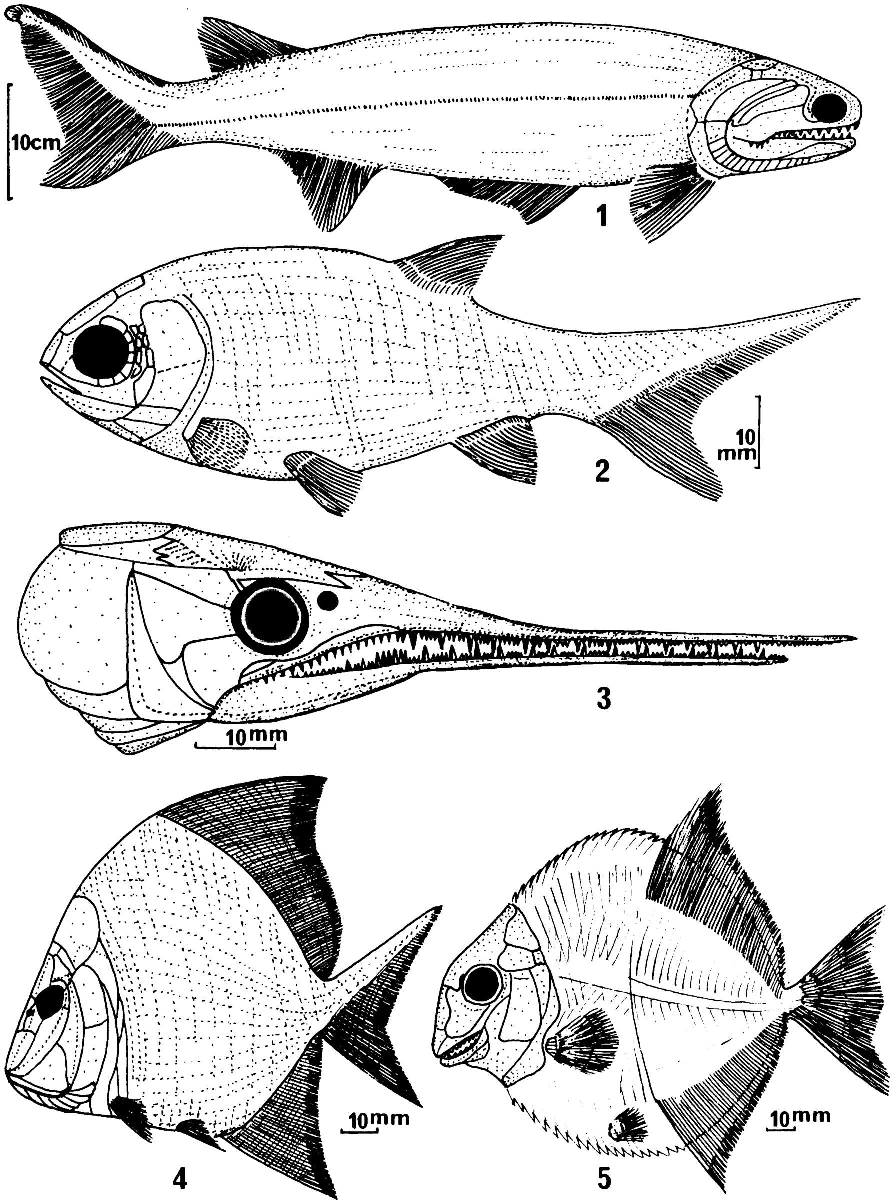


Fig. 3.10. Actinopterygii. **1** *Cheirolepis canadensis*, upper Devonian, Canada, lateral view; **2** *Aeduella blainvillei*, Autunian, Morvan, France; **3** *Belonostomus tenuirostris*, Kimmeridgian of Cerin, Ain, France; **4** *Platysomus superbus*, Carboniferous, England; **5** *Microdon radiatus*, middle Purbeckian, England. (**1** after Lehman 1947; **2** after Heyler 1969; **3** after Saint-Seine 1947; **4** after Moy-Thomas and Bradley-Dyne 1938; **5** after Woodward 1909)

lepis of the Liassic). They are characterized by a symmetrical (homocercal) tail, although the prolongation of the vertebral column is situated in its dorsal lobe. Their endoskeleton was to ossify completely, while the exoskeleton regressed. The pelvic fins migrated forward and the scales became thin and rounded. In the phylogeny of the teleosts proposed by Lauder and Liem (1983) four main groups can be distinguished. That of the Osteoglossomorphs, known from the upper Jurassic, is characterized by the presence of a tongue covered with teeth. The elopomorphs (650 existing species) include the eels. The clupeomorphs (herrings) are known from the lower Cretaceous and are currently represented by 290 species; they exhibit a repeated and independent tendency to lose the teeth and branchial arches. Finally, the euteleosts constitute the most developed group, with 17,000 existing species. The protacanthopterygians include the Salmonidae (trout, salmon), the Ostariophysii (600 species), the catfish (Siluroidae) and the Gymnota (Gymnotoidae) which can generate electricity. The neoteleosts are characterized by a major innovation, the development of a contractile pharyngeal muscle. Among the best-known forms may be mentioned the lantern fish (Myctophidae), which live at a depth of 500 m and ascend to feed on plankton at the surface during the night. To those should be added the perch (percopsiforms), Acanthopterygii, known since the Cretaceous and diversified into the Cyprinodontidae (atherinomorphs) which appeared in the Eocene, the percomorphs: lantern fish (Anomalopidae), flying fish (dactylopteriforms), perciforms (6900 species) some of which are: the freshwater Cichlidae, the boxfish, porcupine fish (Tetraodontidae) and the soles (pleuronectiforms), characterized by the asymmetric position of the eyes.

3.8.3.2 Sarcopterygii

The Sarcopterygii are represented in the fossil record by the onychodontiforms, the porolepiforms and the osteolepiforms, and currently survive as the groups of the Actinistia, Dipnoi, and Tetrapoda. The Sarcopterygii are characterized by the fact that the sole persisting feature of the endoskeleton of the paired fins is the metapterygium, articulating with the girdle by a single element, the humerus or femur.

3.8.3.2.1 Onychodontiforms or Struniforms

This is a small group of the Devonian or Carboniferous, known from *Strunius* (Fig. 3.11) and *Grossius*. Possessing large eyes, a reduced operculum, a solitary external nostril, and teeth devoid of pleated structure, they also had parasymphysial fangs on the mandible which may well have been a gnathostome symplesiomorphy.

3.8.3.2.2 Actinistia or Coelacanthiformes

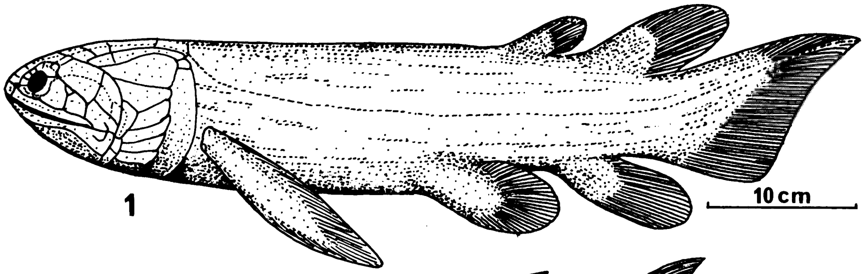
These appeared in the Devonian and persist to the present day as the genus *Latimeria*, regarded as a living fossil (Fig. 3.11). They had two dorsal fins and an anal fin. The heterocercal caudal fin had a trilobed or gephyrocercal appearance (*Latimeria*). The head was covered with large symmetrical plates, the body with cosmoid scales. Their neurocranium was divided into two regions. They had a well-developed olfactory sense and small eyes. The primitive forms had teeth implanted on the palate, and there were other larger teeth of pointed carnivorous type on the jaw margins. The group shows a remarkable structural stability from the Devonian onwards. Juvenile forms of *Rhabdoderma* (Carboniferous) have been found showing the existence of a vitelline sac, as found in the fetus of the present-day *Latimeria*. The lungs were often calcified and preserved in fossils. These fish were represented in the Cretaceous by forms of large size like *Mawsonia tegarnensis*. The existing *Latimeria chalumnae* (Fig. 3.11) has a massive body, paired fins forming lobes, and a diphycercal tail possessing a supplementary lobe in the axis of the body. The short cranium exhibits a marked reduction in the cranial bones and marginal teeth.

3.8.3.2.3 Porolepiformes

This small Devonian group, known mainly from *Porolepis* and *Glyptolepis*, was considered by Jarvik as the ancestor of the Urodela on the disputed hypothesis of a diphyletic origin for the Tetrapoda. In fact, *Porolepis* seems more related to the Dipnoi, as suggested by intermediate forms between the two taxons, like *Youngolepis* or *Diabolepis*.

3.8.3.2.4 Osteolepiformes

Known from the lower Devonian to the lower Permian, these are of the greatest importance from the evolutionary aspect because of the presence in *Eusthenopteron* (upper Devonian of the Baltic countries and Canada, Fig. 3.11) of paired fins supported by an endoskeleton suggestive of the limb skeleton of the Tetrapoda (see Chap. 4). In fact, the pectoral fins were borne on bony elements corresponding respectively to the humerus, radius, and ulna of the anterior limb of the Tetrapoda. Classically, the osteolepiforms, together with the Tetrapoda, were the only Sarcopterygii to have choanae. This character, suspect for Rosen et al. (1981), raises the problem of basing the Tetrapoda within the osteolepiforms. The same author regards the structure of the anterior limb of *Eusthenopteron* (a metapterygial axis of dichotomous structure) as a primitive structure of the Sarcopterygii inherited from the first gnathostomes and not as a specialization heralding the skeleton of the Tetrapoda. The osteolepiforms also include the Panderichthyidae (*Panderichthys, Elpistostege*) (Fig. 3.11) sharing very many synapomorphies with



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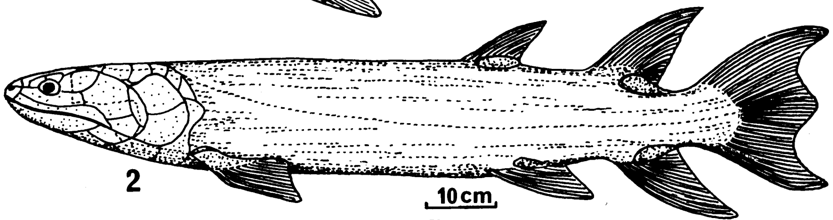

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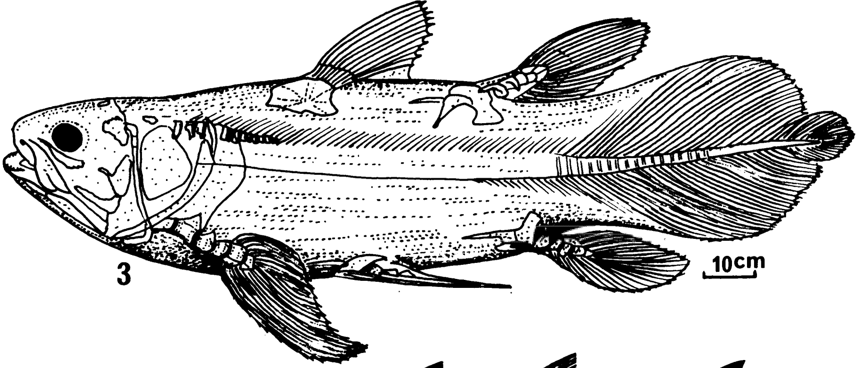

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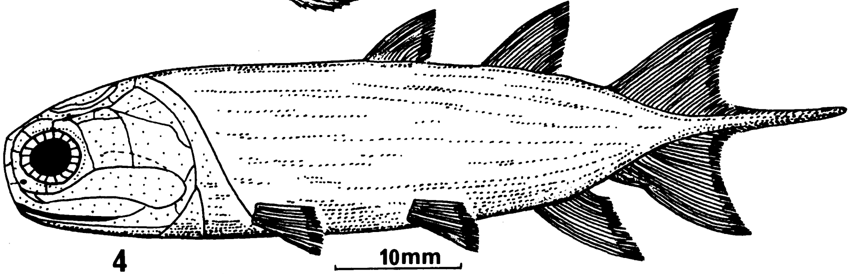

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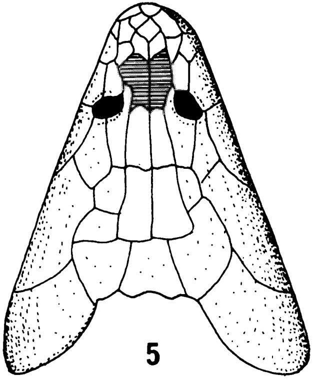

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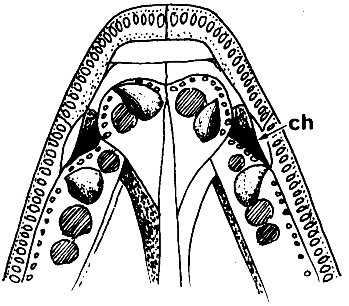

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the Tetrapoda (presence of true frontals and very large choanae), which qualify them for the position of a sister-group of the Tetrapoda, although the skeleton of their paired fins cannot be considered as ancestral to pentadactyl limbs. The other group, that of the Rhizodontidae, to which *Eusthenopteron* is usually attached, is known from large forms in the Carboniferous notable for the covering of the rays of the paired fins by cycloid scales giving a palette-like appearance to the fins.

3.8.3.2.5 Dipnoi or Lungfishes

These appeared in the lower Devonian (*Dipnorhynchus*) and had their greatest expansion in the upper Devonian. They currently persist as three genera: *Neoceratodus* (Queensland, Australia), *Protopterus* (west, central, and east Africa) and *Lepidosiren* in South America. This is a very conservative group which has acquired its specific derived characteristics since the lower Devonian: the arrangement of the cranial bones, grinding dental plates marked by creases. The relationships of the Dipnoans has been much discussed because of the existence of rudimentary lungs, internal nostrils, fins, and scales. It was thought that the Tetrapoda derived from the Dipnoi, since both groups had in common internal nostrils connecting the mouth and the nasal fossae (choanae). In fact, the discovery in the lower Devonian of Yunnan in China of *Diabolepis speratus*, a dipnoan typified by its dental plates, shows that the cranium has a structure much like that of the other Sarcopterygii and, especially, that it seems to have possessed two external nostrils like the other Osteichthyes. The posterior nostril was situated at the edge of the mouth (Fig. 3.12), accounting for its migratory movement towards the middle of the palate where it is found in existing Dipnoans. The internal nostrils of the lungfishes may therefore not be homologous with the choanae of the Tetrapoda; this may simply be a convergence, and there is no longer any justification for classifying Dipnoans and Tetrapoda in the Choanata. In the same Chinese deposit, *Youngolepis praecursor* recalls rather the porolepiforms, possessing both two external nostrils like *Diabolepis* and the labyrinthodont teeth of the Rhizodontidae and the first Tetrapoda. *Youngolepis* may thus be considered as occupying an intermediate position between *Porolepis* (Porolepiforms) and the aggregate of *Diabolepis* and lungfishes (Fig. 3.12) and shows that the Dipnoi and Tetrapoda are the sole existing survivors derived from a common ancestor.

Dipterus valenciennesi of the Scottish Devonian had a fusiform body, a covering of massive scales, two dorsal fins, one caudal and one separat anal fin, as

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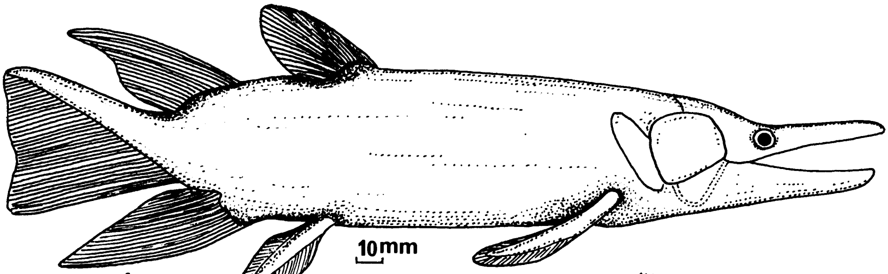
Fig. 3.11. Osteolepiforms, Porolepiforms, Actinistia, and Onychodontiforms. **1** *Holoptychius* sp., upper Devonian; **2** *Eusthenopteron foordi*, upper Devonian; **3** *Latimeria chalumnae*, present-day; **4** *Strunius walteri*, upper Devonian; **5** *Panderichthys rhombolepis*, upper Devonian, lateral view of head showing the existence of frontals (*cross-hatched*); **6** *Eusthenopteron foordi*, anterior part of palate showing position of choanae. (**1, 2, 6** after Jarvik 1954; **3** after Millot and Anthony 1958; **4** after Lehman 1966; **5** after Schulze and Arsenault 1985)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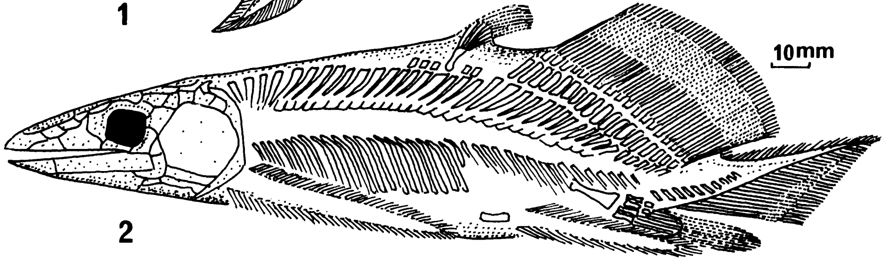
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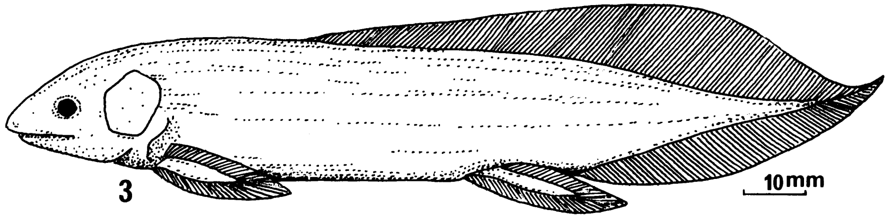
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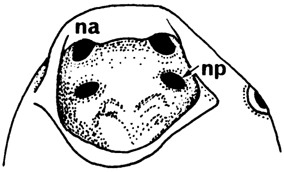
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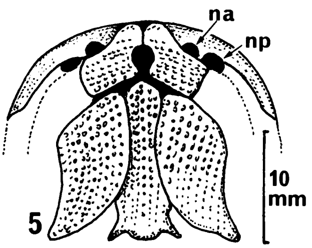
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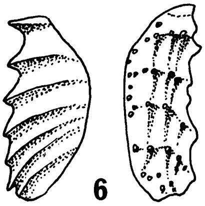

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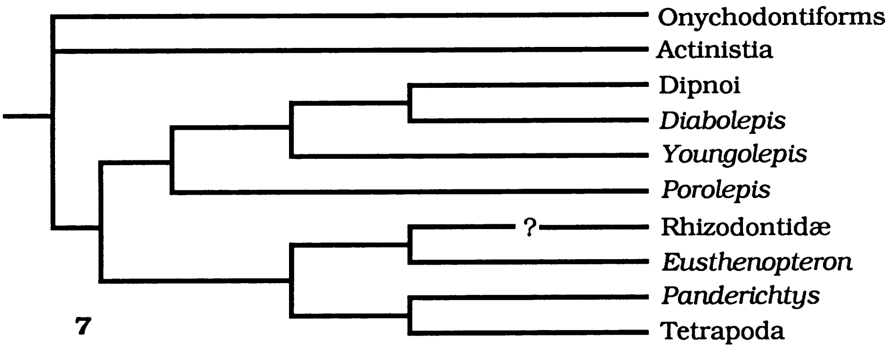
Onychodontiforms
Actinistia
Dipnoi
Diabolepis
Youngolepis
Porolepis
?
Rhizodontidæ
Eusthenopteron
Panderichtys
Tetrapoda

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well as a heterocercal tail. During the evolution of the group, continuous median fins were formed, *Scaumenacia* of the upper Devonian and *Uronemus lobatus* of the Carboniferous representing two stages of this transformation (Fig. 3.12). The evolution of the Dipnoan was further characterized by regression of ossification, replaced by cartilage. The Dipnoans breathed both by gills and lungs, but in periods of drought they survived with the aid of their lungs alone. The oldest species of Dipnoi were marine, but others lived in the fresh water of the continental environments with alternating wet and dry seasons (Devonian old red sandstones). During the dry phases, the present-day *Protopterus* buries itself in the mud in a mucus envelope. The mode of life of the lungfishes has been modified since the Devonian. For practical purposes, almost all the Devonian Dipnoans were marine and often lived in reefs, crunching Brachiopoda. They moved to fresh water in the middle Carboniferous and their first land-dwellers are found in the Permian. Their evolutionary diversification was relatively minor. The central line of the Dipnoans is represented by *Ceratodus* of the Triassic. The existing *Neoceratodus* is a virtually unchanged direct descendant of its Mesozoic ancestor. The African and South American forms have evolved independently, but they have the same gephyrocercal tail and reduced paired fins, descending from a common ancestor which lived when these two continents were joined (a case of vicariance).

3.8.3.2.6 Tetrapoda

These are Sarcopterygii whose paired fins have lost their fringe of dermal rays and have individualized at least five articulated expansions, the digits. The operculum disappeared, leaving in its place a tympanum connected to the inner ear by the hyomandibular, modified as a stapes. These specializations, which may have appeared in the aquatic setting, marked the beginnings of the conquest of the terrestrial environment by this group.

Fig. 3.12. Lungfishes. **1**, *Rhynchodipterus elginensis*, upper Devonian, Scotland; **2** *Fleurentia denticulata*, upper Devonian, Canada; **3** *Uronemus lobatus*, lower Carboniferous; **4** present-day dipnoan, mouth in ventral view showing position of anterior nares (*na*) and posterior nares (*np*); **5** *Diabolepis speratus*, dipnoan of lower Devonian, China, snout in ventral view showing the posterior nares (*np*) still situated outside the mouth as in the other fish. Thus the posterior nares of the lungfishes are not equivalent to the choanae of the Tetrapoda, but the result of a convergence; 6 teeth of *Ceratodus africanus* (left) and of *Ceratodus tuberculatus*, (right) of the Cretaceous, Sahara; **7** hypothesis of phylogenetic relations between the Sarcopterygii. (**1, 3** after Säve-Söderberg 1937; **2, 6** after Graham Smith and Westoll 1937; **4, 7** after Janvier, 1986; **5** after Chang and Yu 1984)

CHAPTER 4

From the Aquatic to the Terrestrial Environment; the Tetrapoda

4.1 Problems of Adaptation

During the later stages of the Devonian, osteolepiforms, doubtless much like *Eusthenopteron* or the Panderichthyidae, acquired characteristics allowing them to live, at least partly, in a continental environment. These were the first tetrapods. For these aquatic animals to be able to live in a terrestrial setting, it was necessary for them to acquire a certain number of adaptations relative to various vital functions: respiration, resistance to desiccation, locomotion, and reproduction.

4.1.1 Respiration

Whereas fish abstract oxygen from the air of water by gills, terrestrial vertebrates remove it from the air by their lungs. This problem was solved thanks to the existence in the teleosts of a swim-bladder functioning either as a hydrostatic organ or as a lung. In the nontetrapodal Sarcopterygii this organ functioned as rudimentary lungs, but it was the gills that were responsible for the greater part of respiration. In the first tetrapodal vertebrates, on the contrary, the opposite was the case, for the lungs were to play the essential role in oxygenation of the animal. The gills played a part only during the larval stages.

4.1.2 Thermoregulation

Thermoregulation and desiccation constitute a vital problem for a terrestrial vertebrate, but not for a fish. There must have been an ecologic factor favoring the tendency to emergence. In fact, research into littoral ecology has shown that the warmer the climate of a region, the more one observes representatives of typically aquatic groups tending toward an air-breathing life. These animals more often leave the water, frequent the highest levels of the tidal zone, and even invade the terrestrial environment. For example, it is noted that crabs of the family of the Blemnidae which live in a tropical zone move about on the rocks in full sunlight, whereas those of our temperate regions remain submerged at low tide, hiding under stones. This is a matter of heat regulation. The risk of desiccation is great for those sheltering in puddles of water, where they become rapidly heated in the sun and risk being cooked. The animal avoids this risk by emerging, for, even if the air temperature exceeds that of the water, evaporation from the moist surface produces cooling, which is the more marked the higher the temperature. When the animal's body is dry and desiccation advances, it submerges again and reemerges. This is a case of true ecologic regulation of body heat by behavior.

4.1.3 Locomotion

While fish move about by undulation of the body and tail, the fins acting as stabilizers, limbs are absolutely essential for terrestrial forms, and the tail then becomes the stabilizer. A terrestrial form must also adapt to gravity, which implies the development of a rigid vertebral column and powerful limbs.

4.1.4 Reproduction

Most fish abandon their eggs in the water without protection. The factors acting to destroy these eggs are so many that to ensure only a few descendants the females must often produce millions of eggs. This is the reproductive strategy termed *strategy r.* For terrestrial vertebrates there are two great reproductive possibilities: to return to the water to lay a great many eggs or to lay eggs on land while ensuring their protection. This second method allows an adequate number of descendants with production of a reduced number of eggs. This type of reproduction is termed *strategy k.*

The Amphibia, whose name means "double life", have not acquired adaptations allowing them to deposit protected eggs in a terrestrial environment. But they have solved the problem of cutaneous respiration. Because of this, they will always be bound to the water for reproduction and their conquest of the terrestrial environment can only be partial.

This mode of reproduction has important consequences for the development of individuals, who will necessarily undergo two successive life stages: an aquatic larval life and a partly terrestrial adult life.

4.2 Adaptations

The appearance of the Tetrapoda corresponds to a transition stage in the history of the vertebrates in their conquest of the terrestrial environment. The problems just cited have been solved by a number of morpho-functional adaptations, as revealed by structural changes in the skeleton.

4.2.1 Skeleton

4.2.1.1 Limbs

The passage to terrestrial life implies the transformation of the fins of fish into the limbs of tetrapod vertebrates, and here several stages may be distinguished.

In the Actinopterygii, the fins (actinopterygium) were made up of large parallel rays articulating with basal segments lodged between the muscles (Fig. 4.1:2).

The nontetrapodal Sarcopterygii have an important structure of paired fins formed of a median axis (axopterygium) bearing a fringe of short rays (Fig. 4.1:4). In the first Sarcopterygii there was a single proximal bone articulating with the scapulocoracoid bone. There are good reasons for thinking that this bone is homologous with the humerus of the fore-limb and the femur of the hind-limb. At the extremity of this single bone there were two articulated bones, corresponding to the radius-ulna or tibia-fibula, to which were articulated other bones in a radiating pattern comparable to the bones of the hand and foot. The pectoral fin of *Eusthenopteron* (Osteolepiform) (Fig. 4.1:5, 7) shows how much this resembled the structure of the fore-limb of a tetrapod.

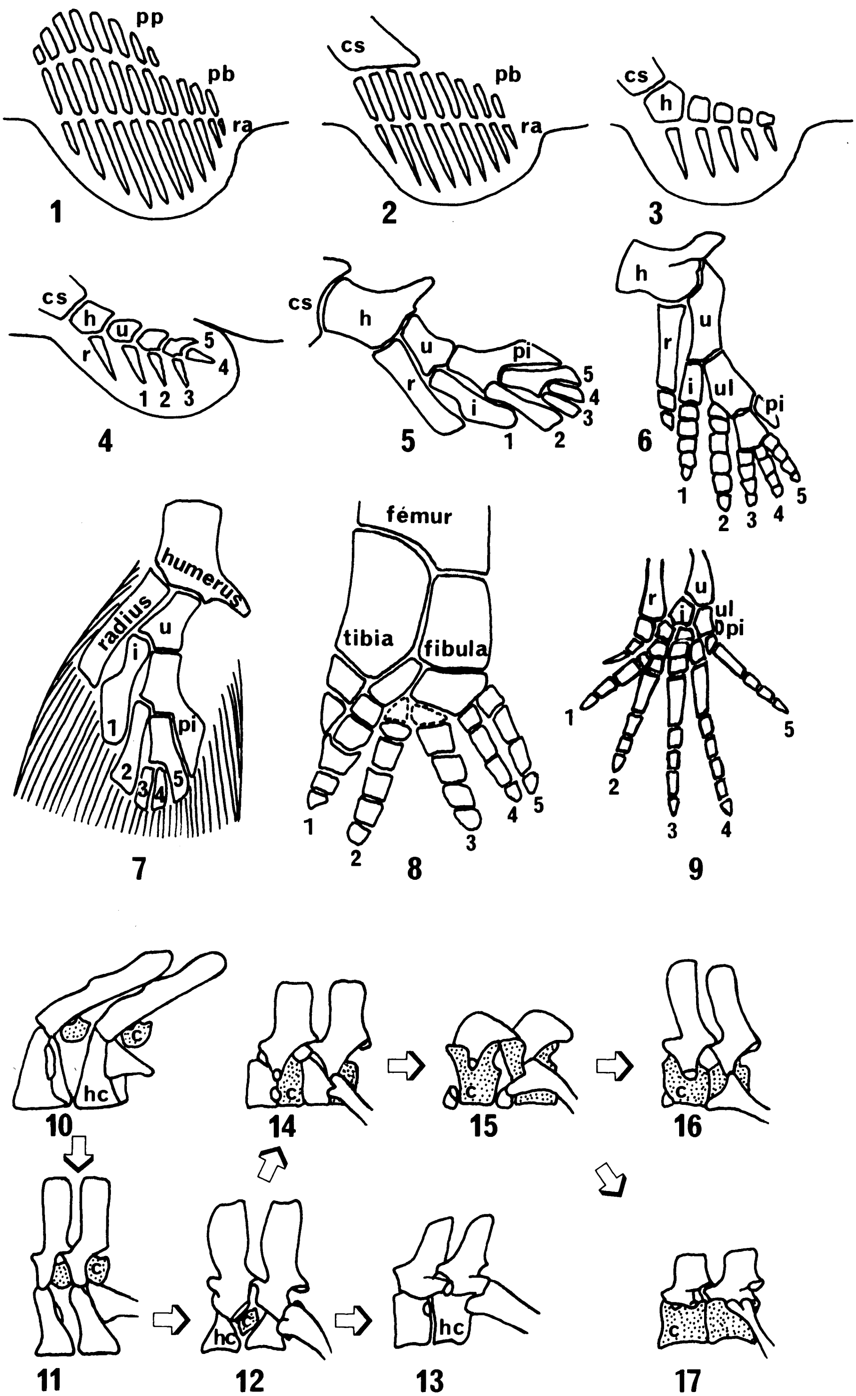
From this structure it is easy to derive that of the limb of the tetrapods, the cheiropterygium (illustrated in Fig. 4.1:6, 9 by the fore-limb of an amphibian), and the hind-limb of *Ichthyostega*, the oldest tetrapod known.

Walking on the ground without support by water implies reinforcement of the limb girdles (interclavicular and sacral) and fixation of the pelvic girdle on the vertebral column. These archaic limbs were heavy and massive.

4.2.1.2 Vertebral Column

Adaptation to gravity is marked by major changes in the structure of the vertebrae. In *Eusthenopteron* and the primitive Tetrapoda the vertebra was formed in its lower part by symmetrical fused elements: two dorsal pleurocentra (or centra) and two ventral intercentra (or hypocentra) of different sizes surrounding the dorsal chord: and in its upper part of two symmetrical fused segments surrounding the spinal cord and carrying a dorsal spine constituting the neurocenter (or neural arch or arcocenter) (Fig. 4.1:10).

Ichthyostega had vertebrae consisting of a large intercentrum and a small pleurocentrum (rachitome type) (Fig. 4.1:11). The neural arches carried zygapophyses providing a strong articulation between the vertebrae. Starting from this structure, two evolutionary tendencies can be observed, but this evolution of the vertebral column is to the present still very hypothetical and subject to revision. One is characterized by the disappearance of the pleurocentra, the vertebral body being formed by the intercentra, leading to vertebrae of stereospondylar type (Fig. 4.1:12, 13). This evolution corresponds to that of a group which returned to aquatic life and had no need of a strong vertebral column. The second tendency,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which corresponds to a perfectioning of adaptation to terrestrial life, is characterized by reduction of the intercentrum. In the embolomeric type (Fig. 4.1:14) the pleurocentrum is as large as the intercentrum, and in the Seymouriamorpha (Fig. 4.1:15) the vertebral body is composed of the pleurocentra alone. This is the first step towards the vertebral structure of the Amniota, totally freed from the aquatic environment. In fact, the vertebrae of the Amniota were derived from this type (Fig. 4.1:16, 17).

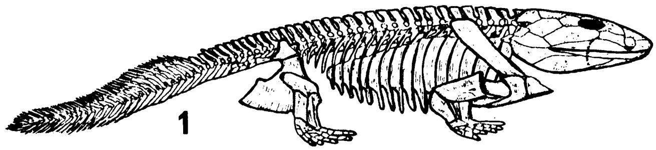
4.2.1.3 Skull

The transition from fish to Tetrapoda is marked by a number of evolutionary trends. There is the backward shift of the orbits and the pineal orifice, the reduction of the parietal and postparietal bones and a flattening of the cranium (Fig. 4.2). The articulation of the skull with the vertebral column is effected by one condyle in the archaic forms and by two in the derived forms. Traces of canals for the sensory organs of the lateral line persist on the cranium of numerous fossil forms. The upper and lower jaws carry teeth, sometimes also the palate. The folds of dental enamel have earned the primitive tetrapods the name of Labyrinthodontes. The very ossified cranium of certain primitive tetrapods of the Primary (*Eryops* among others) and the beginning of the Secondary led them to be termed Stegocephali. This ossification, and also the development of a thick skin often covered with bony plates were adaptions in response to the problem of desiccation.

4.2.2 Reproduction

The need to return to the water for reproduction implies the existence of two life phases for the Amphibia. This double life was made possible by a major innovation: metamorphosis. This must have been the case in the forms of the Primary, as suggested by the existence of the fossil *Protriton petrolei* of the lower Permian of Autun. The fact that gill slits are found, as may be seen in larvae, and that the eyes become smaller in a series of increasing size suggests that *Protriton petrolei* may have been the larva of *Branchiosaurus* (Romer had suggested that *Branchiosaurus* might itself have been the larva of other Stegocephali). Certain features of

Fig. 4.1. Modifications of limbs and vertebrae from the Actinopterygii to the Tetrapoda. **1** actinopterygium; **2** actinopterygium with fused basal elements; **3** axopterygium; **4** axopterygium showing the origin of the five digits of the tetrapoda; **5** pectoral fin of *Eusthenopteron*; **6** fore-limb of archaic tetrapod; **7** pectoral fin of *Eusthenopteron*; **8** hind-limb of tetrapod *Ichthyostega*; **9** fore-limb of evolved tetrapod; *pp* proximal elements; *pb* basal elements; *ra* rays; *cs* scapular girdle; *h* humerus; *u* ulna (cubitus); *r* radius; *p* pisiform; *i* intermedium (lunate); *ul* ulnare (pyramidal); *1, 2, 3, 4, 5* the five digits. (**1, 2, 3, 4** after Vandebroek 1969; **5, 6, 7, 8, 9** after Jarvik 1964). – Evolution of vertebrae in the vertebrates: **10** *Eusthenopteron*; **11** *Ichthyostega*; **12** *Eryops*; **13** Stereospondyl; **14** Embolomere; **15** Seymouriamorph; **16** Synapsid; **17** Diapsid; *c* centrum or pleurocentrum; *hc* hypocentrum or intercentrum. (After Vandebroek 1969)



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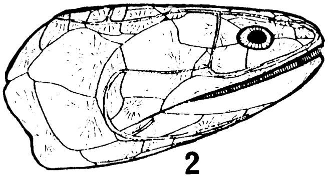

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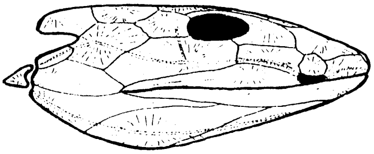

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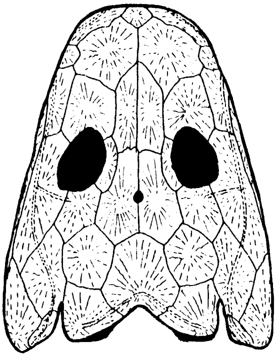

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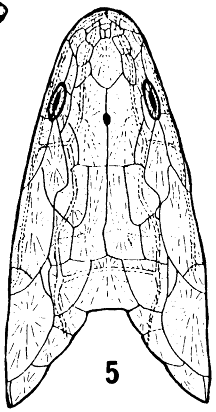

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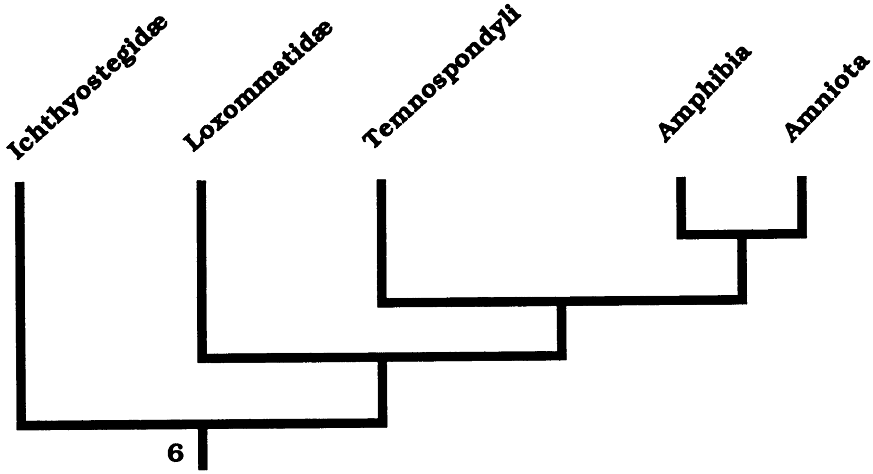
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Loxommatidæ
Temnospondyli
Amphibia
Amniota

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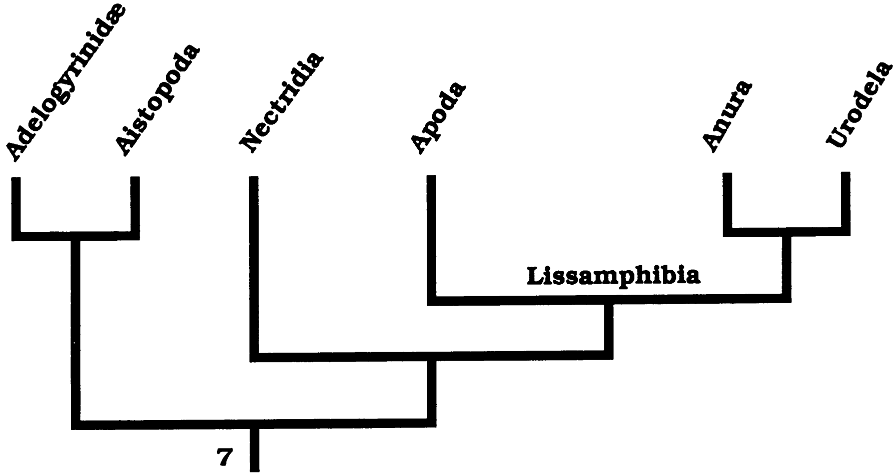
Adelogyrinidæ
Aistopoda
Nectridia
Apoda
Anura
Urodela
Lissamphibia

7

their skeleton (gills?) suggest that the larger branchiosaurs (10 to 18 cm) could be neotenic forms, i.e., that they retained larval characters in the adult state, a matter of developmental heterochrony. Heterochronies were to play a considerable part in the diversification of the Amphibia.

4.3 Paleontological History of the First Tetrapoda

The origin of tetrapods has always been disputed. While the arguments in favor of the traditional view, that they are derived from osteolepiforms are accepted by many (Panchen 1985), Rosen et al. (1981) proposed an alternative hypothesis that the lungfishes are the sister-group of the tetrapods.

With the exception of two small and very primitive groups, the Ichthyostegidae and the Loxommatidae, the Tetrapoda comprise three great groups: the Temnospondyli, the Lissamphibia and the Amniota (Fig. 4.2). To these last it is useful to associate a paraphyletic collection of primitive fossil forms known by the name of Anthracosauria, which herald the true Amniota.

4.3.1 Ichthyostegidae

This group includes the Amphibia which preserved teeth of labyrinthodont type. The oldest have been found in the old red sandstone of the upper Devonian in Greenland (*Acanthostega* and *Ichthyostega*). *Ichthyostega* (Fig. 4.2) is a form in which the characteristics of fish and amphibian are distributed in a mosaic. As compared with *Eusthenopteron*, there is a noticeable change between the proportions of the cranial bones linked with the development of a snout essential for seizing prey (Fig. 4.2).

4.3.2 Loxommatidae and Crassigyrinus

These forms of the lower and middle Carboniferous share with the other Tetrapoda entirely open sensory grooves, but still possess folded teeth (polyplacodont) like *Ichthyostega* and the osteolepiforms, though the folds are simpler than in the other "labyrinthodonts".

They are known only by four genera characterized by keyhole-shaped orbits. The loxommatidae are undoubtedly rather primitive, but their position as a sister-

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Fig. 4.2. *Eusthenopteron* (osteolepiform) and *Ichthyostega* (tetrapod). **1** skeleton of Ichthyostega; **2** lateral view of cranium of *Eusthenopteron*; **3** laterial view of cranium of *Ichthyostega*; **4** dorsal view of cranium of *Ichthyostega*; **5** dorsal view of cranium of *Eusthenopteron*. The passage from osteolepiforms to Tetrapoda is marked by the development of a snout, recession of the eyes and pineal foramen, and shortening of the posterior region of the dermal neurocranium; **6** cladogram of principal groups of Tetrapoda; **7** cladogram of Amphibians. (**1**, **2**, **3**, **4**, **5** after Jarvik 1952, 1954; **6**, **7** after Gardiner 1983)

group of non-ichthyostegid amphibians, as proposed by Gardiner (1983) in Fig. 4.2, has not really been proven. Panchen and Smithson (1988), for example, connect them to the anthracosaurid line, whereas Milner et al. (1986) consider them as a separate group like *Crassigyrinus* (the sole representative of its group), an aberrant animal with enormous quadrangular orbits and a long narrow jaw from the Carboniferous of Scotland (Panchen 1985).

4.3.3 Temnospondyli

Ranging from the lower Carboniferous to the lower Jurassic, they do not exhibit any general characteristics of the Temnospondyli, despite "their uniquely derived hearing system adapted to receiving high-frequency air-borne sound" (Milner et al. 1986) with modifications of the jaw muscles and an open palate with large vacuities. Based on the development of the vertebrae, two tendencies can be distinguished with the intercentra predominating in the Temnospondyli, and the pleurocentra in the anthracosaurs.

The most primitive had rhachitome vertebrae and the more evolved stereospondylar vertebrae (Fig. 4.1). *Eryops*, of the Permian, is a characteristic member of this group, well adapted to terrestrial life (Fig. 4.3). *Eryops* was 1.8 m long and had a wide flat rugose head with large optic notches and teeth implanted on the jaw margins and palate. The vertebral column, the limb girdles and the limbs were strong and massive due to vigorous endochondral ossification. *Trematops* is another example shown in Fig. 4.3.

Springing from the rhachitome vertebrates there developed the group of stereospondylar vertebrates of the Triassic. These animals adapted to the aquatic environment. Although their metamorphosis remained complete, a delay in ontogenetic development resulted in incomplete endochondral ossification and the persistence of cartilages, which became mineralized. They reached a very large size, notably of the skull in relation to the rest of the body (*Metoposaurus*, *Mastodontosaurus*). As shown by de Ricqlès (1979), this evolution was achieved by developmental heterochronies, notably by more or less marked neotenies. In certain forms it is probable that metamorphosis was totally or partially eliminated, leading to morphologies comparable to those observed in larvae or juveniles ancestors of normal ontogenetic development (*Dinosaurus*, *Gerrothorax*, *Benthosuchus*) (Fig. 4.3).

4.3.4 Lissamphibia

Three existing groups of Lissamphibia share numerous synapomorphies, notably pediculate teeth. These are the frogs (Anura), newts and salamanders (Urodela), and the Apoda (Gymnophiones) (Fig. 4.2). To these may be annexed the former "Lepospondyli" (Nectridia, Aistopoda, and Microsauria). The phylogenetic relationships between Lissamphibia and Lepospondyli are not clear.

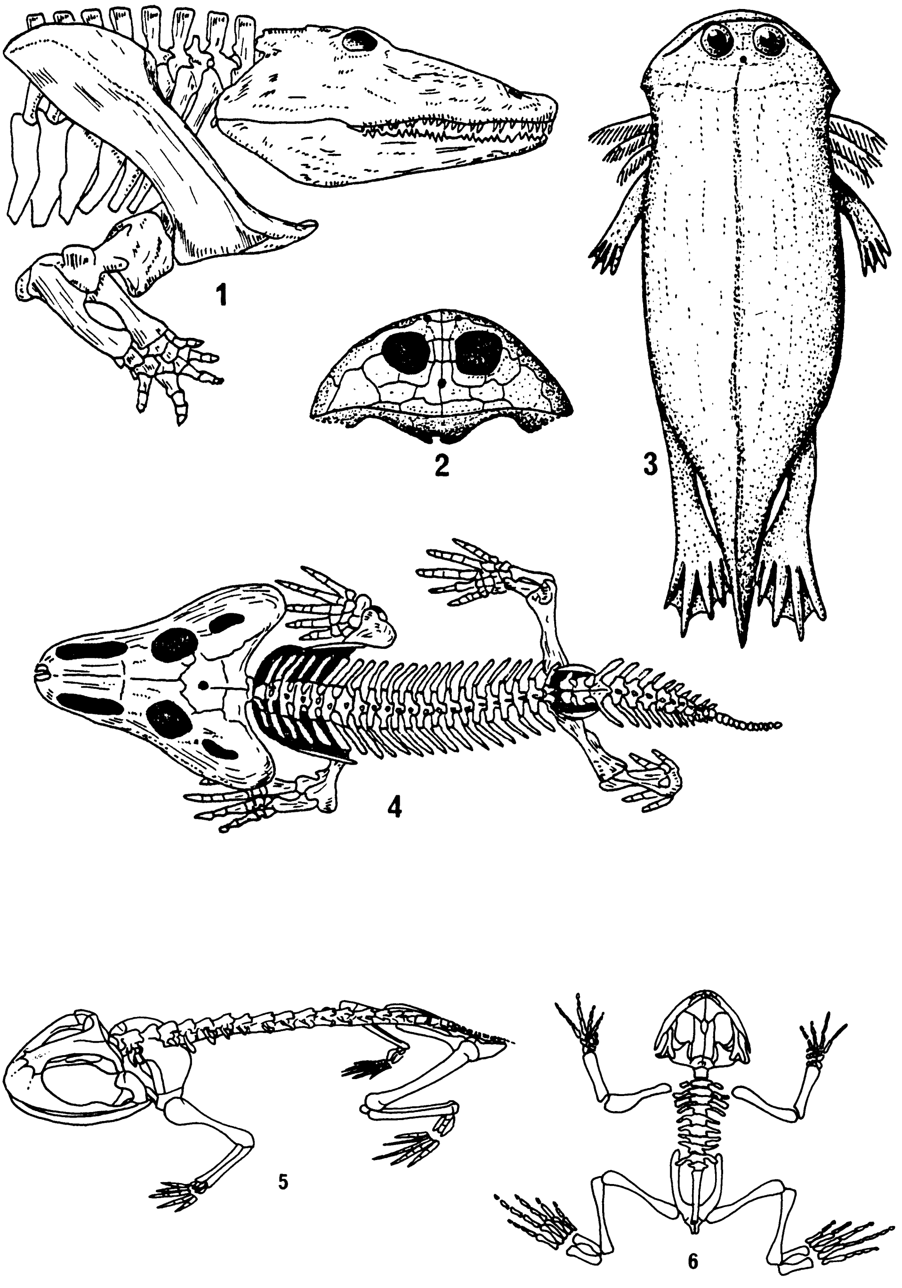

Fig. 4.3. Amphibians. **1** *Eryops*, Texan Permian, anterior part; **2** *Gerrothorax*, dorsal view of cranium; **3** *Gerrothorax*, reconstruction; **4** *Trematops*; **5** *Triadobatrachus*, early Triassic; **6** *Notobatrachus* late Jurassic; (**1** after Miner 1925; **2** after Romer 1947; **3** after Nilsson 1946; **4** after Olson 1941; **5** after Rage and Rocek 1989; **6** after Estes and Reig 1973)

4.3.4.1 Lepospondyli

The unity of the Lepospondyli has been questioned by Bossy (1976), Milner (1980), and Milner et al. (1986). Nectridians and aïstopods are a group of specialized limbless forms with very long body and short tail. They range from Visean to lower Permian. They share derived vertrebral characters (elongate centra, the neural spines fused to the neural arch) not found in microsaurs. This is the reason why Lepospondyli is an unnatural paraphyletic group. As the earliest known aistopod is from the Visean of Scotland and if aïstopods are the sister-groups of the nectridians, then their dichotomy must have occurred at the basal Carboniferous, even in the late Devonian (Milner 1980). Lepospondyli disappeared at the end of the Paleozoic.

The Nectridia diversified into forms that were flattened and broadened (*Diplocaulus*) or snakelike (*Sauropleura*). *Diplocaulus* (Permian) had a very broad horned head and feeble limbs, and doubtless lived at the bottom of streams. The Aistopoda were snakelike animals living on marsh shores of the Carboniferous and Permian. *Ophioderpeton* and *Dolichosoma* are the oldest known forms devoid of limbs. Finally, the Microsaura, regarded by Gardiner (1982) as Amniota and first discovered in the hollow trunks of *Sigillaria* in Nova Scotia (Canada), were abundant in the lower and middle Carboniferous. Microsaurs were small aquatic or terrestrial tetrapods. *Rhynchonkos* from the lower Permian of Oklahoma has been considered as a possible close relative to modern caecilians.

4.3.4.2 Anura

The first indications of anural structure are to be found in *Amphibanus* in the Pennsylvanian, but there exists an enormous hiatus in the fossil record between the stegocephali and present-day Amphibia (frogs, toads). These last can be identified in the lower Triassic of Madagascar with *Triadobatrachus* (Fig. 4.3). This form already had some characteristics of the Anura. True frogs are known from the Jurassic, with a reduced number of vertebrae, the formation of the urostyle (fusion of the last vertebrae) and disappearance of the tail in the adult, a group of adaptations to life at the water's edge and to jumping.

4.3.4.3 Urodela and Apoda

The first Urodela discovered in the middle Jurassic show no major differences from existing members, characterized by an elongated axial skeleton (100 vertrebrae) and a reduction of ossification. The Apoda, burrowing Amphibia of the tropics devoid of limbs, are known in the fossil record since the Cretaceous-Tertiary boundary. Developmental heterochronies have played a very great part in the evolution of the Urodela. It seems that the extent of endochondral ossification ot their endoskeleton varied inversely to their degree of neoteny. The complete blockage of endochondral ossification in the Proteidae resulted in calcified cartilages (de Ricqlès 1986) (see Sect. 4.4.4.1).

4.3.5 Primitive Amniota or "Anthracosauria"

This group includes lines with amniote affinities: the Embolomera of the Carboniferous and the Seymouriamorphs of the Permian. The oldest anthracosaurs are represented by the embolomeres (*Eoherpeton* and *Proterogyrinus*) of the lower Carboniferous. They are thus somewhat older than the oldest amniota known so far from the middle Carboniferous (*Archerpeton* and *Hylononus*). The aquatic embolomeres were large crocodile-like forms. The terrestrial anthracosaurs were smaller, retainning a primitive skull characterized by short-paired tabular horns extending posteriorly from the back of the skull (Panchen 1980). The seymouriamorphs, because of their vertebrae with dominant pleurocentra, seem close to the line(s) which gave rise to the Amniota. *Seymouria*, of the lower Permian of Texas, was for long regarded as an intermediate form between Amphibia and Amniota, but all the characters considered as "reptilian" have been refuted. An egg-like fossil has been discovered in the lower Permian of Texas, but it is not clear whether it is really an egg in the true sense or the egg of amniota. The diadectomorphs (*Diadectes* of the lower Permian of North America) which have been considered otherwise as belonging to the amniota, are included now with the anthracosaurs (Panchen 1980; Heaton 1980).

4.4 Developmental Heterochronies

Study of the evolution of the Stereospondyli has stressed the importance of modifications of the rate of ontogenetic development in the reduction of ossification or the maintenance of a larval morphology. In effect, developmental heterochronies constitute a simple means of important evolutionary change based on acquired structures without any missing-link. In a way, as Jacob expressed it (1977), it is a matter of a real "tinkering", exploiting the possibilities allowed by regulation of the processes of development. There exist four main types of heterochrony (Gould 1977; Alberch and Alberch 1981; McNamara 1986, 1988), on which may be superimposed early or late innovations (Dommergues et al. 1986), summarized in Chapter 1.4 in Fig. 1.2 and 1.3. These developmental heterochronies have been studied in detail in existing amphibians, where the relevant processes and factors have been demonstrated. We shall examine in turn cases of neoteny and then a case of progenesis.

4.4.1 Neoteny

Neoteny corresponds to a delay in somatic development without any modification of sexual maturation. The result is adults exhibiting juvenile characteristics and morphology, or a larval morphology in species with metamorphosis.

The Mexican axolotl (*Ambystoma mexicanum*) is a classic case of neoteny, where in nature aquatic forms exist with external gills, and terrestrial forms without gills. Norris and Gern (1976) have shown that the injection of a small amount of thyroxin into the hypothalamus activates the production of thyroxin and induces metamorphosis in the terrestrial form (Fig. 4.4). Neoteny is therefore regulated by a simple endocrine mechanism controlled by two alleles of a single gene (Humphrey 1967). It has been observed that certain newts which usually metamorphose in warm water marshes become neotenic in the cold waters of mountain environments. Here the tissues do not seem to react to the effects of thyroxin. In fact, the changes induced by hormonal processes may be varied according to the chronology of hormonal action and interactions with the tissues and external factors. It has also been noted that stagnant waters poor in oxygen often contain neotenic forms. These findings account for the neotenic trends of the Stereospondyli, which, by returning completely to aquatic life, are characterized by the persistence of cartilage. There is an equilibrium between the metabolism and the environmental parameters (temperature, oxygen), translated at the histologic level as skeletal neoteny. These hypothyroid endocrine processes seem to be fairly general in the Tetrapoda that re-adapt to aquatic life, as evidenced by the numerous instances of convergence observed. Heterochrony of development has played a major part in the secondary adaptation of the Tetrapoda to the aquatic environment. The transition from the terrestrial to the aquatic setting is marked by rather general transformations resulting from paedomorphosis due to neoteny: reduction of relative size of the limbs, relative elongation of the trunk, reduction of the number of digits, disappearance of the regions of great elongation of the skull preserving the juvenile proportions, more or less complete suppression of metamorphosis, disappearance of certain bones, and especially regression of endochondral ossification of the endoskeleton, pachyostosis, etc. (de Ricqlès 1986, 1989; see Chap. 9.4)

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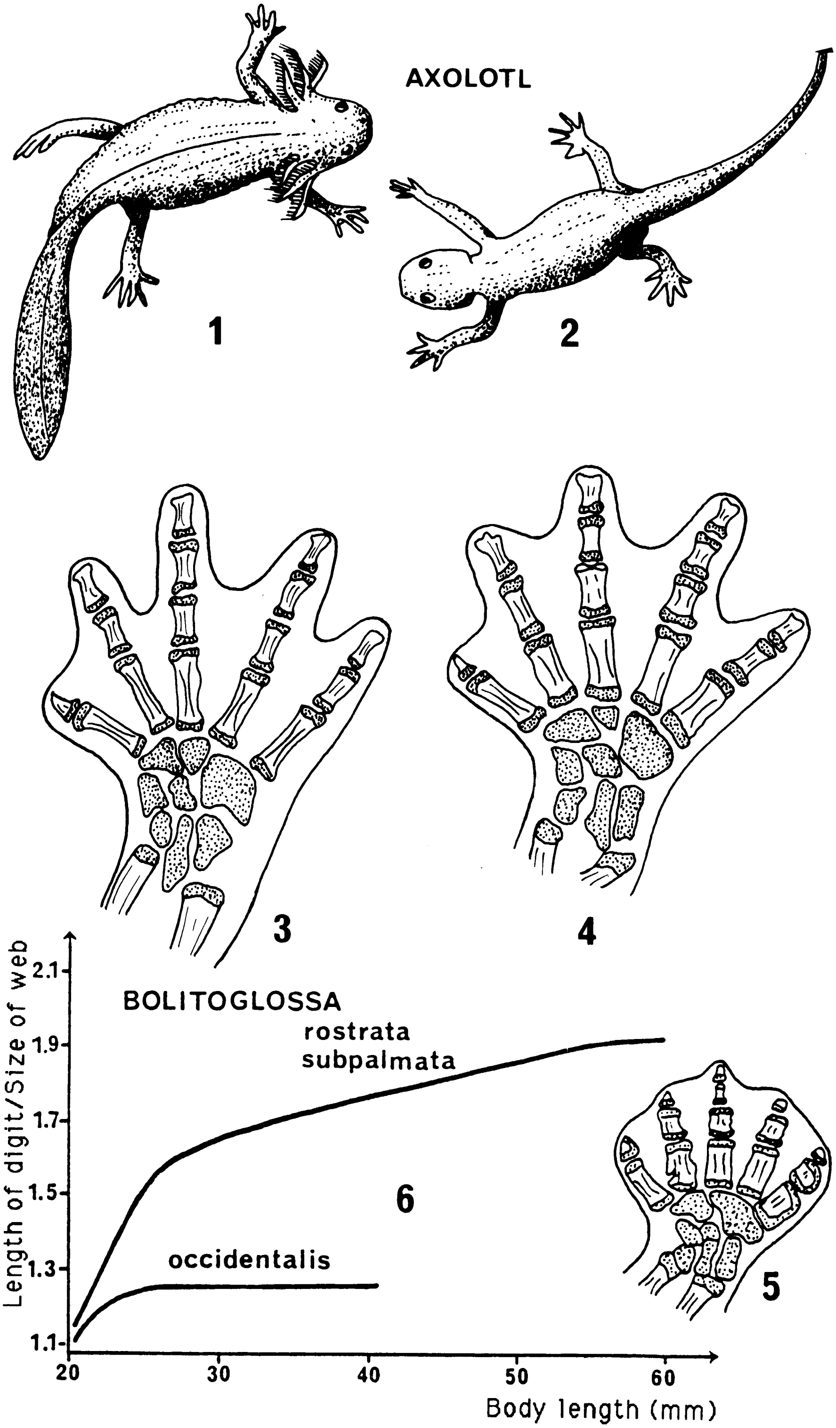
Fig. 4.4. Examples of neoteny and progenesis. The Mexican axolotl retains gills, a flattened tail, and a larval skin though it attains adult size and sexual maturity (**1**). This neotenic paedomorph can metamorphose into a typical terrestrial adult (**2**) by treatment with thyroxin; **3, 4** foot of terrestrial species of the salamander *Bolitoglossa* (**3** *rostrata* and **4** *subpalmata*); **5** foot of arboreal progenetic species *B. occidentalis*; **6** ontogenetic pathways of growth of the foot in the preceding species. Growth is truncated in *B. occidentalis* and the smaller adult foot becomes palmate (**5**). (**1, 2** after Raff and Kaufman 1983; **3** to **6** after Alberch and Alberch 1981)


AXOLOTL
1
2
3
4
BOLITOGLOSSA
rostrata
subpalmata
occidentalis
6
5
Length of digit/Size of web
2.1
1.9
1.7
1.5
1.3
1.1
20
30
40
50
60
Body length (mm)

4.4.2 Progenesis

This is a phenomenon evidenced by an acceleration of sexual maturation without modification of somatic development which curtails the development of the later ontogenetic stages. The outcome is an animal of small size which can reproduce with a larval morphology or a mixture of larval and adult characters. It seems that this phenomenon may favor adaptations to certain milieux where small size and a high reproduction rate are particulary important. For example, Alberch and Alberch (1981) compared three species of salamanders of the genus *Bolitoglossa*: *B.occidentalis*, an arboreal species, and *B.rostrata* and *B.subpalmata*, essentially terrestrial (Fig. 4.4). The arboreal form is smaller than the other two, exhibiting a modification of the foot, which becomes palmate, while the skull has reduced ossification and no prefrontal. These authors have shown that *B.occidentalis* resembles the young of the two other species. All these features suggest an explanation by curtailment of somatic development, i.e., by progenesis.

The cases of neoteny and progenesis discussed for the amphibians illustrate the fundamental role played by these developmental heterochronies in evolution. They make it possible to propose simple mechanisms to explain considerable morphological modifications without having recourse to macromutations, the "hopeful monsters" of Goldschmidt (1940).

CHAPTER 5

The Conquest of the Terrestrial Environment: The Amniota

5.1 Characteristics and Phylogenetic Relationships

The conquest of the terrestrial environment by the Amniota implied resolution of the fundamental adaptive problems related to reproduction and desiccation.

5.1.1 Reproduction

Only total independence from the water could allow effective conquest of the continents. This autonomy was granted to the "reptiles", birds, and mammals by the appearance of the *amniotic egg*, an egg protected against desiccation by a calcareous or resistant shell permeable to air. The amnion is a fluid-filled cavity in which the embryo floats, thus exhibiting an aquatic phase. Nutrient materials are accumulated in the vitelline sac, while the allantoic sac for excreta also plays a respiratory role. The egg laid on land, when it hatches, liberates a newborn animal capable of surviving in the terrestrial setting. An egg-like fossil from the lower Permian of Texas has been attributed without formal proof to the amniota. It is proper to mention the difficulty of determining a fossil amniote on the basis of a skeleton since the amnion is observable only in existing specimens; but there is one osteologic feature specific to present-day amniotes, the presence of an axis in addition to the atlas which is not present in the amphibia.

5.1.2 Thermoregulation

Whereas the skin of the Amphibia has an important respiratory role and must always remain moist, the Amniota were to become covered with a scaly layer impermeable to water. The excreta were extracted in the form of solid uric acid in the cloacal cavity, where the transport water was reabsorbed. The continental environment is marked by swings of temperature, often very great. Most of the "reptiles" are exothermal, using solar heat to increase their temperature. The histologic structure of the dinosaurs suggests that they may have been heterothermal, with a raised metabolism and a special thermal physiology intermediate between the exothermy of the other lepidosaurs and the homeothermy of the birds and mammals.

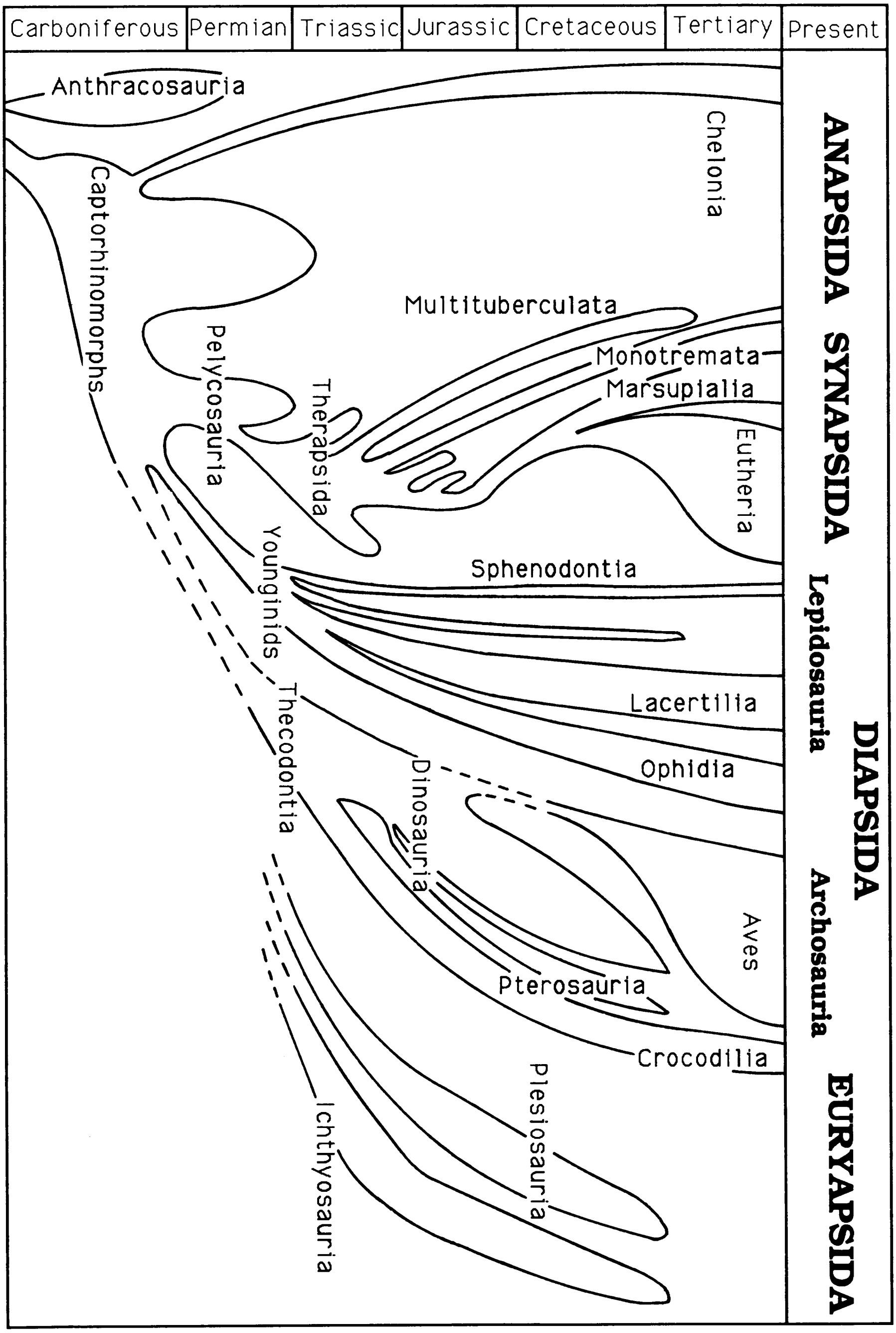


Fig. 5.1. Phylogenetic relationships of the Amniota (after Janvier et al. 1980)

5.1.3 Phylogenetic Relationships

It has long been known that the concept of a class of reptiles has no phylogenetic significance. The Amniota constitute a monophyletic assemblage within which cladistic analysis makes it possible to identify three monophyletic groups: the turtles, the Therapsidae and mammals, the Lepidosauria (Sphenodontia, lizards, snakes) and the Archosauria (Dinosaurs, Pterosaurs, birds and crocodiles) (Fig. 5.1).

5.1.4 Cranial Structures

Four types of cranial structure can be distinguished in the Amniota and have long been used in classification (Watson 1917) (Fig. 5.2). These structures reflect different implantations of the masticator muscles.

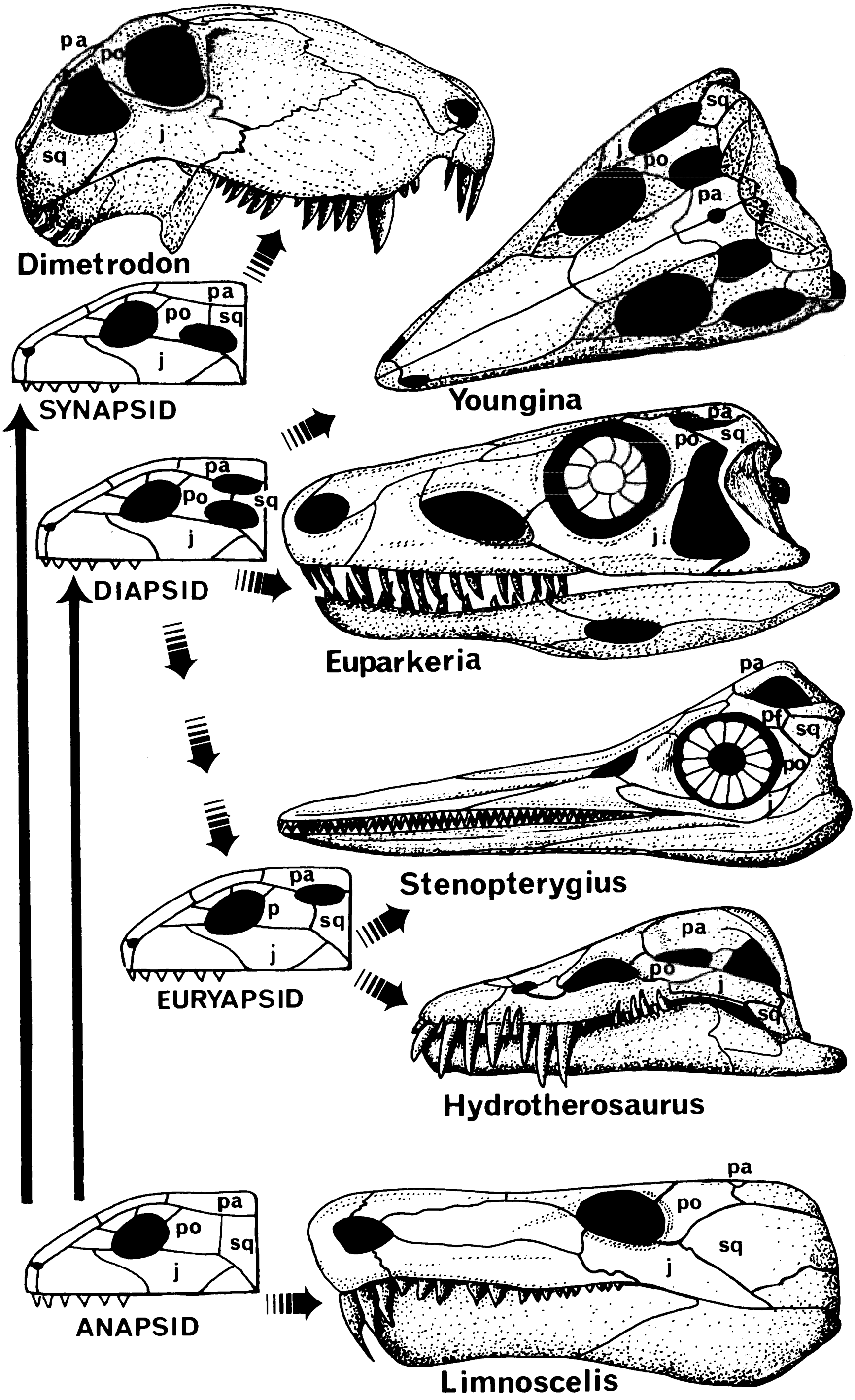
The oldest forms, the anapsids of the end of the Carboniferous and the marine and terrestrial turtles, had a skull devoid of a temporal fenestra behind the orbit (anapsid type). *Limnoscelis* (Captorhinomorph) is an example in Fig. 5.2.

The Therapsidae and mammals had a synapsid skull with a single temporal fenestra situated below the arch formed by the squamosal and postorbital (example: *Dimetrodon*, a pelycosaur, Fig. 5.2). In the dinosaurs, pterosaurs, crocodiles, and sphenodontia, the skull possesses two temporal fenestrae situated on either side of the squamoso-postorbital arch (diapsid type) (e.g., *Euparkeria*, a thecodont, and *Youngina*, a eusuchian, Fig. 5.2). The lizards only retain one of the originally present two fenestrae, whereas the snakes last both of them.

Another, so-called euryapsid, structure observed in the plesiosaurs, nothosaurs, placodonts, and ichthyosaurs, is manifested as a temporal fenestra situated very high above the squamosopostorbital arch. Kuhn-Schnyder (1967) and Mazin (1982) have shown that this structure was derived from an inferior fossa which opened ventrally. From this structural stage the plesiosaurs (e.g., *Hydrotherosaurus*), nothosaurs, and placodonts derived. Subsequently, the reconstitution of this interrupted barrier in a high position led to reinforcement of the postorbital region, as observed in the primitive ichthyosaurs. Finally, in the evolved ichthyosaurs (e.g., *Stenopterygius*) the increase in the size of the eye brings about posterior extension of the postfrontal, which partly constitutes the inferior temporal bar (Mazin 1985). Thus the euryapsid structure would be derived from the diapsid (Fig. 5.2).

5.2 The First Amniota

The oldest known amniotes are *Hylonomus* and *Archerpeton* of the middle Carboniferous of Nova Scotia, discovered in the hollow trunks of *Sigillaria*. Pre-upper Permian amniota are represented by captorhinomorphs, pareiosaurs, mesosaurs, pelycosaurs and aeroscelidians.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ANAPSID
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Limnoscelis

5.2.1 Captorhinomorphs

Hylonomus and *Romeria* of the middle Carboniferous were small predators provided with a single row of maxillary teeth for an insectivorous regime. They preceded *Limnoscelis* (Fig. 5.2), *Captorhinus*, and *Labidosaurus* of the lower Permian of the USA, whose skull, 7 cm long, possessed two to three rows of maxillary teeth. This series (Fig. 5.3) is continued with *Captorhinikos-Kahneria* (middle Permian of the USA) and *Gecatogomphius* (upper Permian of the USSR) and culminates in *Moradisaurus* of the Niger with a skull reaching 42 cm. There is thus a major increase of size in the series and an increase of dental rows to the number of 11–12 in *Moradisaurus*. De Ricqlès (1980) suggests that the captorhinomorphs originated by progenesis in a selective regime, and that the series evolved as the result of hypermorphosis in a selective k regime.

5.2.2 Procolophonia and Others

Besides the Procolophonia of the Permian of the USSR and the Triassic of South Africa, comparable in size to our lizards, Pareiosaurs of very great size (2.4 to 3 m), have been described with a short tail, massive limbs, and broad feet. These forms were doubtless herbivores. The Mesosaurs were aquatic Amniota with a tapering skull of piscivorous type, identified form the Permian in Africa and South America.

5.3 Turtles

The Chelonia are known from the Triassic to the present day. *Proganochelys* of the Triassic has all their characteristics, notably the carapace of dermal bones fused with the pectoral girdle. This turtle still had palatal teeth and could not retract its head, limbs, and tail under the carapace like modern turtles. Turtle have been long considered as a primitive and relict group. Gaffney (1975) shows that two major lineages (cryptodires and pleurodires) arose early in their history and repeatedly evolved parallel adaptations. Most of the differences between the crytodires and pleurodires are related to the palatoquadrate bones. From Proganochelydia were derived the Pleurodira, whose neck could be moved sideways to

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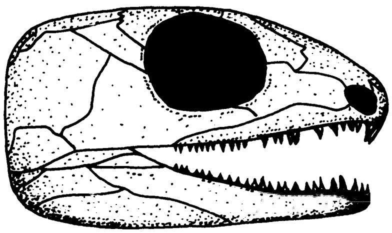
Fig. 5.2. Cranial structures of the Amniota. Anapsid type (without temporal fossa): *Limnoscelis* (Captorhinomorph); euryapsid type (temporal fossa above the sq-po arch: *Hydrotherosaurus* (plesiosaur); the Ichthyosaurs have a euryapsid type derived from a diapsid type by loss of the inferior opening (convergence) (e. g., *Stenopterygius*); diapsid type (two fossae): *Euparkeria* (thecodont) and *Youngina* (eusuchian); synapsid type (one fossa below the sq-po arch; *Dimetrodon*, pelycosaur); *j* jugal; *po* postorbital; *pa* parietal; *sq* squamosal (L. after Romer 1956; H. after Welles 1952, E. and Y. after Broom 1924; D. after Romer and Price 1940)



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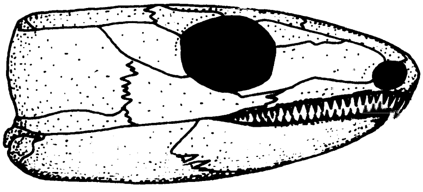

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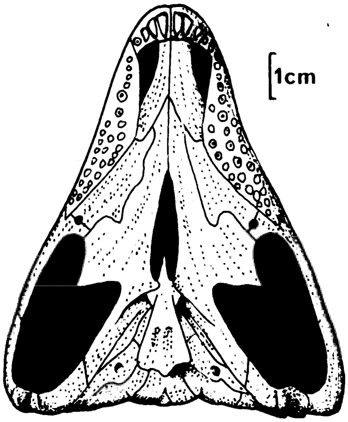

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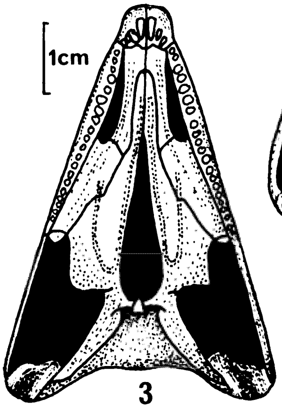

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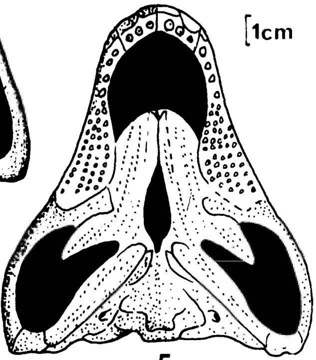

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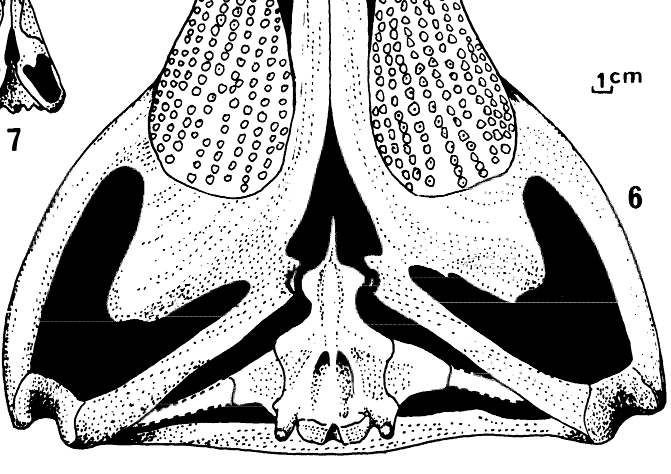

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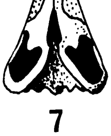

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protect the head under the carapace, and the Cryptodira, where this movement occurred from front to back by a S-bend of the neck. These turtles no longer had palatine teeth, but a horny beak. Numerous Cryptodira became adapted to an aquatic environment with a reduced ossification, flattening of the carapace, and phalanges. Some turtles may attain great size, like the present-day giant tortoise of the Galapagos measuring 1.5 m and weighing 250 kg, and the marine leathery turtle of 1.8 m and 500 kg.

5.4 Lepidosauromorpha

Being present in the Permian and Triassic, the lepidosauromorphs include younginids and lepidosauria: the Squamata (lizards, snakes and amphibaenians) and Sphenodontidae (*Sphenodon* and its fossil relatives). The old paraphyletic stem-group of the Eosuchians has been discontinued as the result of cladistic analysis (Rage 1982; Benton 1985). Whereas the younginids are well established among the lepidosauromorphs, the Prolacerta have been rejected to the archosauromorphs, and the paliguanids and kuehneosaurids to Diapsida of uncertain position.

The paliguanids, *Paliguana* and *Blomosaurus*, certain lizard-like forms from the late Permian to early Triassic of South Africa, are classified as relatives of the lepidosauromorphs.

5.4.1 Younginiformes

Youngina from the Permian of South Africa (Fig. 5.2) had the appearance of an about 40 cm long lizard. Its triangular skull exhibits a diapsid structure with a large pineal orifice and two large lateral eyes. Some recent tangasaurids, namely *Kenyasaurus* and *Tangasaurus*, are also included with the younginoids.

5.4.2 Sphenodontia

Known since the early Triassic (*Palacrodon*), the group persists into the Jurassic with *Homeosaurus* and *Kallimdon* (less than 20 cm long), leading to the present-day relict *Sphenodon* (Hatteria or Tuatara) ressembling an iguana.

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Fig. 5.3. The Captorhinomorphs. **1** *Romeria prima*, lateral view of skull; **2** *Captorhinus aguti*, lateral view of skull; **3** *Romeria texana*, palatine view of skull; **4** *Captorhinus* sp., compiled palatine view of skull; **5** *Captorhinikos chozaensis*, palatine view of skull; **6** *Moradisaurus grandis*, palatine view of skull; **7** *Captorhinus*, palatine view of skull on some scale as **6**.(**1** and **3** after Clark and Carroll 1973; **2** after Gaffney and McKenna 1979; **4**, **5** after Olson and Barghausen 1962; **6**, **7** after de Ricqlès and Taquet 1982; **1** to **7** after de Ricqlès 1984)

5.4.3 Lizards

The lizards are characterized by their special form of mandibular articulation. The base of the temporal fossae was opened, therefore the quadrate became mobile and its ventral extremity was freed. The true lizards appeared in upper Jurassic and developed in the upper Cretaceous where forms close to the present-day monitors, the Mosasaura, adapted to marine aquatic life. Reaching up to 10 m in length, the mosasaurs had a trunk as long as the tail, short limbs, and a head with pointed teeth except for *Globidens*. They disappeared in the upper Cretaceous. Today, the lizards are widely diversified into 3300 species, from the geckos with adhesive digits to the desert Agamidae, the crested iguanas and the monitors of Komodo (Sunda islands), reaching 3 m in length.

5.4.4 Snakes

These have a very lightly constructed cranium, poor material for fossilization. The shift backwards of the articulation between quadrate and mandible and the fact that the two mandibles are not joined permanently in front, but connected by a ligament at the position of the symphysis allowing them to spread apart, facilitate wide opening of the mouth. The two temporal fossae have disappeared as the arcs delineating them have been eliminated. Teeth are implanted along the complete length of the jaw, some being associated with venom glands. In the fossil state the snakes are for the most part known only by their vertebrae, as for the two oldest snakes: *Lapparentophobis* of the lower, and *Simoliophis* and *Pouitella* of the "middle" Cretaceous. They have become widely diversified into 2300 existing species. According to Rage (1982), the snakes and the Amphisbaenidae (a group with limb regression) are the sister-group of the lizards.

5.5 Archosauromorpha

These are characterized by a preorbital fossa.

5.5.1 Rhynchosauria

Rhynchosaurs are known from the mid-Triassic of England (*Rhynchosaurus*) and Tanzania (*Stenaulorhynchus*). *Scaphonyx*, a large heavy form up to several metres long, comes from the late Triassic of Brazil and Argentina. Their skull exhibits considerable broadening in the posterior part and possesses an edentate hooked beak. In contrast to the generally held belief, the rhynchosaurs are not related to the Sphenodontia.

5.5.2 Archosauria

As demonstrated by Gauthier (1984), the archosaurs are a monophyletic group united by 26 synapomorphies, encompassing the crocodiles, birds, and certain fossil taxa. Some of the latter, the Pseudosuchia, including Parasuchia, Aetosauria, and Rauisuchia, are closely related to the crocodiles. Other groups, the Ornithosuchia, including *Euparkeria*, ornithosuchids, *Lagosuchus*, Pterosauria, and non-avian dinosaurs are closer to birds (Fig. 5.4).

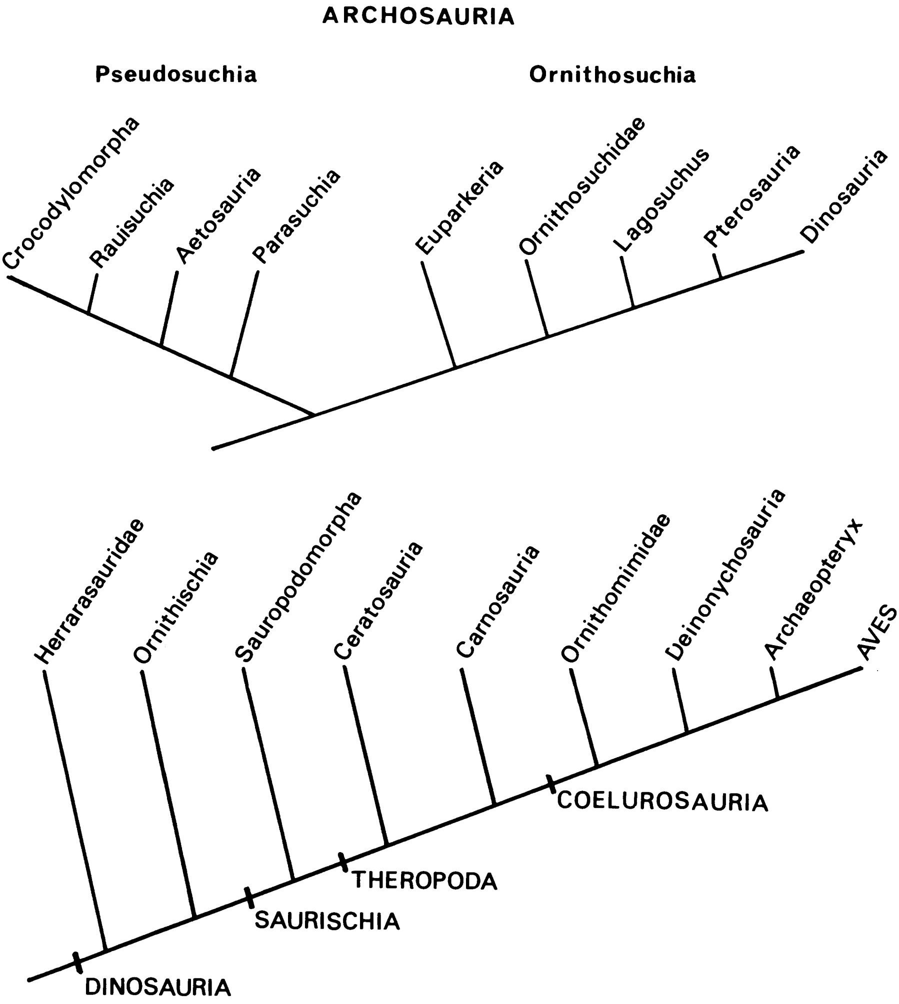


Fig. 5.4. Phylogenetic relationships of archosaurs, (After Gauthier and Padian 1984)

Euparkeria (Fig. 5.2), of the lower Triassic of South Africa, 60 cm long, was partly biped with a tail acting as a stabilizer. The skull, with two temporal fenestrae and an anteorbital opening, had a typical archosaur structure. The teeth were implanted in alveoli. The group diversified into carnivorous forms, some small (*Lagosuchus*) and some large (*Ornithosuchus*).

5.5.3 Dinosaurs

5.5.3.1 Characteristics and phyletic relationships

The traditional term "dinosaur" (terrible lizard) includes two groups: the Saurischia and the Ornithischia, distinguished by the structure of the pelvis, skull, and limbs.

The Saurischia (Fig. 5.5) had a triradiate pelvis without a prepubis and teeth extending along the jaws. Most of the carnivores were bipeds, with hind-limbs of avian appearance; but the herbivores were characterized by a return to the quadripedal state with massive feet usually carrying claws.

The Ornithischia (Fig. 5.5) had a tetraradiate pelvis with a distinct ilium, ischium, pubis, and prepubis. They all possess a distinguishing bone in front of the jaw, the predentarium which does not have teeth. When this bone grows longer, it

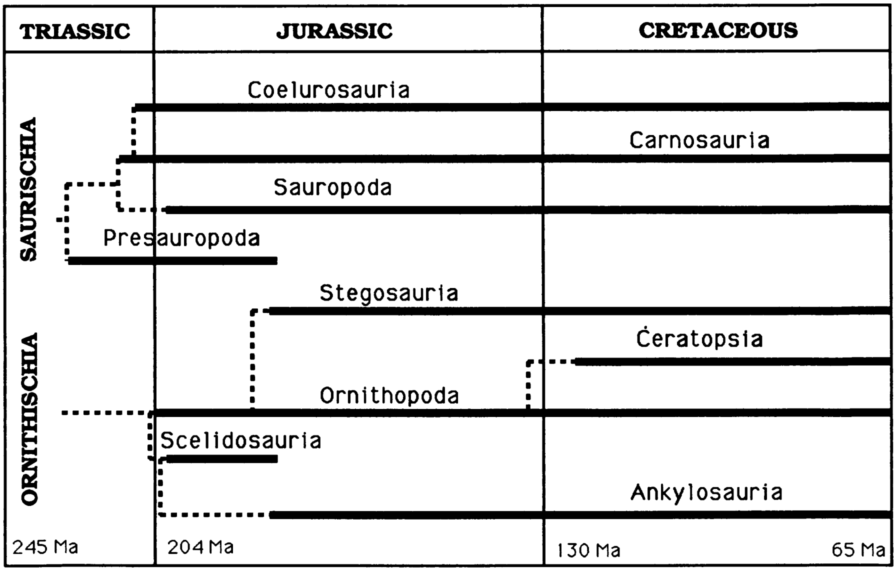


Fig. 5.5. Phylogenetic relationships and fossil record of the dinosaurs (after data of Lambert et al. 1983)

takes the shape of a beak from the lower jaw. The upper untoothed part of beak forms through widenning of the premaxillaes which loose their teeth. Certain groups became quadripedal again and had feet terminating in flat nails or hooves rather than claws.

The phylogeny of the Dinosauria (Fig. 5.4) as revised by Gauthier and Padian (1984), shows that Ornithischia and Saurischia are monophyletic taxa. The Saurischia include Sauropodomorpha and Theropoda. The Theropoda are divided into Ceratosauria, Carnosauria (*Allosaurus* and Tyrannosauridae), and Coelurosauria. As defined by Gauthier and Padian (1984), the Coelurosauria include birds (Aves), Deinonychosauria (Dromaeosaurs and Saurornithoidids), Ornithomimidae, as well as some other forms such as *Coelurus*, *Ornitholestes*, and *Campsognathus*. Thus, within the Coelurosauria, the Deinonychosauria appear to be the sister-group of *Archaeopteryx* and birds.

Figure 5.5 shows the phyletic relationships between the different families of dinosaurs (Lambert 1983).

Staurikosaurus, as well as *Herrarasaurus*, appear to be the oldest and most primitive dinosaurs, appearing at the boundary between middle and upper Triassic in South America. However, they are too primitive to fit within either the Ornithischia or the Saurischia. By mid-Carnian times (early upper Triassic), the ornithischians and saurischians had diverged from each other (Padian 1986).

5.5.3.2 Saurischia (Fig. 5.6)

The Saurischia diversified into two main groups: the biped and carnivorous Theropoda and the quadripedal herbivorous Sauropoda.

The Theropoda were constructed on a bipedal model for which *Coelophysis*, a coelurosaur of the final Triassic of North America, provides a standard example. About 3 m long, *Coelophysis* was a light animal because its bones were hollow. The long strong hind-limbs of avian type had three main digits and two reduced digits ending in claws. The fore-limbs were short. The long flexible neck carried a long narrow head with two large temporal and preorbital fenestrae. The jaws bore pointed teeth. The very long tail acted as a stabilizer. The size of the Coelurosaur varied from that of a chicken to that of a large ostrich.

Springing from this type, the diversification of the Theropoda (Fig. 5.5) is indicated by a reinforcement of the hind-limbs, an often considerable atrophy of the fore-limbs (*Tyrannosaurus*), shortening and thickening of the neck (Carnosaurs) or a slender elongated neck (Ornithomimosaurs) and a more or less large head with jaws with pointed teeth or ending in a birdlike beak (Ornithomimosaurs, Oviraptorids, Caenagnathids). The Theropoda reached considerable size, becoming the largest carnivores that have ever existed. *Allosaurus*, at the end of the Jurassic, might have reached 12.8 m in length and 4.9 m in height, while *Tyrannosaurus* in the Cretaceous (North America and China) and *Tarbosaurus* (Mongolia) were 1 to 14 m long and 5 to 6 m tall and must have weighed over 6 tons. The skull alone of *Tyrannosaurus* was 1.2 m long, with teeth of 18 cm.

Among the Theropoda, the Spinosaurs had a special morphology, the development of vertebral spines forming a dorsal keel as seen in the Pelycosaurs (see Chap. 7.1). Some specialists also place *Archaeopteryx* within the Theropoda, a position that will be discussed in connection with the origin of the birds (Chap. 6.3.1).

The Sauropoda are represented in the Triassic and the early Jurassic by the Prosauropoda. The majority were quadripedal, as were the Sauropoda of the Jurassic and Cretaceous. They were characterized by a small head carried on a very long neck, a massive body supported by a heavy skeletal armor, fore-limbs shorter than the hind-limbs with a claw on each thumb, and a very long tail. The variations on this structural plan relate to the lengths of the neck and tail. The Prosauropoda included the smallest known dinosaur, *Mussaurus*, the young of which were 20 cm long and the adults about 3 m (final Triassic). The Sauropoda reached considerable size and weight, 18 m in length and 9 tons in the case of *Cetiosaurus* (Jurassic of Europe and North Africa), 27 m and 70 tons for *Brachiosaurus* (Jurassic of Colorado and Africa) and at least 30 m and perhaps 55 tons for *Ultrasaurus* (a large *Brachiosaurus*?) of the terminal Jurassic of Colorado, larger than the famous *Diplodocus* which did not exceed 27 m and 10.6 tons (Fig. 5.6).

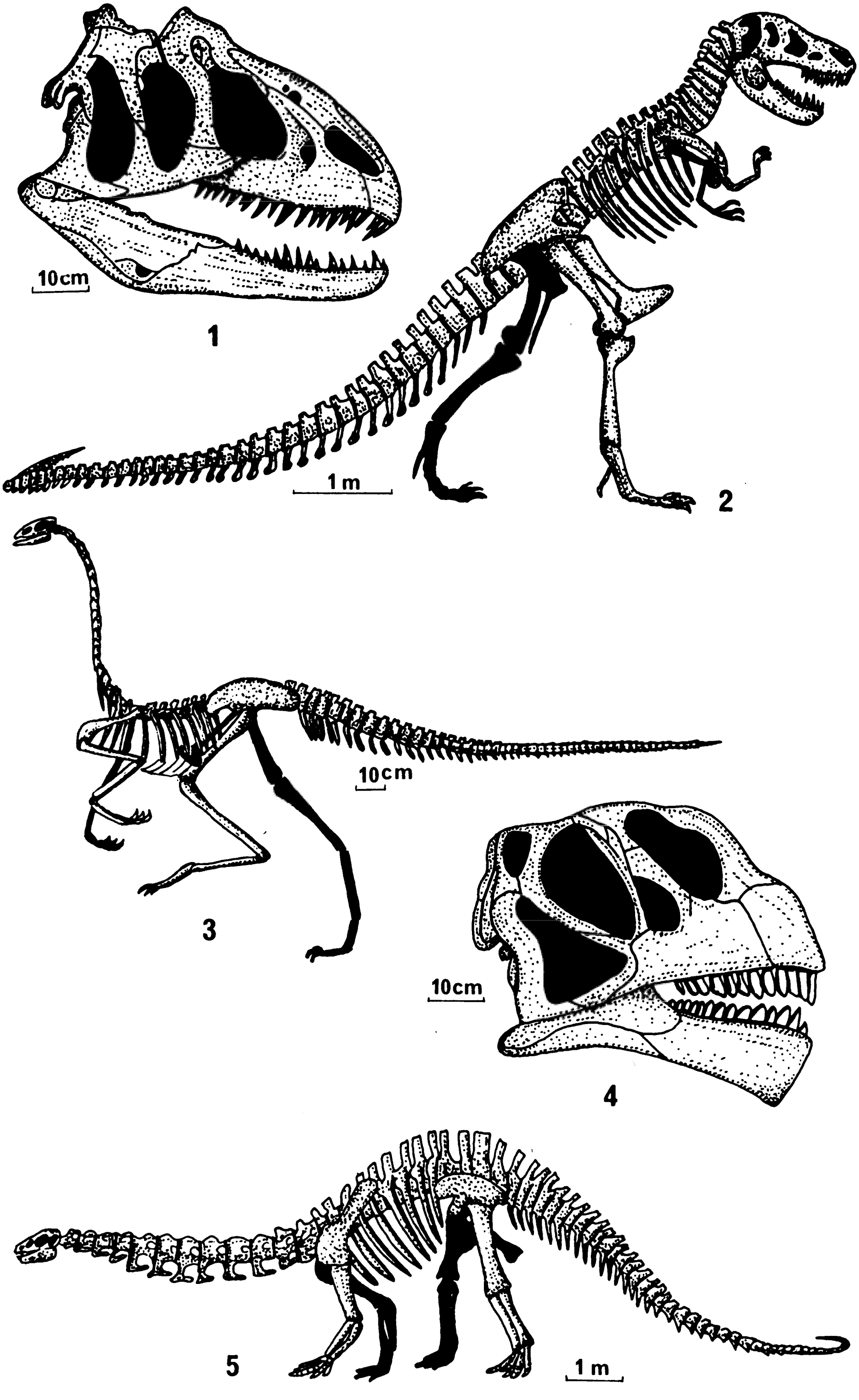
The considerable mass and the recession of the nostrils to the summit of the head in some of these animals led specialists to regard them as semiaquatic herbivores with only their head emerging. They are now interpreted as terrestrial giraffe-like dinosaurs living in herds.

5.5.3.3 Ornithischia (Fig. 5.7)

These fall into four main groups: the Ornithopods, Stegosaurs, Ankylosaurs, and Ceratopsids.

The Ornithopod appeared at the end of the Triassic and the start of the Jurassic. Initially, these were small bipeds (Fabrosaurs, Hypsolophodonts and Heterodontosaurs) which gave rise to larger herbivores, the Camptosaurs at the end of the Jurassic-lower Cretaceous, the Iguanodonts, Hadrosaurs and Pachycephalosaurs (upper Jurassic-Cretaceous). The head became increasingly large, with a tendency to loss of the front teeth and their replacement by a horny beak. Various protuberances developed on the summit of the Hadrosaurs, Lambeosaurs, Pachycephalosaurs (Fig. 5.7). Measurements of natural isotope abundances of ^{13}C

Fig. 5.6. Saurischian dinosaurs. **1** *Allosaurus valens*, carnivorous theropod, upper Jurassic; **2** *Tyrannosaurus rex*, carnivorous theropod, upper Cretaceous, skeleton; **3** *Struthiomimus altus*, therapod of upper Cretaceous, skeleton; **4** *Camarasaurus supremus*, upper Jurassic, cranium; **5** *Brontosaurus excelsus*, upper Jurassic, skeleton. (**1** after Gilmore 1920; **2, 3, 4** after Osborn 1898; **5** after Marsch 1888)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and ^{15}N on fossil organic matter (bone collagen) from terminal Cretaceous *Anatosaurus* suggest that its diet consisted to terrestrial plants, some of them growing in arid environments (Bocherens et al. 1988).

The Stegosaurs of the middle Jurassic and the Cretaceous were derived from bipedal Ornithischia, as evidenced by fore-limbs shorter than their hind-limbs. On their back they had a double row of alternating triangular plates and the tail bore two pairs of bony spines. *Stegosaurus*, 9 m in length and weighing 18 tons, was the largest of the stegosaurs, which disappeared at the beginning of the Cretaceous. The group is represented in Fig. 5.7:3 for the genus *Kentrosaurus*.

The Ankylosaura, or armed dinosaurs, may be derived from the Scelidosaura of the Jurassic had their body covered with rows of bony protuberances. They may also be primitive ornithopods or related to Stegosaurs, Quadrupeds with short fore-limbs, their large bodies were covered with an armor formed of heavy bony polygons bearing spines, especially on the tail. In *Ankylosaurus*, 6 m long, the tail ended in a bony mass acting as a mace. The small teeth and horny beak indicate a herbivorous regime.

The Ceratopsia, or horned dinosaurs, appeared in the lower Cretaceous and underwent rapid diversification at the end of the Cretaceous. *Psittacosaurus*, of the lower Cretaceous of Mongolia, is the oldest ceratopsian, semi-bipedal, with its head ending in a parrot's beak. The Protoceratopsia of Mongolia and Canada were characterized by a very special form of skull in which the parietals and squamosals extended backwards to form a ruff or nuchal covering, whose size might reach a quarter or a third of the body surface (Fig. 5.7:2, 4). The skull ended in front in a horny beak. *Protoceratops* (1.8 m, 1.4 tons) is one of the best known because of the series of specimens of different ages and the nests of a dozen eggs discovered in Mongolia. The evolution of the Ceratopsids was characterized by a great increase in size (9 m, 5.4 tons) and by the development of ruffs of very great size lightened by fenestrae (*Torosaurus*). The ruff itself was sectioned into six spines in *Styracosaurus*. Most of the ruffs were adorned with a pair of more or less developed horns and a large nasal horn. *Ceratops* had three short horns, *Monoclonius* a large nasal horn, *Triceratops* a small nasal horn and two large frontal horns (Fig. 5.7:2). The horns of the Ceratopsids recall those of the African antelopes and are thought to have served for combats between males. Their abundant remains in some regions suggests a herd life.

5.5.3.4 The Disappearance of the Dinosaurs

The dinosaurs began to disappear gradually, their decline starting slowly during the Turonian and Senonian, to become suddenly dramatic at the end of the Cretaceous with numerous other groups (pterosaurs, ichthyosaurs, plesiosaurs, etc), some authors estimating that 75% of animal and plant species became extinct. The most absurd hypotheses have been invoked to explain this. The three most recent theories invoke the encounter of the earth with an asteroïd cloud (Alvarez et al. 1980), a phase of intense volcanism (Courtillot et al. 1986), or an

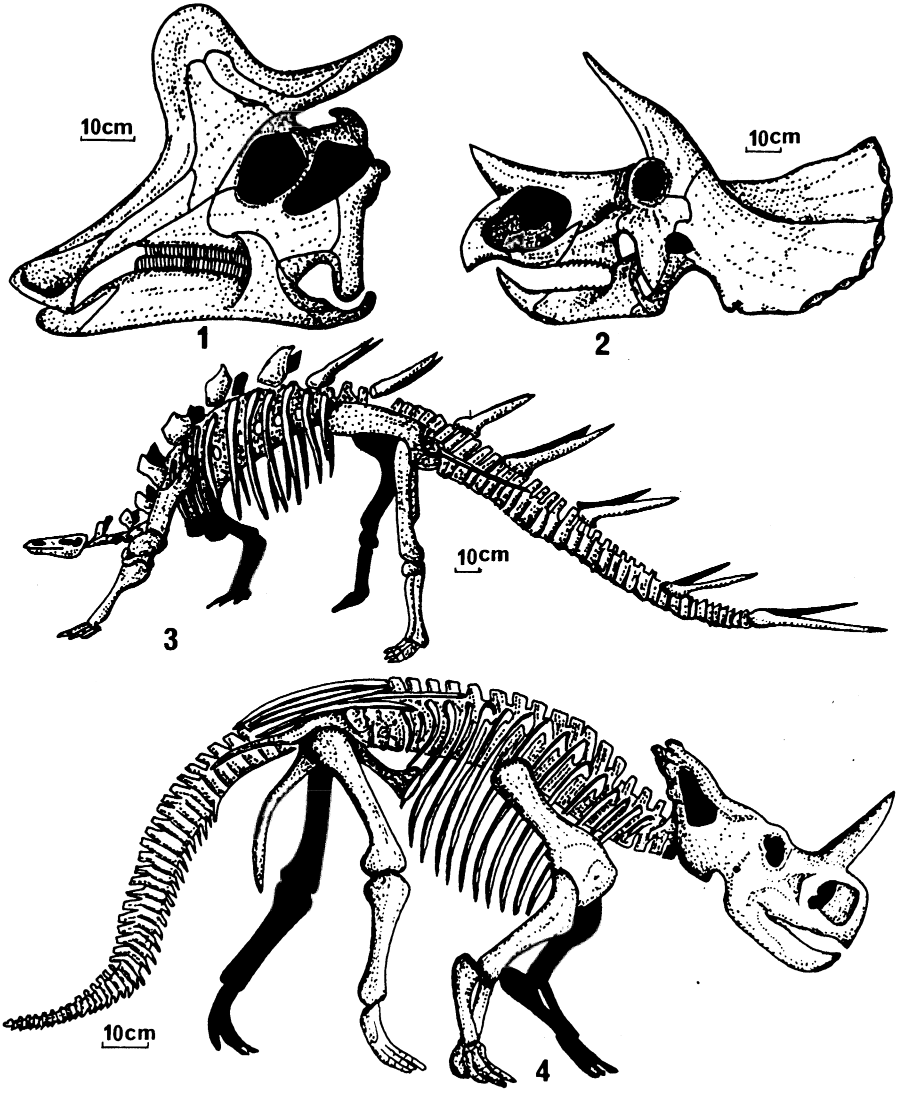


Fig. 5.7. Ornithischian dinosaurs. **1** *Lambeosaurus lambei*, ornithopod, upper Cretaceous; **2** *Triceratops prorsus*, ceratopsid, upper Cretaceous; **3** *Kentrosaurus aethiopicus*, stegosaur, upper Jurassic; **4** *Monoclonius nasicornus*, ceratopsid, upper Cretaceous. (**1** after Lull and Wright 1942; **2** after Hatcher et al. 1907; **3** after Janensch 1925; **4** after Brown et al. 1940)

extensive regression of the epicontinental seas (Ginsburg 1984). A combination of the latter two theories could explain the disappearance of the marine organisms living in the epicontinental seas, the volcanic production of iridium leading to the destruction of plancton (an important link in the nutritional chain), and the cooling of the world climate to a more continental state. However, they fail to explain adequately the persistence of groups like the Eosuchia, crocodiles, lizards, snakes, and turtles.

5.5.4 Birds

These are Archosaura whose phyletic relationsships are still very debatable, bearing feathers, and adapted to flight. They will be discussed in detail in Chapter 6.3, which deals with this adaptation.

5.5.5 Pterosaurs

These have been regarded as archosaurs originating from "thecodonts". Wild (1978), however, demonstrated that two late Triassic genera (*Endimorphodon* and *Peteinosausus*) were more clearly related to the eosuchians (*Youngina*) and thus are not true archosaurs. Their anteorbital fenestra is considered to be a convergent feature. Their most parsimonious position at present is within the archosauromorpha, as the sister-group of all other archosauromorphes. Gardiner (1982), however, considered them to be a sister-group of the Aves. Further work is thus necessary to solve the problem of their phylogenetic relationships. These will be discussed in Chapter 6.3 dealing with the adaptation to flight.

5.5.6 Diapsids incertae sedis: Kuehneosaurids

Kuehneosuchus from late Triassic fissure deposits of England and *Icarosaurus* from North America had very long ribs bearing a membrane. The apophyses were rather long, but insufficient to connect the membrane to the body. They became adapted to gliding flight like the existing *Draco* lizards.

5.5.7 Crocodiles

The oldest crocodiles known are the Protosuchia of upper Triassic and lower Jurassic. Small in size (around 1 m), with a short snout and quite long limbs, the continental and aquatic Protosuchia, a paraphyletic group, had bodies entirely covered with bony plates. After we find the marine crocodiles, the Mesosuchia, a paraphyletic group. The Teleosauridae, with a long snout and narrow dentate jaws, which could reach up to 4 m in length, were piscivores resembling the existing gavials. They lived in rather shallow epicontinental seas. The Metriorhynchidae, adapted to aquatic life in deeper seas, faded out during the lower Cretaceous (Buffetaut 1979).

The regression of the seas at the end of the Jurassic, by extending the continental domain and the great alluvial plains, favored the development of the crocodiles in a terrestrial setting and in fresh water. This led to the sudden appearance of the Atoposauridae (40 cm), terrestrial carnivores, and the Goniopholidae, large animals with a broad snout similar to existing alligators. In the lower Cretaceous, on the continent of Gondwana, there developed the Pholidosauridae with giant forms like *Sarcosuchus*, whose skull measured 1.8 m, with a body of 11 m. After the separation of Africa and South America by the south Atlantic in the middle Cretaceous, the Libycosuchidae in Africa and the Notosuchidae in South America exhibit a certain degree of convergent evolution with short snouts. The crocodiles survived the phenomena which brought about the disappearance of the dinosaurs, plesiosaurs, and mosasaurs.

The eusuchians, represented by the recent Crocodylidae, the Gavialidae, and the Alligatoridae, make their appearance during the upper Cretaceous. However, the doubious forms of lower-Cretaceous age must be kept in mind. In the southern land-masses the Dyrosauridae, late Mesosuchia of great size (up to 9 m), became adapted to piscivorous or durophagous regimes. In the South America of the Tertiary, other Mesosuchia, the Baurusuchidae and Sebecidae, were characterized by narrow snouts and laterally compressed teeth with serrated ridges. The persisted until the Sebecidae Pliocene. In the northern hemisphere, the crocodiles which were abundant in the Miocene became rare with the climatic cooling of the upper Miocene and Quaternary. On the other hand, they remained diversified in Africa and America, where they gave rise in the upper Cretaceous to giant forms (*Phobosuchus*) 15 m in length. From the Protosuchia to the Mesosuchia and Eusuchia, the crocodiles were characterized by the transition from amphicele biconcave vertebrae to procelous vertebrae with a concave anterior surface and a posterior convex surface, and by the backward recession of the internal nostrils following the development of the secondary palate, thus connecting the external nostrils and the pharynx.

5.6 Ichthyosaurs

The Ichthyosaurs appeared in the lower Triassic and were aquatic forms with a hydrodynamic body whose shape resembled that of the dolphins. This was a case of convergence between ichthyosaurs and cetaceans. The elongated skull with a single temporal fossa (see Chap. 5.1.4) had a very large orbit with sclerotic plates (*Ophthalmosaurus, Stenopterygius*: Fig. 5.2) and a long slender snout. In the primitive ichthyosaurs the teeth were inserted in alveoli, but in the evolved forms the pointed teeth of the same size were implanted in a longitudinal groove. The same evolution is to be seen in the Cetacea, another convergence between two groups of quite different metabolism, the ichthyosaurs being incapable of regulating their internal temperature (poikilotherms), while the Cetacea have a constant temperature (homeotherms) (Mazin 1985). The biconcave vertebrae were very numerous and the body ended in a hypocercal tail. The extremities of the limbs were characterized by a hyperphalangism and hyperdactylism increasing their surface area and giving them a palette shape. They also possessed a dorsal fin without bony support. They seem to have been ovoviviparous. Their phyletic relationships have not yet been settled. They disappeared prior to the uppermost Cretaceous, most probably at the Cenomanian-Turonian boundary.

5.7 Plesiosaurs

Derived from unknown diapsid forms, these appeared in the Triassic (nothosaurs and pachypleurosaurs). They diversified into two groups: that of the pliosaurs with a short neck and very elongated head (3–4 m) and that of plesiosaurs with a very long neck (up to 75 vertebrae) and a very small head (*Muraenosaurus* of the Jurassic, *Hydrotherosaurus*: Fig. 5.2). *Elasmosaurus*, one of the last forms of the upper Cretaceous, exceeded 10 m. Their paired fins exhibited hyperphalangism, but never hyperdactylism.

5.8 Placodontia

These were marine forms whose body was sometimes enveloped in a sort of carapace (*Placochelys*). Their crushing teeth were slab-like, indicative of a durophagous regime (*Placodus*). They are known only from the Triassic. The Placodontia have commonly been considered to be relatives of the Sauropterygian nothosaurs and plesiosaurs (Romer 1956). By their shared derived characteristics they are closely related to the diapsids (Sues 1987).

CHAPTER 6

The Conquest of the Aerial Environment

Three very different groups have conquered the aerial environment: the Pterosaurs, the birds, and the Chiroptera or bats (mammals). They constitute an excellent example of convergence.

6.1 The Constraints of Flight

The requirements of adaptation to flight are restrictive. Flying animals must overcome the problem of gravity. They must be light and have powerful muscles to ensure movement of their wings. The bones are usually hollow, with thin walls. They need wings, derived from transformation of the fore-limbs. In the Pterosaurs the wing is supported by the fourth digit, in the birds mainly by the second and in the Chiroptera by the last four digits (Fig. 6.1). The powerful muscles are attached to the broadened sternum, which bears a median crest or carina in the birds. The bearing surface of the wings is formed by a membrane in the Pterosaurs and Chiroptera, by feathers in the birds. The hind-limbs must fulfill the function of landing. Flight calls for powerful vision (birds) or a system of radar guidance (bats) and a delicate sense of balance. The cerebellum includes the centers for balance and muscle coordination essential to flight. It is therefore very developed in the Pterosaurs, and especially in the birds, where it attains maximal structural complexity. Finally, flight implies increased metabolism and an elevated temperature. While birds and bats are warm-blooded animals, the pterosaurs, essentially cold-blooded, were covered with a long, dense, thick coat (*Sordus pilosus*) that doubtless facilitated heat regulation.

6.2 Pterosaurs

The Pterosaurs appeared in the Triassic and were initially represented by the Rhamphorhynchoidae, then by the Pterodactylidae. *Rhamphorhynchus*, of the Jurassic, was 60 cm long (Fig. 6.2) and had a diapsid type of skull. The front of the skull and the mandibles bore pointed teeth. The tail was twice as long as the body in front of the pelvis and carried a lozenge-shaped rudder. The alar membrane must have been attached to the small weak limbs.

They were succeeded by the Pteranodontidae in the Cretaceous. In these the tail was reduced, or even absent. The mandibles carried teeth in *Anurognathus*

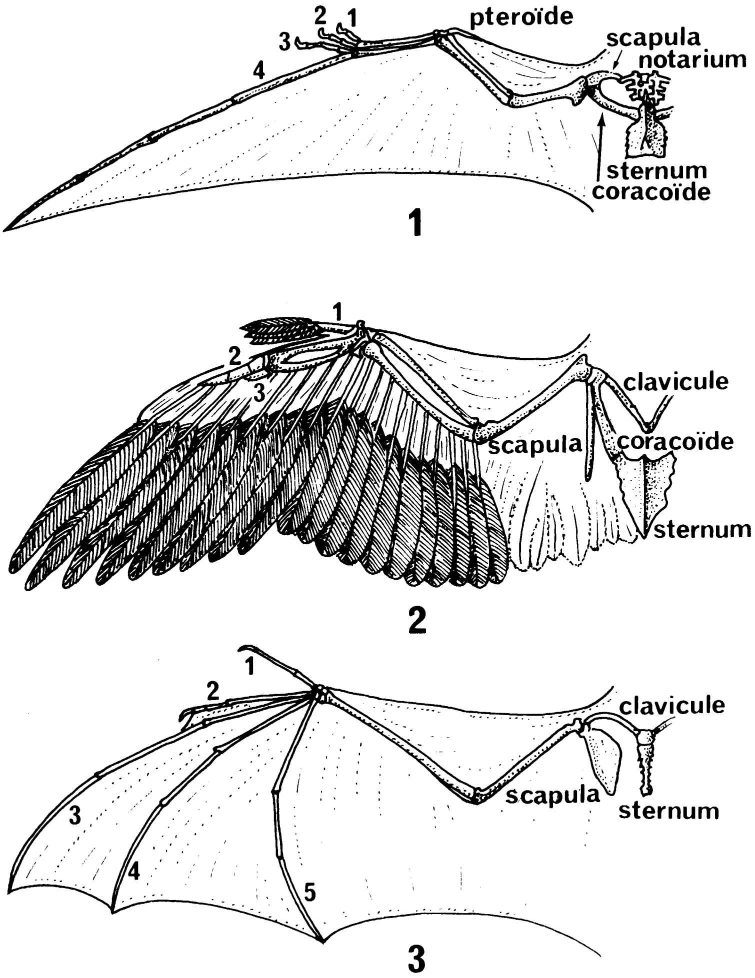
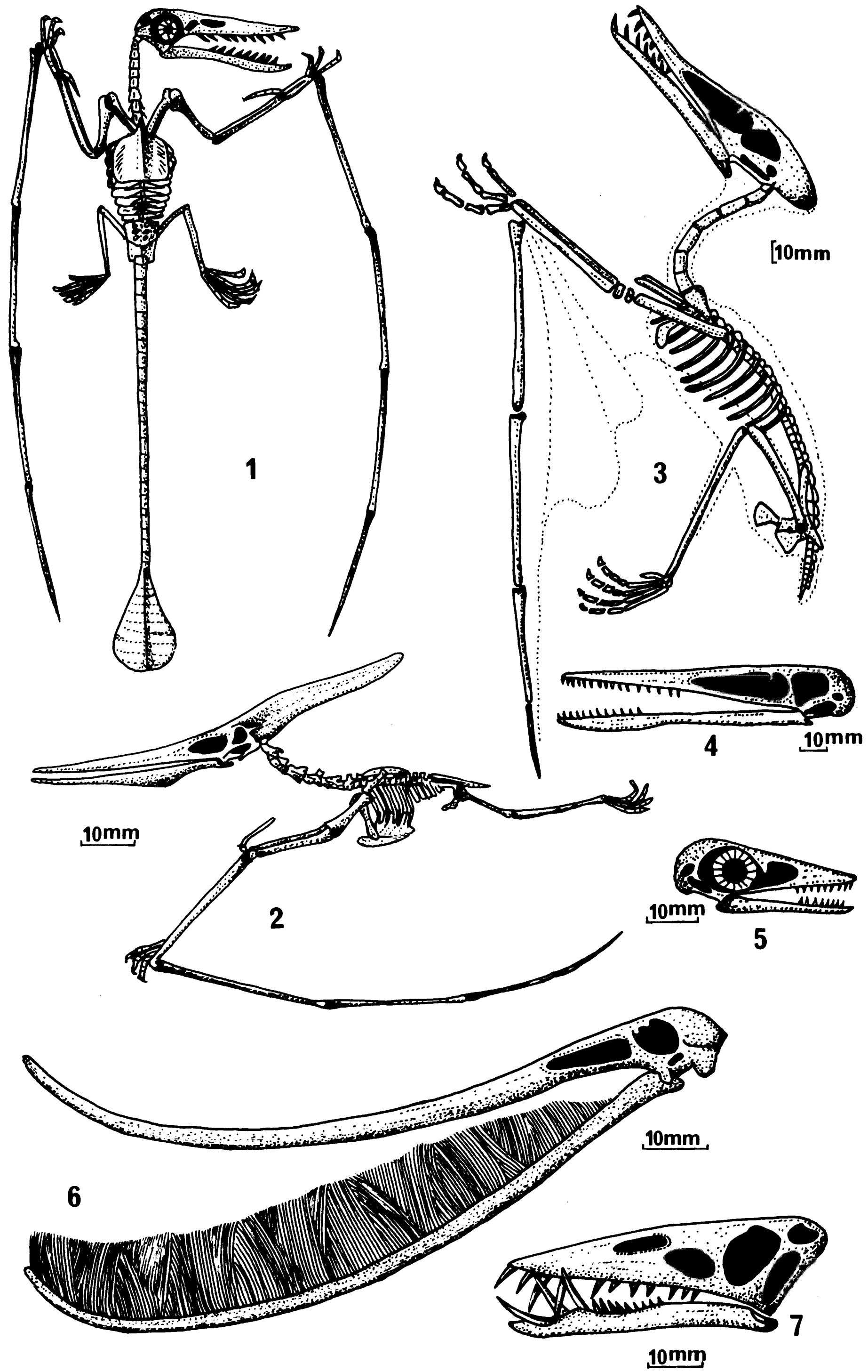


Fig. 6.1. Comparison of wings of pterosaur (**1**), bird (**2**) and bat (**3**). The wing is supported by the 4th digit in pterosaurs, by the 2nd digit in birds, and by the 2nd, 3rd, 4th, and 5th digits in bats (After Langston 1983)

Fig. 6.2. Pterosaurs. **1** *Ramphorhynchus gemmingi* (upper Jur.); **2** *Pteranodon* (cretaceous piscivore); **3** *Gallodactylus canjuersensis*, Portlandian of the Var; **4** *Pterodactylus antiquus*; **5** *Pterodactylus kochi*; **6** *Pterodaustro* (planktivore ?); **7** *Dorygnathus*. (**1** after Williston 1892 – 1893; **2** after Easton 1904; **3, 4, 5** after Fabre 1981; **6, 7** after Langston 1983)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(an insectivore), kinds of wattles in *Pterodaustro* (planktonivore?) or were without appendages. *Pteranodon* (upper Cretaceous) seems to have been a fish-eater, the fish being stored in a crop as in pelicans. *Pteranodon* (Fig. 6.2) had a span of 7.5 m, but the record belongs to *Quetzalcoatlus northropi* of Texas, with a span assessed at 11–12 m and a weight of 86 kg, the biggest flying animal yet identified. These were soarers.

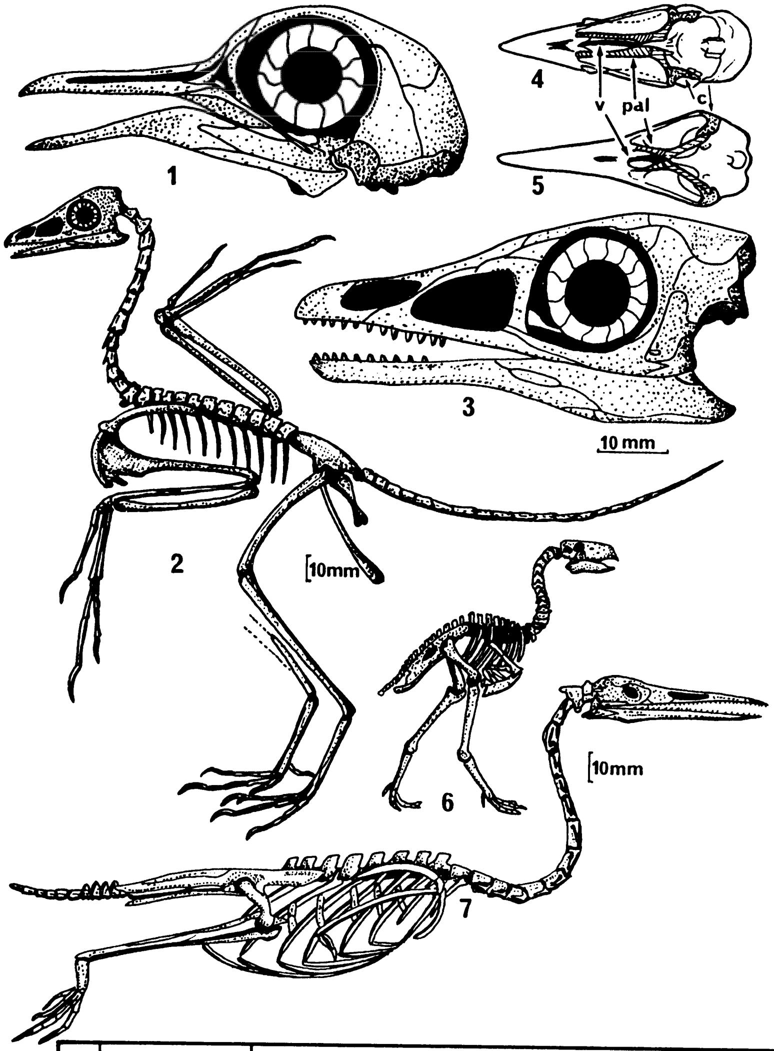
6.3 Birds

6.3.1 Archaeopteryx

Six specimens have been discovered in the Jurassic of Bavaria exhibiting a mixture of archosaurian and avian characters, the most surprising of which is the presence of feathers. Without these, *Archaeopteryx* would never have been considered a bird. The size of a pigeon, it had an elongated skull with jaws carrying teeth and a broad eye with a sclerotic annulus. There was no sternal carina and the bones were not hollow. The hindlimb had no tarsometatarsus, the single bone of birds formed by fusion of the tarsus and metatarsus. The two clavicles formed a wishbone and the tail was long. The phyletic relationship of this animal are still very debatable. Colbert and Romer place it within the dinosaurs, Ostrom (1973) among the Coelurosaurs. According to Walker (1972) and Whetstone and Martin (1979), it was related to the crocodiles, but Hecht and Tarsitano (1982) place it in the "thecodonts", between *Euparkeria* and *Lagosuchus* (Fig. 6.3). Finally Ostrom's conclusions (1974) were sustained by over 120 synapomorphies (Gauthier 1984; Padian 1982; Gauthier and Padian 1984). *Archaeopteryx* is the earliest and most primitive taxon considered as a bird and may be regarded as the sister-group to all other birds (Fig. 5.4). As established by cladistic analysis, avian characters were already present in theropods before bird evolved. In many cases the avian form of these characters is only slightly modified over the non-avian form (Gauthier and Padian 1984).

Two major theories of the origin of avian flight have been competing. The "arboreal" theory proposed the idea that avian flight began in trees. But *Archaeopteryx* lack any obvious arboreal adaptations of the skeleton. The challenging theory, the "cursorial" theory, supposed that birds' ancestors were terrestrial

Fig. 6.3. Birds. **1** skull of pigeon; **2** *Archaeopteryx*, reconstruction of skeleton; **3** *Archaeopteryx*, cranium; **4** neognathous palatine vault of Carinates (*c* quadrate; *pal* palatine; *v* vomer); **5** paleognathous palatine vault (Ratites and some Carinates); **6** *Diatryma*, Eocene; **7** *Baptornis advenus*, reconstruction of skeleton; **8** cladogram illustrating hypothesis for phylogenetic relationships of taxa relevant to the early history of birds (**1, 2, 3** after Heilman 1926; **4, 5** after Portmann 1950; **6** after Matthew and Granger 1917; **7** after Martin and Tate 1967; **8** after Cracraft 1988)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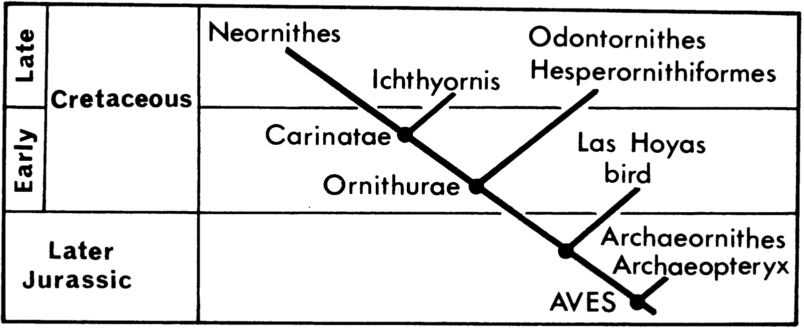
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Ichthyornis
Odontornithes
Hesperornithiformes
Carinatae
Ornithurae
Las Hoyas bird
Archaeornithes
Archaeopteryx
AVES

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bipeds with long arms and legs, prehensile hands, and hindlimb proportions adapted for fast progression (Ostrom 1974). Finally, Gauthier and Padian (1984) proposed a terrestrial theory built on Ostrom's predictive functional analysis of the forelimb, without the insect net function, taking also into account the Caple et al. (1983) calculations about flight: "the wings begin to beat, especially the outer portion, which provides thrust, some of which is converted into lift. As speed increases, the thrust generated by the wings and legs is taken over by the wings; the bird is now moving too fast for its legs to keep up with it, and it is airborne. To land, the flight speed is slowed by a combination of increased flapping amplitude and increase angle of attack: the bird descends and slows enough to reach maximum running speed, and the legs touch the ground. Once on the ground, the bird uses both legs and wings to brake incremently". There is also the hypothesis of Gardiner (1982), who, taking the view that paleontologic arguments add nothing to the biologic data, is prepared to acknowledge the collectivity of dinosaurs and birds as constituting the sister-group of the mammals.

6.3.2 Landmarks in the History of the Birds

Four subclasses of birds are actually recognized. The Archaeornithes for *Archaeoteryx*, the Enantiornithes, the Odontornithes (Hesperornithiformes and Ichthyornithiformes) and the Neornithes for all the modern birds (Fig. 6.3).

The Enantiornithes includes *Enantiornithes leali* from the uppermost Cretaceous of Argentina (Walker 1981).

A primitive bird, found in the Neocomian of Spain (Sanz et al. 1988) possibly the sister-group of Ornithurae (all birds except *Archaeopteryx*), leads to the idea that the aquatic Hesperornithiformes were probably secondarily flightless.

The fossils of birds are rare and their history is poorly known. In the Cretaceous, *Ichthyornis*, the size of a sea-swallow, had a marked carina whereas *Hesperornis* and *Baptornis* (Fig. 6.3.) were about 1.8 m long, with very reduced wings and adapted to swimming. Numerous groups became differentiated from the end of the Cretaceous: grebes, pelicans, divers, flamingos, waders, etc. Other groups appeared in the Tertiary. Among these, the Ratita, minus a carina and unsuited to flight, attained a great size: the ostriches with their Eocene representative *Eleutherornis*, *Aepyornis titan* of Madagascar (3 m tall, weighing 450 kg) and the moas (*Dinornis maximus*) of New Zealand (3 m) which became extinct in historical times. As well as the Ratita, the Carinata (with a carina) also gave rise to wingless forms of great size and a very powerful beak, like *Diatryma* of the Eocene of Europe and North America (head 45 cm) and *Phororhacos* of the Miocene of South America (head 70 cm). The columbiforms also gave rise on the Mauritius and Reunion islands to a large wingless pigeon, the dronte or dodo (*Raphus cucullatus*). Among the 8600 existing species of birds, 5150 are passeriforms, little known in the fossil record.

The great wingless birds of the Paleocene were redoubtable predators and must have replaced the dinosaurs ecologically before the appearance of the large mammals. The large wingless Quaternary forms were insular and their disappearance was brought about by man.

The world's largest flying bird was a Teratornithidae, considered be relatives to the New World vultures. *Argentavis magnificens*, found in the late Miocene of Argentina (Campbell 1980), weighed between 160 and 170 pounds with a 25-feet wingspan. The Teratornithidae became extinct at the end of the last Ice Age. The last *Teratornis merriami* found in the asphalt deposits at Rancho La Brea, Los Angeles (about 10,000 years ago) weighed about 36 pounds and had a 12-feet wingspan.

A revision of the classification of birds by Sibley and Ahlquist (1986) by means of the method of hybridization of DNA molecules has shown numerous and astonishing convergences, for example between the vultures of the Old and New Worlds, the former being related to the sparrowhawks and eagles, the latter to the storks. This method has made it possible to reconstruct the complex paleogeographic history of the Corvidae (warblers, thrushes, etc.), from Australia to western Eurasia, Africa, east Asia and America.

6.4 Chiroptera

These are mammals which, from the lower Eocene, had acquired adaptation to flight by the development of an alar membrane (patagium) stretched between the neck and digits (Fig. 6.1). Thanks to their system of orientation by ultrasonic emission, they were able to acquire a nocturnal cave-dwelling existence. The Microchiroptera were fossilized from the Eocene, the Megachiroptera from the Oligocene.

CHAPTER 7

The Radiations of Mammals

7.1 From Pelycosaurs to Mammals

Within a line of Cotylosaurs the first group with a synapsid cranial structure originated, that of the Pelycosaurs. This gave rise to several lines constituting the group of the Therapsidae, of which one or more gave rise to the mammals.

7.1.1 Pelycosaurs

These appeared in the upper Carboniferous and persisted until the middle Permian.

Romer and Price (1940), believing that the Pelycosaurs consisted of three adaptive radiations, subdivided the order into three suborders, the Ophiacodontia, Edaphosauria, and Sphenacodontia. Pelycosaurs possess derived characters such as broad anteriorly tilted occipital plate and a reduced post-temporal fenestrae. These groups are not monophyletic and have been reduced by Reisz (1980) to six taxa (Fig. 7.1).

7.1.1.1 Eothyridae

Eothyris parkeyi and *Oedalops campi* are small pelycosaurs with the jugals excluded from the ventral margin of the cheek and a rounded posterior border of the squamosal providing poor separation between the cheek and occipital part of this bone.

7.1.1.2 Caseidae

These are small to very large pelycosaurs characterized by greatly enlarged external narial openings, narrow squamosals, large anterior pineal foramen, dorsolateraly expanded ribs. The skull of *Casea broilii* is small in relation to the body and possesses a large temporal fossa.

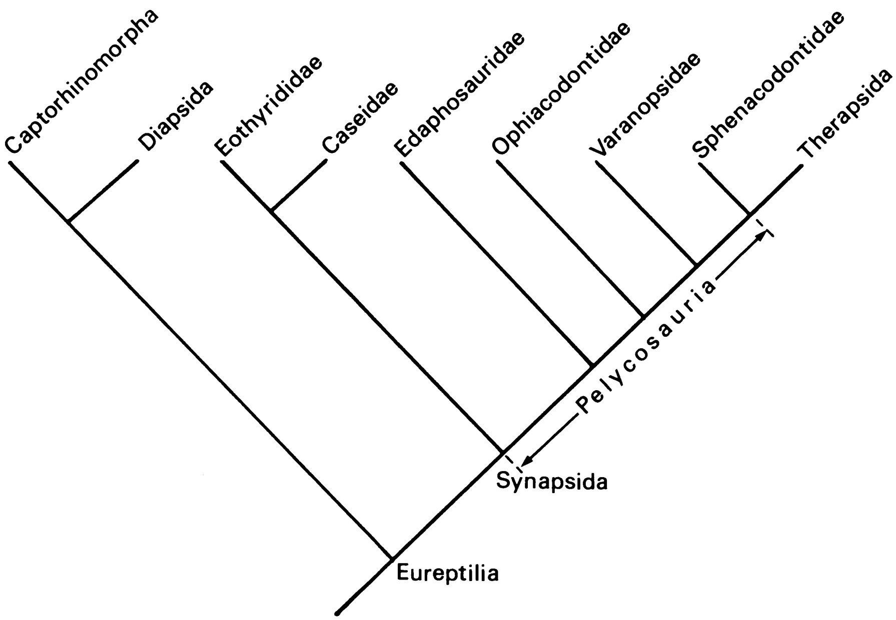

Fig. 7.1. Phylogenetic relationships of pelycosaurians. (After Reisz 1980)

7.1.1.3 Edaphosauridae

These are small to very large herbivorous pelycosaurs characterized by massive crushing dentition, broad frontals, and greatly elongated neural spines with successive thickenings forming a high dorsal carina (*Edaphosaurus cruciger*).

7.1.1.4 Ophiacodontidae

These are small to large carnivorous pelycosaurs with elongated nasals. In *Ophiacodon*, a 2.4-m-long piscivore, the dorsal vertebrae have become compressed anteroposteriorly increasing the skull-to-trunk ratio from 64%. *Varanosaurus* had the form of a large lizard 1.5 m long (Fig. 7.2) with a long tail. The narrow elongated skull with a long mandible had the eyes set far back.

7.1.1.5 Varanopsidae

Varanops, *Aerosaurus*, and *Varanodon* are carnivorous pelycosaurs of moderate size with skull-table deeply incised above the orbits.

7.1.1.6 Sphenacodontidae

The skull exhibits greater dental differentiation and large jugal muscles allowing wider opening of the mouth. Certain pelycosaurs like *Dimetrodon*, and subsequently all the Therapsidae possessed an angular expanded by a reflected lamina. *Dimetrodon* was also characterized by elongation of the vertebral apophyses into a high carina, doubtless connected by a membrane considered to have had a role in heat regulation. *Dimetrodon* lived in the great delta at the beginning of the Permian and could reach 3.3 m in length and a height of 1.3 m (Fig. 7.2).

7.1.2 Therapsidae

The Therapsids appeared in the lower upper Permian, flourished in the upper Triassic, and became extinct in the middle Jurassic. They are particularly known from the continental deposits of South Africa. The temporal fenestra of the skull, bounded below by the zygomatic arch, expanded to allow the passage of powerful masticator muscles; the quadrate bone became smaller. In the more evolved forms there is a secondary palate formed by the premaxillaries, maxillaries, and palatines, defining the nasal cavity and separating it from the mouth. The teeth diversified into incisors, canines, and molars. The occipital condyle became double. The ribs and vertebrae were differentiated regionally and the elongated limbs were held alongside the body. The differentiation of mammalian structure took place in dispersed order, characters appearing in mosaic and evolving at different rates in the various groups. The phyletic relationships observed are those proposed by Reisz (1980) and Kemp (1984).

7.1.2.1 Dinocephalians

Characterized by a temporal fossa expanded dorso-ventrally, and by large incisors, the Dinocephalians included herbivorous forms, the Titanosuchia (*Titanosuchus, Jonkeria, Moschops*) and carnivores, the Brithopids (*Titanophoneus, Anteosaurus*) (Fig. 7.2). *Moschops* had particularly thick skull bones (11.5 mm) and a large massive body (3 m in length, 1 ton). This pachyostosis is interpreted in terms of head-to-head combat.

7.1.2.2 Anomodonts

These were exclusively herbivorous Therapsids, from the end of the Permian to the end of the Triassic, characterized by enlargement of the temporal fenestra. *Otsheria* and *Venjukovia* of the USSR have differentiated teeth (Venjukovoidea). The Dromosaurs of Southern Africa (*Galepus*) have a temporal fenestra smaller than the orbit. The Dicynodonts constitute a group in which the extreme characteristics of herbivores are manifested by the disappearance of the incisors, lower canines and posterior teeth, the upper canines being transformed for defense. The temporal fossa is very large and extended to behind the occipital condyle. Three groups of dicynodonts can be distinguished: *Kingoria, Robertia,* and *Dicynodon*. This last group was to have a new expansion in the Triassic with *Lystrosaurus*, an animal of amphibian tendency, and *Kannemeyeria* (lower Triassic) (Fig. 7.2), *Dinodontosaurus* (middle Triassic), *Stahleckeria* and *Placerias* (upper Triassic), reaching the size of the great Dinocephalians.

7.1.2.3 Gorgonopsidae

The Ictidorhinids, and Gorgonopsids were the first carnivorous therapsids, dominating the final Permian. They are identified by the great development of the canines, their short nose in some Gorgonopsids and a mandible possessing a coronoid apophysis. *Rubidgina* (Fig. 7.2) and *Lycaenops* are two representatives of the group with a size varying from 50 cm to 2 m.

7.1.2.4 Therocephali

From the final Permian to the start of the Jurassic the Therocephali were essentially carnivores, but certain small forms must have been insectivorous and others herbivorous (*Bauria*). While the more primitive forms had no secondary palate (*Crapartinella*), this characteristic appeared in the Ictidosuchia, the Scaloposauridae (*Ericiolacerta*) and the Bauridae. The group possessed well-developed incisors and complex post-canine teeth with numerous cusps (*Bauria*). (Fig. 7.2).

7.1.2.5 Cynodonts

These appeared at the end of the Permian, flourished in the Triassic, and some persisted into the Jurassic. Derived from primitive therapsids, they are characterized by the development of the dentary, which came to articulate with the squamosal in the more evolved forms (mammalian articulation). The teeth became complex, with cusps, and a secondary palate developed. *Dvinia* (Permian of the USSR) is the most primitive and precedes the group of the Galesaurids (*Thrinaxodon*) (Fig. 7.3). Two groups of herbivores appeared in the lower Triassic, the

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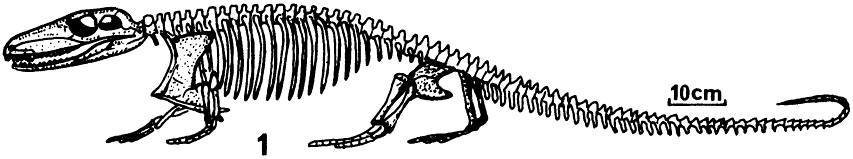
Fig. 7.2. Pelycosaurs and therapsids. **1** *Varanosaurus*; **2** *Dimetrodon*; **3** *Moschops*, lateral view of skull; **4** *Titanophoneus*, lateral view of skull; **5** *Rubidgina*, lateral view of skull; **6** *Kannemeyeria*; **7** *Bauria*, lateral view of skull; **8** *Bauria*, dorsal view of skull. (**1,2** after Romer and Price 1940; **3** after Boonstra 1969; **4** after Orlov 1958; **5** after Sigogneau 1970; **6** after Pearson 1924; **7, 8** after Brink 1963)



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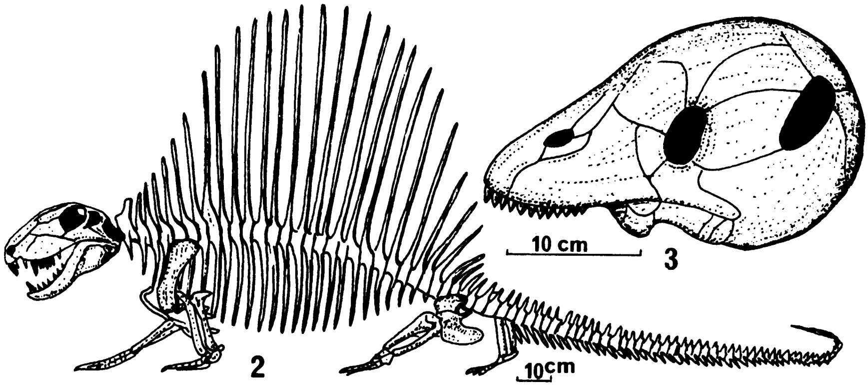

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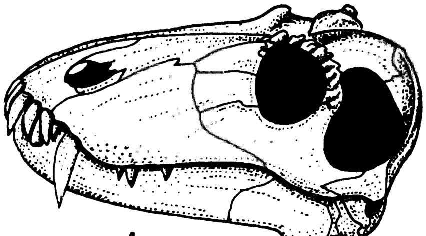

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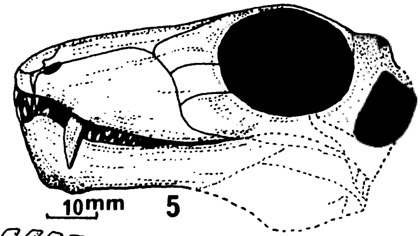

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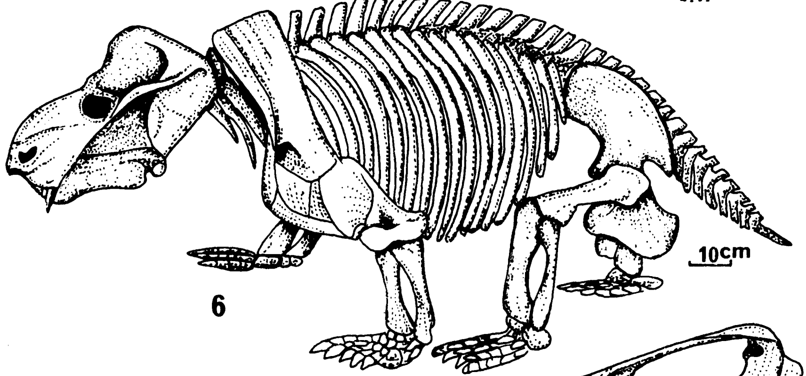

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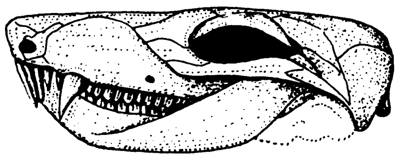

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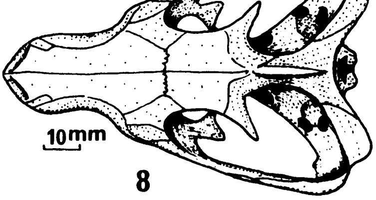

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Diademodontids and the traversodontids. The tritylodontids were also herbivores, known from the lower (*Tritylodon)* to the upper Jurassic (*Oligokyphus, Stereognathus*) (Fig. 7.3). They had the temporal fenestra confluent with the orbit, as in the mammals, and post-canine teeth with three rows of tubercles in a crescent. Among the other Cynodonts, which were all carnivores, are classed the cynognathids and the chiniquodontids (*Probelesodon*: Fig. 7.3), with a close relation of

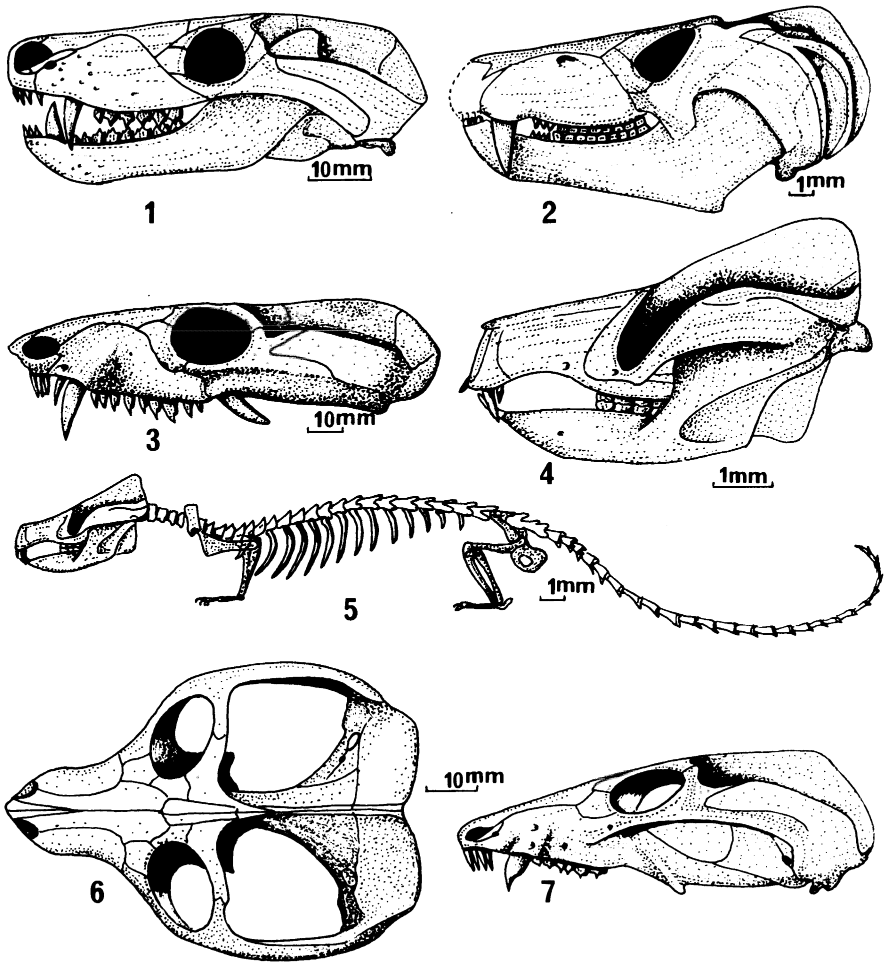


Fig. 7.3. Therapsidae. **1** *Thrinaxodon* (cynodont), lateral view of skull; **2** *Diademodon* (cynodont), lateral view of skull; **3** *Probelesodon* (chiniquodont), lateral view of skull; **4** *Oligokyphus* (tritylodont), lateral view of skull; **5** *Oligokyphus*, reconstruction of skeleton; **6** *Probainognathus* (Probainognathidae), dorsal view of skull; **7** same, lateral view of skull. (**1** after Parrington 1946; **2** after Brink 1963; **3** after Romer 1969; **4, 5,** after Kühne 1956; **6** after Romer and Lewis 1973; **7** after Romer 1970)

the latter, *Probainognathus*, the first to have a dentary-squamosal articulation (Fig. 7.3). This articulation also exists in *Diarthrognathus* (trithelodontids), where the articular process of the dentary, grown prominent, comes into contact with the squamosal to form a second articulation lateral to that of the quadrate-articular. These were animals of small size with a skull of 6 to 7 cm (Fig. 7.4).

7.2 Acquisition of Mammalian Characteristics

The transition from therapsids to mammals is well summed up in terms of physiology, since all the systems of active or vegetative life underwent major transformations, or at least a notable perfecting: nutrition, respiration, locomotion, reproduction, intelligence. The skeletal changes reflect only part of these transformations. One of the most interesting concerns the transition from the therapsid articulation between the articular and the quadrate to the mammalian articulation between the dentary and the squamosal, and the transformation of the middle ear. It is now clear that the use of the dentary-squamosal articulation as the diagnostic character of the Mammalia is seriously challenged by the discovery of the articulations of *Diarthrognathus* and *Morganucodon*.

7.2.1 From Therapsid to Mammalian Articulation

The lower jaw of present-day and fossil lepidosaurs and archosaurs, as well as that of the therapsids, comprises several bones: the dentary, angular, prearticular, and the articular ensuring articulation with the condyle of the quadrate bone. In *Dimetrodon* the dentary has increased to occupy two-thirds of the mandible. Further, the articular develops a retroarticular process and the angular a lateral reflected lamina defining a gutter open below. The dentary is extended upwards to form a coronoid apophysis (Fig. 7.4). In the cynodonts it comes to constitute the mandible almost by itself, the articular and angular being very reduced. This change was brought about muscular restructuring and modified mandibular mechanics by the formation of teeth with complex crowns and the development of mastication. *Probainognathus* (Fig. 7.3) and *Diarthrognathus* (Fig. 7.4) had a double articular structure which clarifies the functional transition from one to the other. Crompton (1958) showed that in *Diarthrognathus* the articular process of the dentary sketches a rudimentary condyle which is embedded in a cavity of the squamosal, and in fact this articulation functions parallel with that of the articular-quadrate in the same transverse axis. In the Jurassic the mammalian articulation is the only one that persists, the bones of the former therapsid articulation having acquired other functions in the middle ear. Devillers (1981) stresses a cardinal fact: at the beginning of ontogenesis in a marsupial the mammalian embryo possesses only an articular-quadrate articulation of therapsid type, and it is only in the course of embryonic development that the dentary grows considerably to

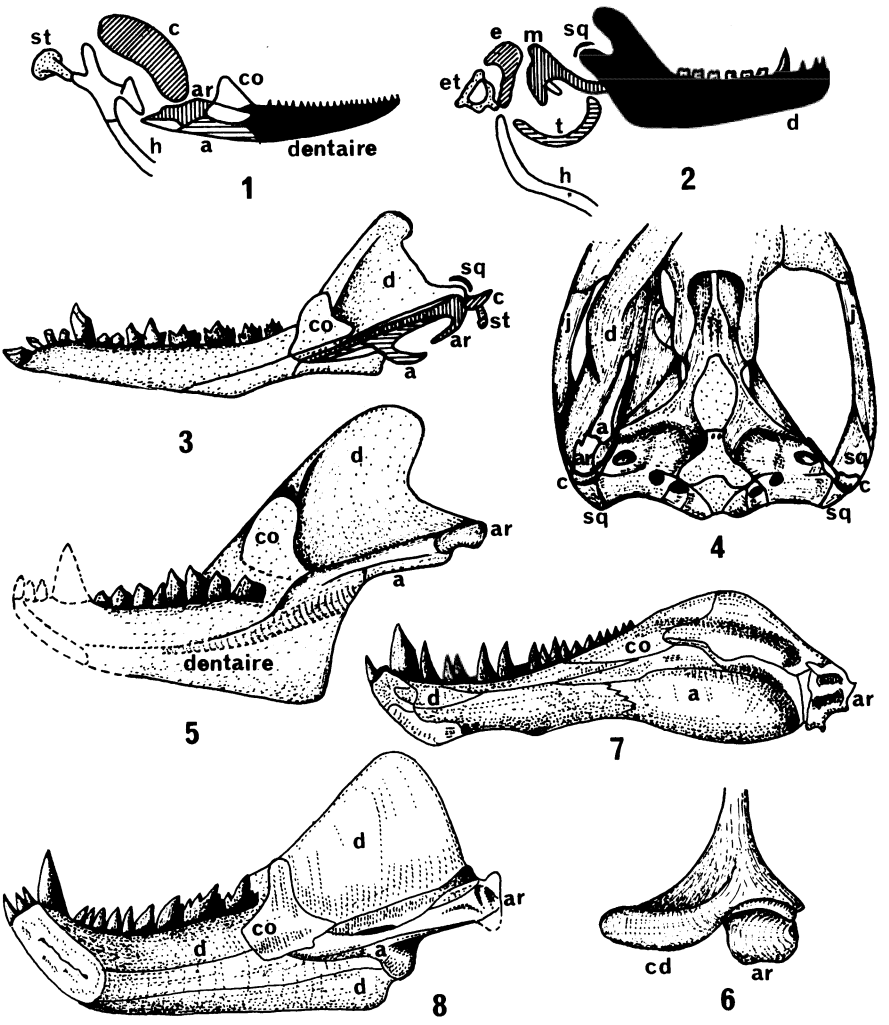


Fig. 7.4. From the therapsid to the mammalian mandibular articulation. **1** mandible of existing lepidosaur with articulation between articular and quadrate; **2** mandible of mammal with articulation between dentary and squamosal and structure of middle ear showing homologies: quadrate = incus, articular = malleus, angular = tympanic; **3** *Eozostrodon* (Rhaetian), mandible with double articulation; **4** *Diarthrognathus* (upper Triassic), inferior view of cranium, on left mandible in place showing articular-quadrate and dentary-squamosal contacts; **5** *Diarthrognathus*, mandible; **6** *Diarthrognathus*, posterior view of articular region of mandible showing condyles of dentary and articular situated side by side on the same axis; **7** *Dimetrodon*, mandible; **8** *Cynognathus* (Triassic), mandible; *a* angular: *ar* articular; *c* quadrate; *d* dentary; *cd* condyle of dentary; *e* incus; *et* stapes; *h* hyoid; *j* jugal; *m* malleus; *sq* squamosal; *st* stapes; *t* tympanic (**1, 2** after Gaupp 1913; **3** after Parrington 1971; **4** after Crompton 1958; **5, 6** after Crompton 1963; **7** after Romer and Price 1940; **8** after Kermack et al. 1973)

establish the new dentary-squamosal articulation. This change is possible linked with complex heterochronies of development.

7.2.2 Structure of the Middle Ear in Mammals

Research in embryology, comparative anatomy and paleontology has shown that the bones which formed part of the therapsid articulation played an essential part in auditory function in mammals following their passage into the middle ear. Thus, it is known that the malleus is the homolog of the articular, the incus of the quadrate, the stapes of the columella and the tympanic bone of the angular. The history of the therapsids shows that those bones which took part in the mandibular articulation were progressively reduced and concentrated in the postero-internal zone of the mandible. Reference to the marsupial embryo shows that the cartilaginous mandible articulates with a cartilaginous element homologous with the quadrate, ossification of which gives rise to the incus. The malleus is derived by ossification of the posterior part of the mandibular cartilage, the handle of the malleus which is applied to the tympanum being derived from the curved prolongation homologous with the retroarticular process of *Dimetrodon*. The rest of the mandibular cartilage disappears. The tympanum is stretched on the tympanic bone derived from the reflected lamina of the angular. While these homologies are now well demonstrated, the anatomic and functional evolution of the middle ear in the therapsids is not yet understood.

7.2.3 Other Mammalian Characteristics

The development of teeth with complex crowns permitting mastication and faster digestion may not be unconnected with the acquisition of homeothermy increasing the energy requirements. The development of the diaphragm, activating respiration and increasing metabolism, is doubtless also associated with this, as is the appearance of insulatory hairs. The existence of the latter is suggested by the presence of points of implantation of vibrissae on the muzzle involving the development of sebaceous glands. The development of the mammary glands so typical of mammals must have been contemporaneous, doubtless like the development of viviparity. The presence of marsupial bones in the tritylodonts suggests the appearance of these characteristics from the lower Jurassic. Analysis of therapsid evolution confirms De Beer's concept of mosaic evolution. This is a very important concept in the sense that it demonstrates the modality that all the components of an organism may have different speeds or rates of evolution. Thus, the therapsids did not evolve harmoniously towards the mammalian condition. The limbs became mammalian very early, but the skull of a cynodont (e.g., *Cynognathus*), though almost that of a mammal, encloses a brain of therapsid size and organization. The brain did not become mammalian until very late in the Jurassic.

7.3 Mesozoic Mammals

Once the mammalian stage of skull structure was acquired, this was not further modified in the mammals. The influence of evolution was to be essentially on the dental apparatus. These new criteria are the more important since the forms of the Secondary are known virtually only from jaws and teeth. From their appearance in the Rhaetian, 200 Ma ago, there can be observed representatives of two main groups of mammals, Prototheria and Theria (Fig. 7.5), which differ in the construction of the skull wall and the shape of their teeth. Clemens (1986), however, suggested that the interpretation of a basic dichotomy separating mammals into a therian and a non-therian group might have to be abandoned in future.

The evolutionary roots of the mammals are found in the Triassic, the oldest record being a haramyid in Germany. The reassignment of many faunas to the early Jurassic fills a gap in the fossil record. It appears that mammals were widely dispersed throughout Laurasia (haramyids, morganucodontids, kuehneotheriids) and Gondwana (kuehneotheriids) prior to the fragmentation of the super-continents. Most of the mammalian groups known from the late Jurassic and early Cretaceous of the northern hemisphere, made their appearance already by the mid-Jurassic (Clemens 1986).

Figure 7.6 sets out the phyletic relationships of the mammals according to Novacek and Wyss (1986) based on the distribution of 68 characters.

7.3.1 Prototheria

These are currently represented by the Monotremata (*Ornithorhynchus* and *Echidna*), which are oviparous forms. The Mesozoic Prototheria resembled the Triconodonts, Docodonts, and Multituberculata. The discovery of the Cretaceous monotreme *Stereopodon* with a dental structure of the theria and not of the prototheria, suggests that the viviparous nature made its appearance rather late in the development of the mammals.

7.3.1.1 Triconodonts

Known essentially from mandibles and teeth from the upper Triassic to the upper Cretaceous, these were insectivorous animals of very small size (less than 35 cm) with a low elongated jaw bearing incisors, canines, premolars, and molars. A milk dentition preceded the definitive dentition. The molars had a large central cusp flanked by two low cusps, the respective sizes of which constitute the diagnostic features of the group (Fig. 7.7). We may mention *Eozostrodon* (= *Morganucodon*) of the European Rhaetian, *Triconodon* (Jurassic) and *Alticonodon* (upper Cretaceous). The Amphilestidae (*Amphilestes* and *Phascolotherium*) of the Bathonian are generally considered as triconodonts, but the presence of a scapulo-coracoid of therian type raises the problem of their phyletic relationships. The occurrence

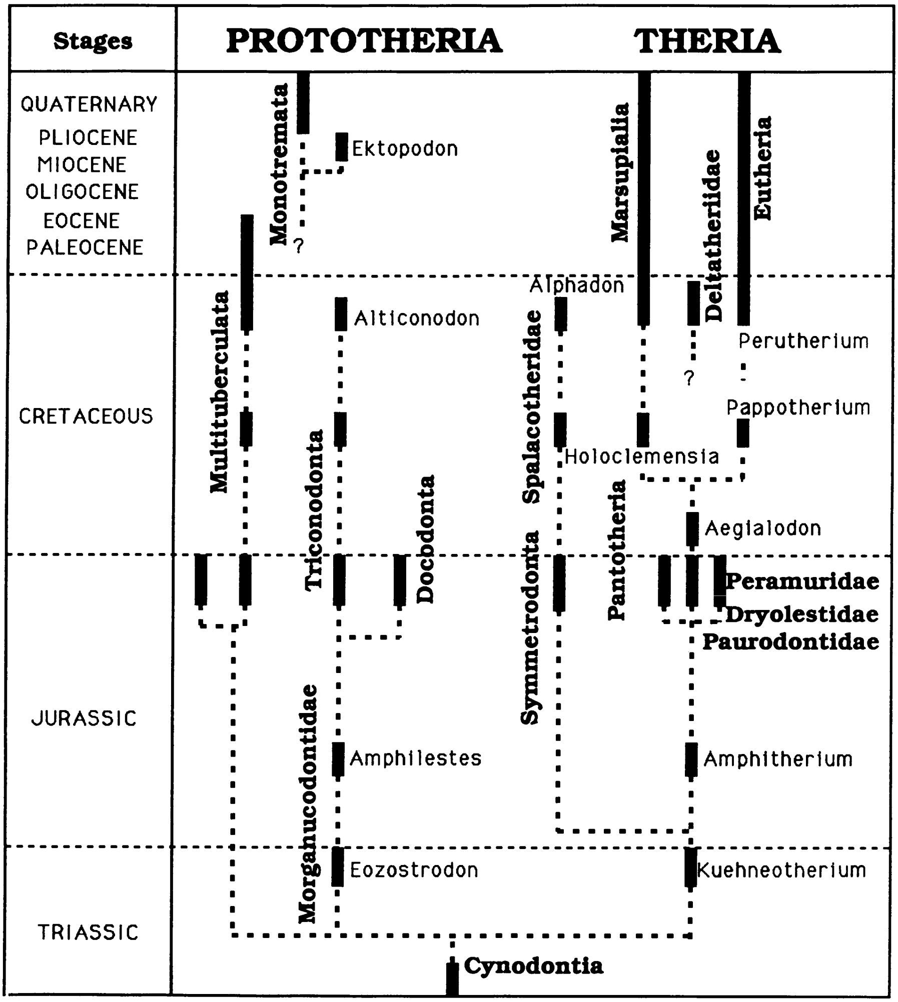


Fig. 7.5. Phylogeny of the mammals. (After Hoffstetter 1976)

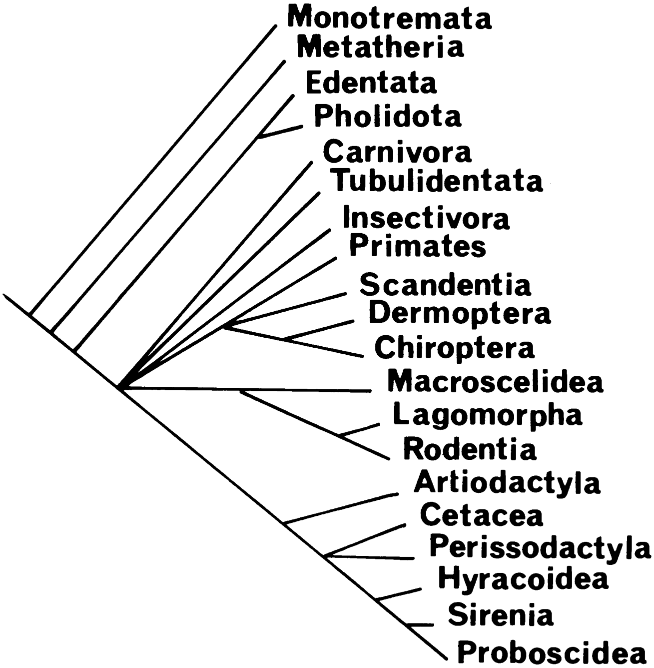


Fig. 7.6. Phylogenetic relationships of the mammals. (After Novacek and Wyss 1986)

of the triconodont *Gobiconodon* in Mongolia and North America suggests some faunal interchange during the early Cretaceous.

7.3.1.2 Docodonts

These are forms of the middle and upper Jurassic, characterized by the development of complex subquadrangular molars (*Docodon*).

7.3.1.3 Multituberculata

Appearing at the end of the Jurassic, they persisted to the end of the Eocene, having developed in the Paleocene a real radiation, especially in North America. They are characterized by a pair of prominent lower incisors which give them the appearance of a rodent, inferior premolars with a cutting edge, often of large size, and by molars with a number of major tubercles arranged in parallel rows. The short massive possessed a strong mandible and a diastema between incisors and premolars, for there were no canines (Fig. 7.7). The oldest forms were the Plagiaulacoidae, succeeded in the upper Cretaceous by the Ptilodontoidae and the Taeniolabidoidae. The functional interpretations of the dentitions in these two groups support the idea that the multituberculated, co-evolving with the angiosperms, occupied a spectrum of ecologic niches analogous to that of the rodents (herbivores, omnivores, insectivores).

7.3.2 Theria

The Theria are currently represented by the marsupials and placentals, known since the Albian, and also include the Symmetrodonts and the Eupantotheria (Fig. 7.5). Pantotheria, which are suspected to include the ancestors of marsupials and placentals, occurred in Laurasia (North America and Europe) and Gondwana (Africa) in the late Jurassic.

7.3.2.1 Symmetrodonts

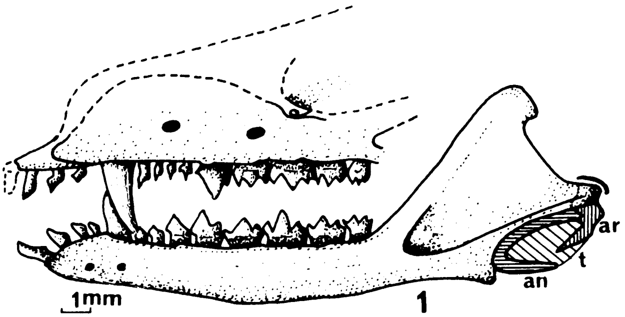
These were animals the size of shrews known from isolated mandibles and teeth. *Kuehneotherium* of the Rhaetian-Liassic had trituberculate molars (Fig. 7.7). In view of the absence of an angular process on the dentary and its dental morphology, *Kuehneotherium* is related to the Amphidontidae (*Manchurodon*) and the Spalacotheridae (*Spalacotherium*) (Fig. 7.7) of the end of the Jurassic and the end of the Cretaceous respectively.

7.3.2.2 Eupantotheria

These are characterized by an angular process of the dentary and by broadened upper molars without a protocone; they are distinguished as Amphitheridae, Dryolestidae, Peramuridae, and Paurodontidae (Fig. 7.8).

7.3.2.3 Appearance of the Tribosphenic Molar

Dental differentiation into incisors, canines, and molars was achieved in the cynodonts. The first mammals had triconodont molars, but from the end of the Jurassic or the beginning of the Cretaceous the tribosphenic molar appeared, which was to characterize the marsupials and placentals. This term relates to the action of the protocone of the upper molars which is embedded like a pestle in the mortar formed by the talonid of the lower molars. The nomenclature employed here is the classic contribution of Osborn, but it should be realized that Vandebroek (1961), considering the dental homologies expressed by the old nomenclature as inexact, has proposed a new and relevant terminology that is unfortunately



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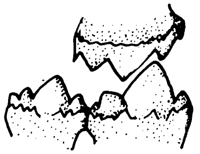

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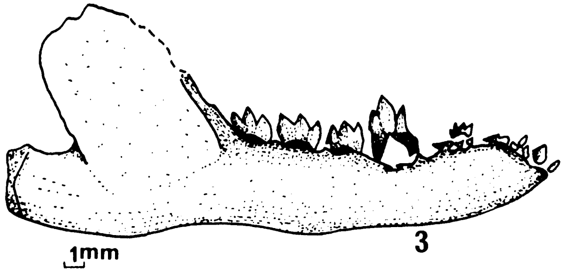

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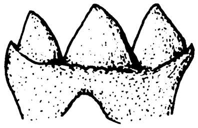

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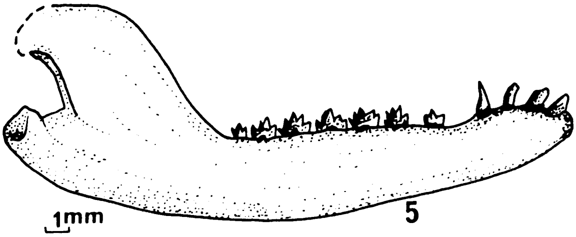

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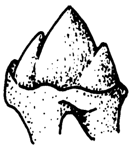

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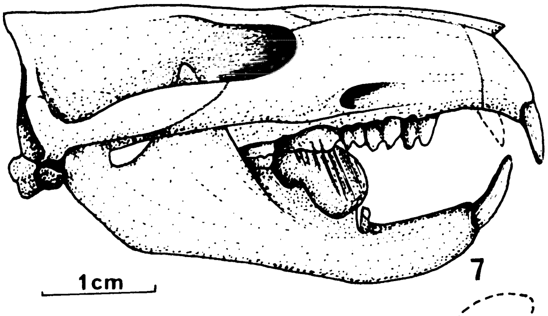

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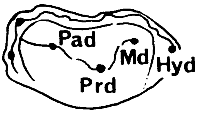

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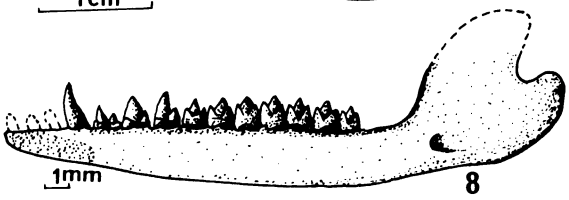

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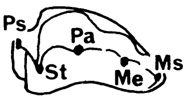

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unused. Figure 7.9 shows the two nomenclatures applied to the upper and lower tribosphenic molars. The phylogenetic development of the structures of the molars from the therapsids to the more complex mammals is still very debatable. The protocone seems to have appeared in *Aegialodon* of the Wealdian, as suggested by the wearing facets of the lower molars. Starting from the Aegialodontidae (*Aegialodon*, *Kielantherium*) there were to develop the potential ancestors common to the Marsupials and the Placentals, what Patterson (1956) has called the mammals of metatherian (marsupial)-eutherian (placental) grade. Included in these are *Holoclemensia* (Fig. 7.8) and *Pappotherium* (Albian of Texas), the Deltatheriidae of Asia and *Endotherium* of Manchuria, but their relationships are still very debatable.

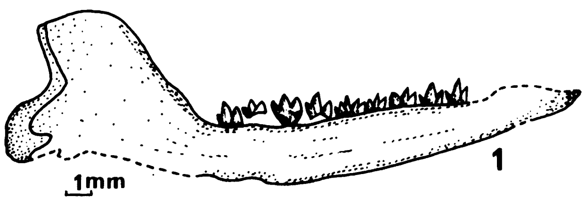
7.3.2.4 Marsupials and Placentals, Two Sister-Groups

These two groups are distinguished by particular characteristics which cannot be derived from the one of the other but have emerged from a common Cretaceous ancestor (Hoffstetter 1975). In the marsupials, dental replacement involves only the third premolar and they have four molars per half-jaw and a pseudovagina. The placentals have lost the marsupial bone which existed in the therapsids, possess a reduced number of incisors and an elaborate placentation, and have acquired a connection between the cerebral hemispheres. All the Theria are viviparous, but in their development the marsupials exhibit characters indicative of oviparous ancestors (a fine envelope around the egg). The dichotomy between marsupials and placentals is considered to result from the opening-up of the Atlantic Ocean in the Cretaceous, as their history given below will show.

7.4 Marsupials (Fig. 7.10)

The origin of the marsupials is still very debatable, but recent paleontologic discoveries in Antarctica, South America, Africa, and Asia allows reconsideration of their history in a new light (Crochet 1986). The cradle of the marsupials is the southern hemisphere and doubtless corresponds to the former continent of Gondwana. Indeed, at the end of the Cretaceous (70 Ma) there were in South America

Fig. 7.7. Mesozoic mammals. **1** *Eozostrodon*, reconstructed mandible and maxillary (*an* angular; *ar* articular; *t* tympanic); **2** *Eozostrodon* teeth; **3** *Triconodon*, mandible; **4** same, teeth; **5** *Phascolotherium*; **6** same, teeth; **7** *Ptilodus montanus*, Multituberculate, skull and mandible in lateral view; **8** *Spalacotherium*, mandible; **9** *Kuehneotherium*, lower tooth (*Pad* paraconid; *Prd* protoconid; *Md* metaconid; *Hyd* hypoconulid). **10** *Kuehnotherium*, upper tooth (*Pd* parastyle; *St* stylocone; *Pa* paracone; *Me* metacone; *Ms* metastyle). (**1,2** after Parrington 1971; **3, 4, 5, 6** after Owen 1871; **7** after Gregory and Simpson 1926; **8** after Cassiliano and Clemens 1979; **9** after Kermack et al. 1968; **10** after Cromptom and Jenkins 1968)



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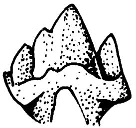

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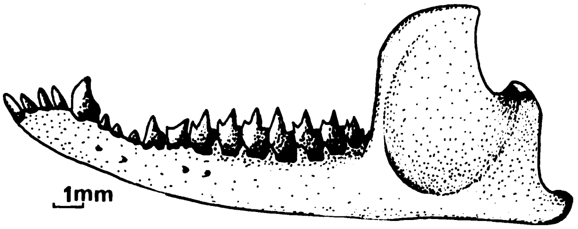

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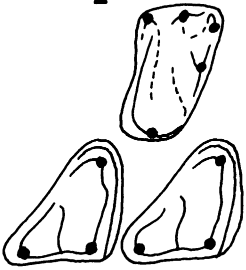

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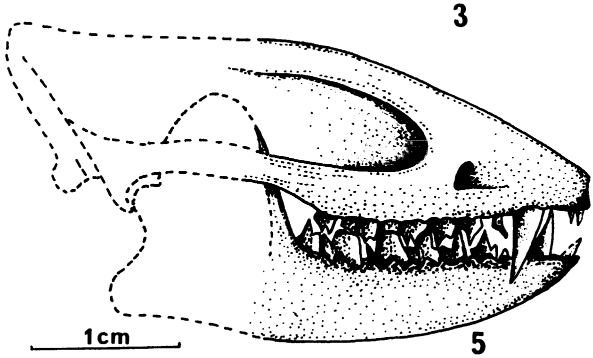

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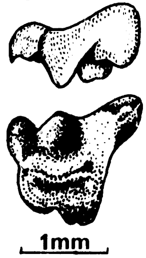

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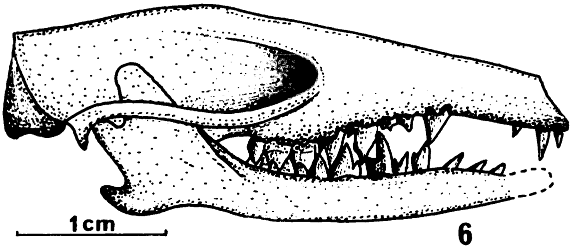

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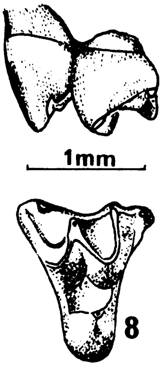

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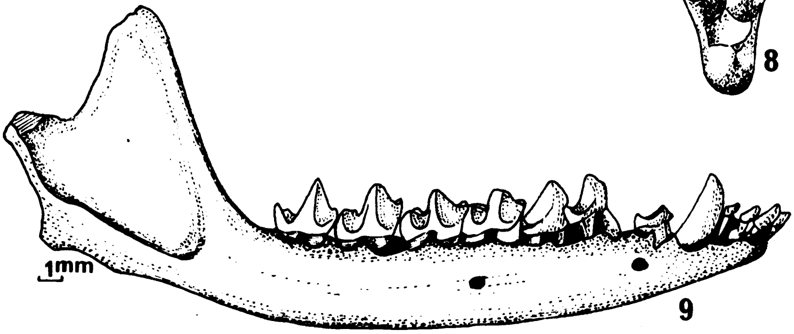

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ancestors of the marsupials which were to diversify and spread into South America, North America, Europe, Africa, and Asia. The earliest record of marsupials mammals in South America is located at Tiupampa (Bolivia) in the upper Cretaceous (Maestrichtian). They are represented by 11 genera (Marshall and de Muizon 1988): a Peradectidae (*Peradectes austrinum*), a Microbiotheriidae (*Khasia cordillerensis*), six Didelphidae (*Pucadelphis andinus, Incadelphis antiquus, Mizquedelphys pilpinensis, Andinodelphis cochabambensis, Tiulordia floresi, Jaskhadelphys minutus*), two Caroloameghiniidae (*Kollpania tiupampina, Roberthoffstetteria nationalgeographica*) and one Borhyaenidae (*Allqokirus australis*). This fossil record demonstrates that marsupials were abundant and taxonomically different by Late Cretaceous time in South America. It suggests that marsupials had a pre-Maestrichtian history on that continent. A first phase of the radiation of the marsupials is documented in the upper Cretaceous of North America (*Glasbius*, *Aquiladelphis*, *Didelphodon*, *Alphadon*), but only the *Alphadon* branch was to develop as far as the upper Miocene. This first phase of radiation is associated with *Garatherium mahboubii*, discovered in the lower Eocene of El Kohol (Algeria) (Mahboubi et al. 1983), whose ancestor must already have been in Africa in the terminal Cretaceous and have undergone an endemic evolution there. In effect, this first phase of diversification must have taken place before the definitive opening-up of the South Atlantic which geophysicists estimate to have occurred around 100 Ma ago, between the lower Cretaceous and the start of the upper Cretaceous. In the lower Eocene the marsupials became dispersed in Eurasia with *Peratherium cuvieri*, Cuvier's famous opossum, in France, *Peradectes* in the middle Paleocene (50 Ma) of Belgium, and the first Asiatic marsupial discovered in the Oligocene of eastern Kazakhstan. Grouped with these forms is the marsupial discovered in the middle Oligocene (33 Ma) of Fayum in Egypt (*Peratherium africanum*) and a peradectine unearthed at Kasserine (Tunisia) in the lower Eocene (53 Ma), *Kasserinotherium tunisiense* (Crochet 1986). The presence of these African marsupials with European affinities could have resulted either from a southern extension of the zone of geographic distribution of the Eurasiatic forms, or by the passage of a potential ancestor present in the upper Cretaceous of South America into Eurasia via Africa, then towards North America, at around 55 Ma (Paleocene-Eocene boundary). This last hypothesis implies residual connections between South America and Africa via the ridge of Rio Grande and Walvis after the opening-up of the Atlantic Ocean. In South America,

Fig. 7.8. Mesozoic mammals and Cenozoic marsupials. **1** *Amphitherium*, lateral view of mandible; **2** *Amphitherium*, tooth; **3** *Crusafontia*, dryolestid, lateral view of mandible; **4** *Crusafontia*, occlusal view of molars; **5** *Deltatherium*, lateral view of cranium and mandible; **6** *Zalambdalestes lechei*; **7** *Holoclemensia texana*, labial view of molar above, occlusal view below; **8** *Garatherium mahboubii*, labial view of upper molar above, occlusal view below; **9** *Peratherium*, lateral view of mandible. (**1, 2** after Owen 1871; **3, 4** after Krebs 1971; **5, 6** after Kielan-Jaworowska et al. 1979; **7** after Slaughter 1971, modified by Kielan-Jaworowska et al. 1979; **8** after Crochet 1984; **9** after Crochet 1979)

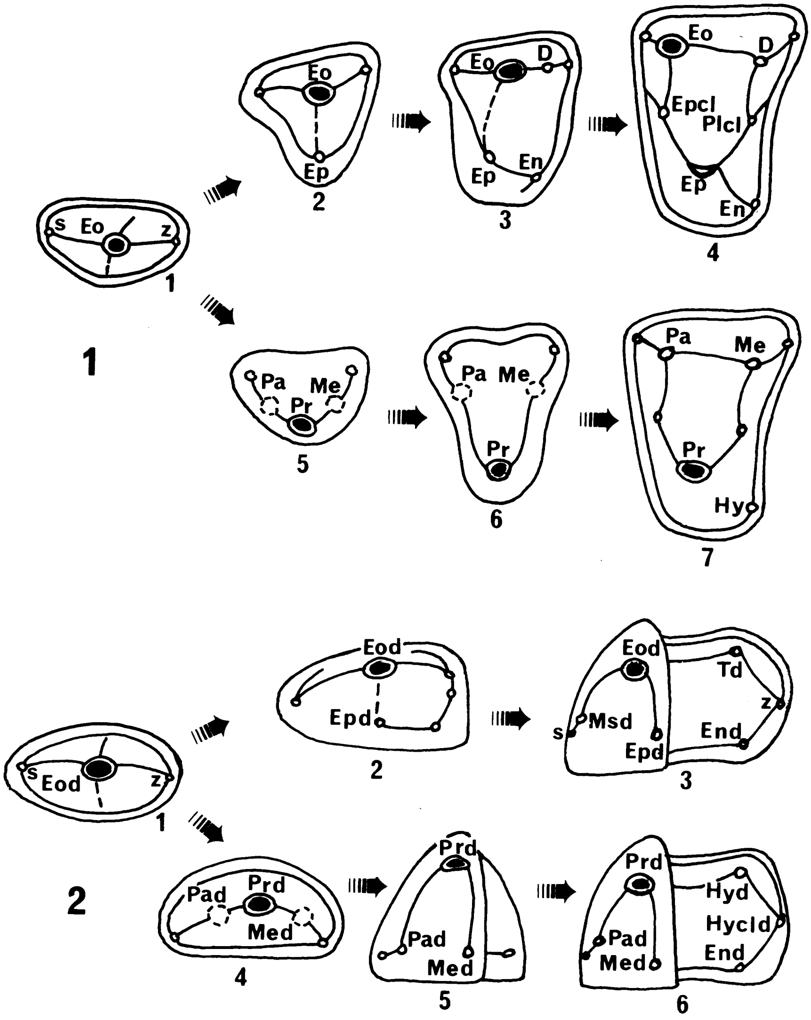


Fig. 7.9. Evolution and nomenclature of dental cusps. **1** Origin of cusps of tribosphenic upper molars: **1, 2, 3, 4** after the theory of Vanderbroek – *Eo* Eocone; *Ep* epicone; *S* mesiostyle; *Z* distostyle; *D* distocone; *En* endocone; *Epcl* epiconule; *Plcl* plagioconule; **5, 6, 7** after the theory of Cope and Osborn, nomenclature of Cope and Osborn – *Pr* protocone; *Pa* paracone; *me* metacone; *Hy* hypocone. Origin of cusps of tribosphenic lower molars: **1, 2, 3** according to Vandebroek (1961, 1969); Vandebroek's nomenclature – *Eod* eoconid; *S* mesiostylid; *Z* distostylid; **4, 5, 6** according to Cope and Osborn; their nomenclature – *Prd* protoconid; *Pad* paraconid; *Med* metaconid; *Hyd* hypoconid; *End* entoconid; *Hycld* hypoconulid

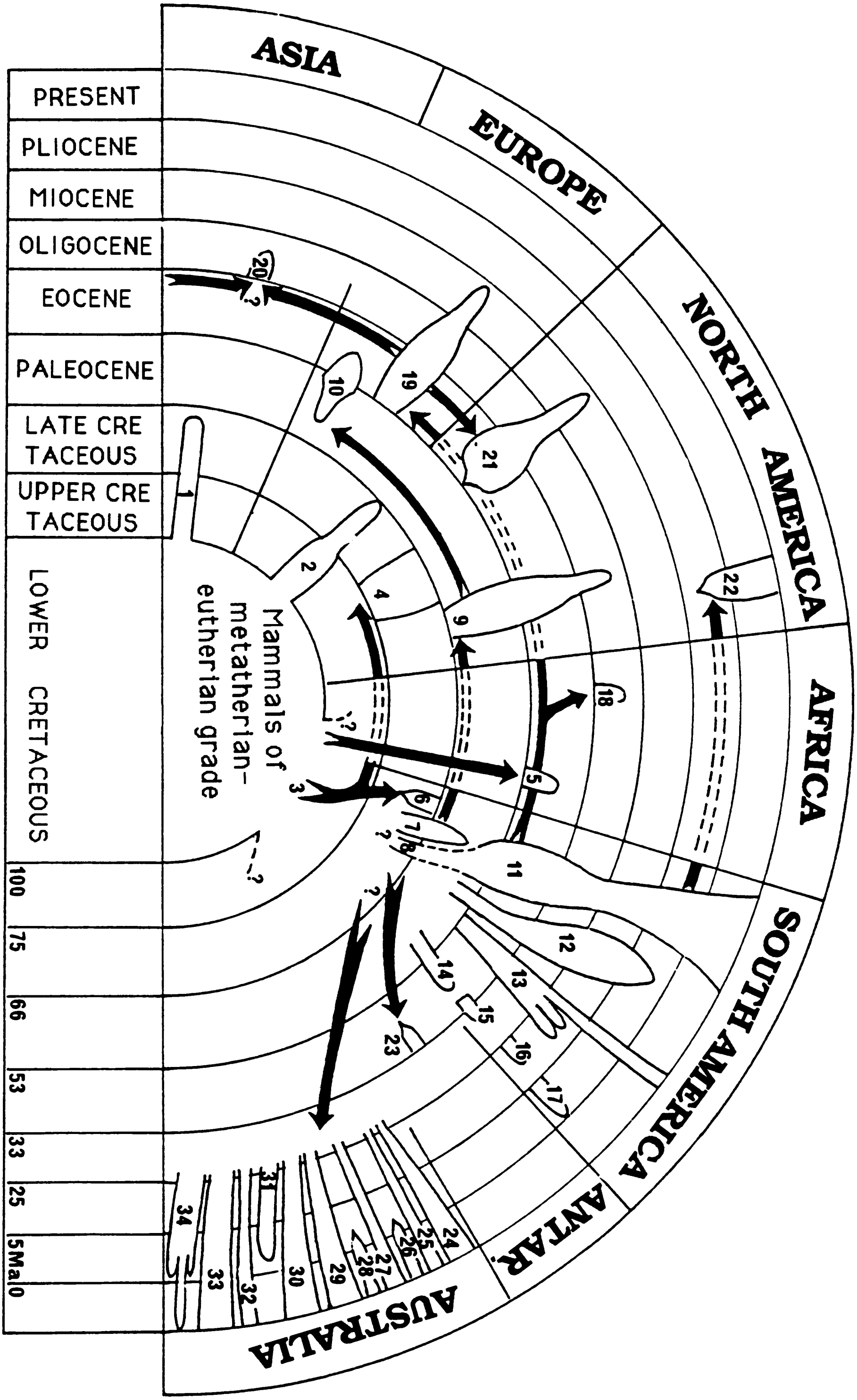
Alphadon and the Didelphidae gave rise to a major radiation of carnivores and insectivores. The Didelphidae (*Protodidelphis*) persisted until the Pleistocene with *Didelphis*, which migrated into North America as far as Canada in recent times. Others, like *Marmosa* and *Monodelphis*, did not go beyond Central America. The Borhyaenidae represent the carnivores in South America with *Prothylacinus* (wolf type), *Borhyaena* (hyena type), *Chasicostylus* (cat type) and *Thylacosmilus* (machaerodont type) (Fig. 7.11). These disappeared at the end of the Pliocene with the arrival of the placentals. The existing Caenolestidae (rat opossums) are living fossils of a group widely spread in the Tertiary. The Argyrolagidae of the Pliocene (*Argyrolagus*) recall the Australian *Antechinomys* (kangaroo mice). A marsupial has been discovered in the Eocene of the Antarctic, which supports the hypothesis of a passage of the marsupials into Australia via this zone. Marsupials have been found in the upper Oligocene of the Australia-New Guinea region (*Wynyardia*), but their great diversity implies an older colonization. Among the Dasyuroidae may be mentioned the Tasmanian wolf (*Thylacinus*), which lived in Australia in the Pleistocene, the marsupial cats (*Dasyurus*), the marsupial mice (*Antechinomys*), marsupial ant-eaters (*Myrmecobius*), and marsupial moles (*Notoryctes*). In these last there may be noted the convergence of form with *Necrolestes* of Patagonia and the Chrysochloridae of Africa. The Peramelidae (bandicoots), of lagomorphic habit, are known from the Pliocene (*Ischnodon*) and the Pleistocene (*Perameles*). Finally, the Phalangeridae, very widely distributed on the islands of Papuasia, became differentiated into *Phalanger* (couscous), *Phascolarctos* (koala), known from the Miocene (*Litokoala*), the Wombatidae (a rodent adaptation) identified from the Miocene (*Rhizophascolonus*), the Macropodidae (kangaroos), including the wallabies (from the Pliocene) and giant fossil kangaroos (*Procoptodon*) 3 m tall. Another group, that of the Diprotodontidae, gave rise to giant forms the size of an ox in the Holocene (*Diprotodon*: Fig. 7.11).

The diversification of the marsupials is interesting from the evolutionary aspect since, in the absence of the placentals, they produced numerous types morphologically identical with those observed in the placentals. These convergences (Fig. 7.11) within two sister-groups underline the close connection between morphology and the ecologic niche, but when the placentals came into competition with them they were rapidly eliminated. Their paleobiogeographic history will be dealt with in Chapter 10.3. Figure 7.10 shows the stratigraphic and geographic distribution according to Crochet (1986).

7.5 Placentals

7.5.1 Mesozoic Placentals

The oldest placentals derive from the Aptian or Albian of Mongolia. These are the Leptictids (*Gypsonicops, Kennalestes*) and the Zalambdalestidae (Fig. 7.8) (*Zalambdalestes, Barunlestes*). Also known from the upper Cretaceous are the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LATE CRETACEOUS
UPPER CRETACEOUS
LOWER CRETACEOUS
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first Condylarthra (*Protungulatum*), primates (*Purgatorius*), and forms of still indeterminate affinities (*Endotherium*). While the Insectivora, Carnivora, Perissodactyla-Artiodactyla and primates became differentiated at the end of the Cretaceous, the Dermoptera, Chiroptera, Rodentia and Cetacea seem to have appeared a little later. As for the Xenarthra, Pholidota, Tubulidenta, Lagomorpha, Hyracoidae, Proboscidae, and Sirenia, their origin is completely unknown.

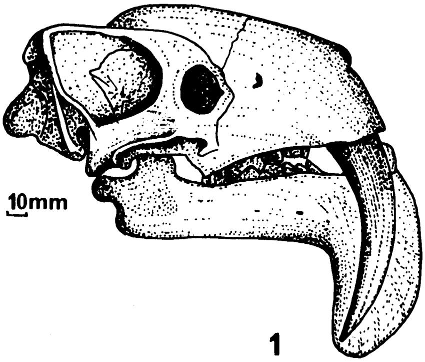
7.5.2 Radiations of the Placentals

Emerging from Asiatic forms, the placentals were to exhibit numerus radiations from the beginning of the Tertiary, ending in the existing fauna. Most of these groups became diversified in a continental environment, but the Chiroptera conquered the air (see Chap. 6.4) and the Sirenia, Pinnipedae, and Cetacea the seas. As it is out of place here to analyse in detail the evolutionary history of the numerous groups of mammals, we shall briefly sketch the different types of specializations achieved before studying in detail concrete cases (Perissodactyla, rodents, primates) offering an approach to the problems of evolution.

7.5.3 Insectivora and Dermoptera

Characterized by molars with pointed tubercles and V-shaped crowns, the Insectivora diversified into hedgehogs (Erinaceidae), shrew mice (Soricidae) and moles (Talpidae). To them are assigned the Galeopithecidae (Dermoptera) and the group of elephant shrews, the Macrosceledidae.

Fig. 7.10. Marsupial radiations in different continents. *1* Deltatheridae in Mongolia; *2* mammals of metatherian-eutherian grade in North America; *3* first marsupial radiation in South America dispersal into North America (*4 Alphadon*, *Glasbius*) Africa (*5*) with the descendant of El Kohol (Algeria): *Garatherium* (*5*) and South America (*6 Pediomyides*; *7 Peradectes*; *8 Alphadon*). Second radiation of *Peradectes* which dispersed into North America (*9*) and Europe (Belgium: *10*). In South America there developed the Didelphidae (*11*), Borhyaenidae (*12*), Caenolestidae (*13*), Polydolopidae (*14*), Groeberiidae (*15*), Necrolestidae (*16*) and Argyrolagidae (*17*). Third dispersal of marsupials of South America into Africa (*18*: *Kasserinotherium*, Tunisia; *Peratherium*, Egypt) and Eurasia (*19*: *Peratherium* into Europe; *20* a marsupial in Asia). It is not known whether this dispersal took place via Africa or via North America (*21*). A recent dispersal of marsupials from South America took place towards North America (*22*). From South America, the marsupials dispersed into Antarctica (*23* Seymour) and Australia and Papuasia, where they gave rise to a major radiation: *24* Dasyuridae and Myrmecobiidae; *25* Thylacinidae; *26* Notoryctidae; *27* Peramelidae; *28* Tarsipedidae; *29* Phalangeridae; *30* Thylacoleonidae; *31* Wynyardidae; *32* Wombatidae; *33* Macropodidae; *34* Diprotodontidae. (*Antar* Antarctic). (After Hoffstetter 1975 and Crochet 1986)



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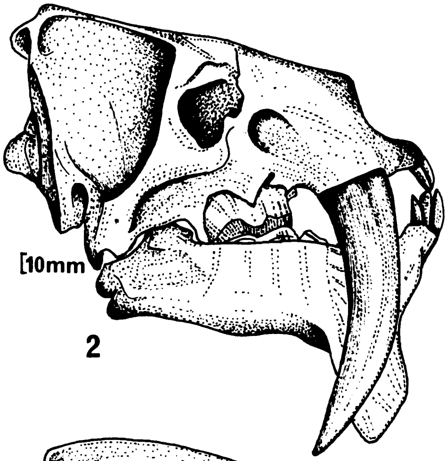

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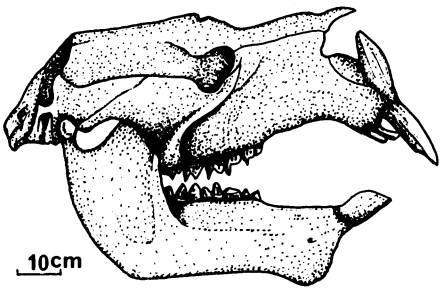

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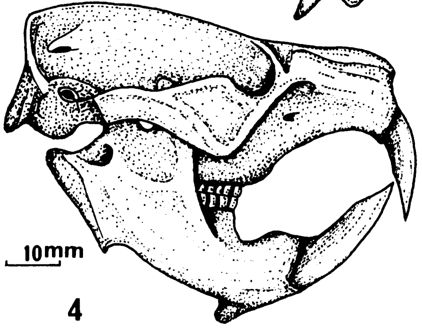

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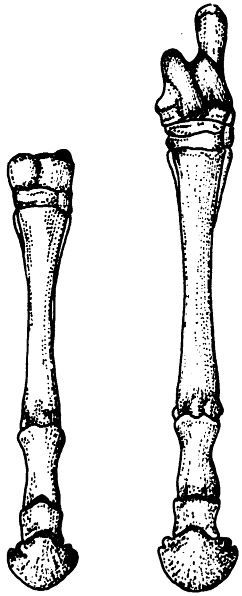

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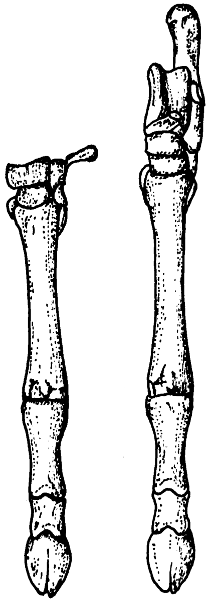

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7.5.4 Pantodonta

Pantodonts are known in South America only from the upper Cretaceous (Maestrichtian) of Tiupampa (Bolivia) where they are represented by *Alcidedorbignya inopinata* (de Muizon & Marshall 1987). This fossil suggests a common ancestry for pantodonts and tillodonts, and supports the inclusion of the Tillodontia with the Pantodontia. Pantodonts are also known from the early Paleocene to early Oligocene of Asia and from the middle Paleocene to late Eocene of North America. This discovery of *Alcidedorbignya* suggests a southern origin for this group which spread to North America by the end of the Cretaceous and then to Asia. It does, however, not have any descendants in South America.

7.5.5 Taeniodonta and Amblypoda

The taeniodonts constitute the first radiation of Paleocene-Eocene Herbivora whose teeth, covered with streaks of enamel, acquired continuous growth. The Amblypoda rapidly attained a large size, associated with skull bearing protuberances and with sabre-shaped canines (*Uintatherium*, the size of a rhinoceros).

7.5.6 Condylarthra

Possesing an astragalus with a spherical articulating head, the Condylarthra (a paraphyletic group) gave rise to a great variety of groups on every continent. The Condylarthra are represented in the upper Cretaceous (Maestrichtian) of Tiupampa (Bolivia) by three species: *Tiuclaenus minutus, Molinodus suarezi* (Hyopsondontidae Mioclaeninae), and *Andinodus boliviensis* (Phenacodontidae) (Marshall & de Muizon 1988). The Arctocyonidae, which had both large canines and grinding teeth, gave rise to the most carnivorous of the Condylarthra, the Mesonychidae (*Andrewsarchus*). *Phenacodus* is one of the best known of the Condylarthra. The Tubulidentata (with teeth traversed by tubes) have phyletic relationships with the Condylarthra (*Orycteropus*, from the Miocene to the present). The Condylarthra are the ancestors of the ungulates. In South America they gave rise to the notungulates, Litopterna, and Astrapothera, in North America and Eurasia to the Perissodactyla and the Artiodactyla.

Fig. 7.11. Convergences between marsupials and placentals. **1** *Thylacosmilus atrox*, marsupial of Pliocene of Argentina; **2** *Barbourofelis fricki*, placental feline of Pliocene of Nebraska; **3** *Diprotodon*, marsupial of Australian Pleistocene; **4** *Palaeocastor*, placental rodent of lower Miocene, Europe; **5** *Equus* (holarctic perissodactyl of Pleistocene, manus (*left*) and foot (*right*) with a single digit; **6** *Thoatherium*, (Proterothera, ungulate of Miocene of South America): manus (*left*) and foot (*right*) with a single digit (drawn to same scale as **5** to show convergence, though actually much smaller than **5**). (**1** after Riggs 1934; **2** after Schultz et al. 1970; **3, 4** after Schindewolf 1950; **5, 6** after Simpson 1951)

7.5.7 Ungulata of South America

Notungulata are represented in the upper Cretaceous of South America by *Perutherium altiplanense* (Grambast et al. 1987) at Laguna Umayo (Bolivia) and by *Gondwanatherium patagonicum* from the Campanian at Los Alamitos (Argentina), the earliest placental mammal yet known (Bonaparte 1986). They persisted there until the beginning of the Quaternary during the arrival of the more evolved placentals. The Notungulata culminated with *Toxodon* in the Pleistocene. The Litopterna exhibited an astonishing convergence in the evolution of their limbs with that of the Equidae in which the lateral digits were reduced to lead to a monodactylism of the third digit (Fig. 7.11). The Astrapothera up to the Miocene had canines developed for defense, a trunk, and teeth recalling those of the rhinoceros.

7.5.8 Perissodactyli

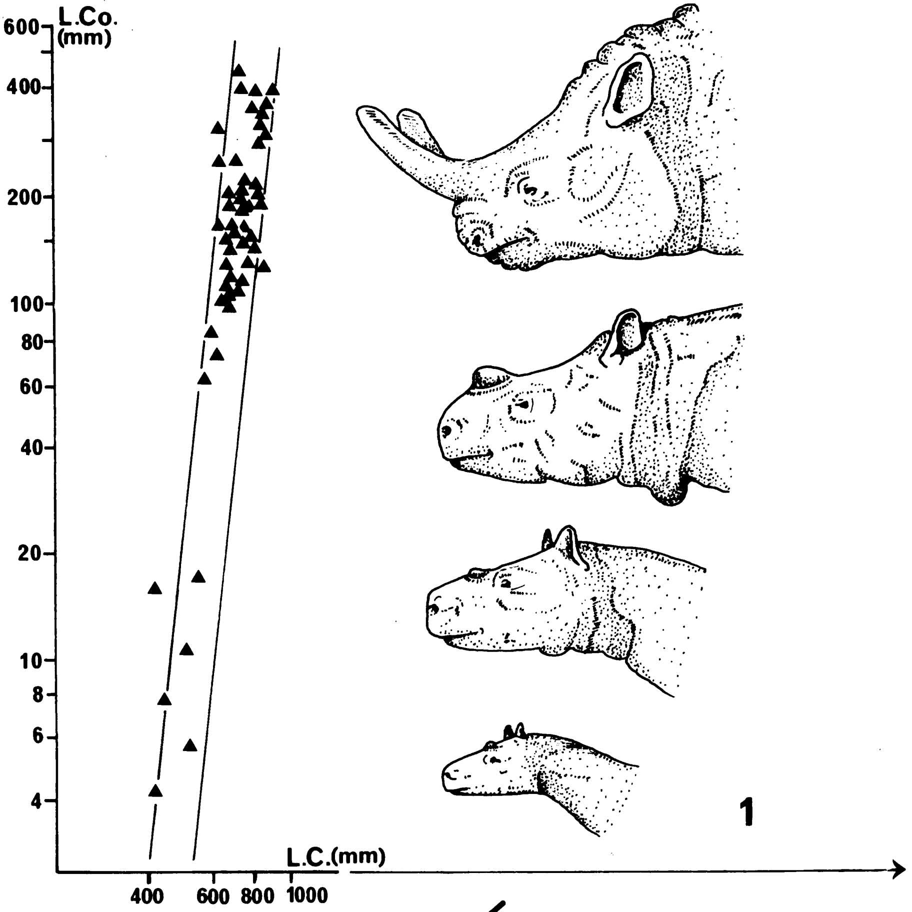
Resembling the tapirs, rhinoceri, and horses, these were characterized by the axis of their foot passing through the middle of the median (third) digit. They emerged from Condylarthra of the type of *Tetraclaenodon* and differentiated into Hippomorphs (Titanothera, Palaeothera and horses), Ceratomorphs (tapirs, rhinoceri) and Ancylopoda (Chalicothera).

7.5.8.1 Titanothera

Appearing at the start of the Eocene in North America, these constitute a good example of evolutionary trends (Osborn 1929; Hersh 1934; McKinney and Schoch 1985) with a very considerable increase in size, shortening of the face, and the development of frontonasal horns. These trends are expressed in a succession of forms: *Lambdotherium* and *Eotitanops* (lower Eocene), *Palaeosyops* and *Mesatirhinus* (middle Eocene), *Manteoceras* and *Duchesneodus* (middle-upper Eocene) and *Brontops, Brontotherium, Allops* and *Menodus* (lower Oligocene). They migrated into Asia, where they gave rise to forms with very developed and fused nasal horns (*Embolotherium*) (Fig. 7.12). The analysis of Hersh (1934) showed

►

Fig. 7.12. Evolution of the Titanothera. **1** Diagram of Hersh (1934) showing variations in length of horns (*L. H.*) in relation to length of base of cranium (*L. C.*) in logarithmic coordinates. This diagram seems capable of interpretation in terms of heterochronisms by a hypermorphosis. In fact, treatment of the same data (*L. H.* = log. length of horns; *L. C.* = log. length of cranial base) on the arithmetic scale (**2**) show that the Oligocene forms differ from the Eocene by a predisplacement (earlier start of development of horns) and that among the four Oligocene genera considered (**3**) *Allops* and *Brontotherium* have accelerated development of all characters, while in *Menodus* and *Brontops* there is a dissociation between development of the horn and of the rest of the skull. Only in *Menodus* development of the horn is accelerated compared with *Brontops*, the rest of the skull having retarded development. (After McKinney and Schoch 1985)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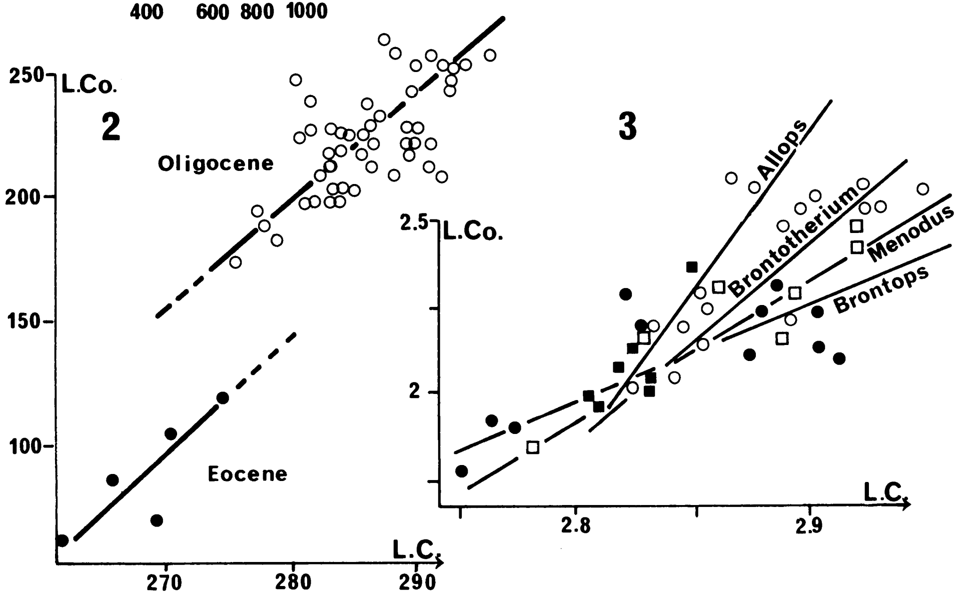
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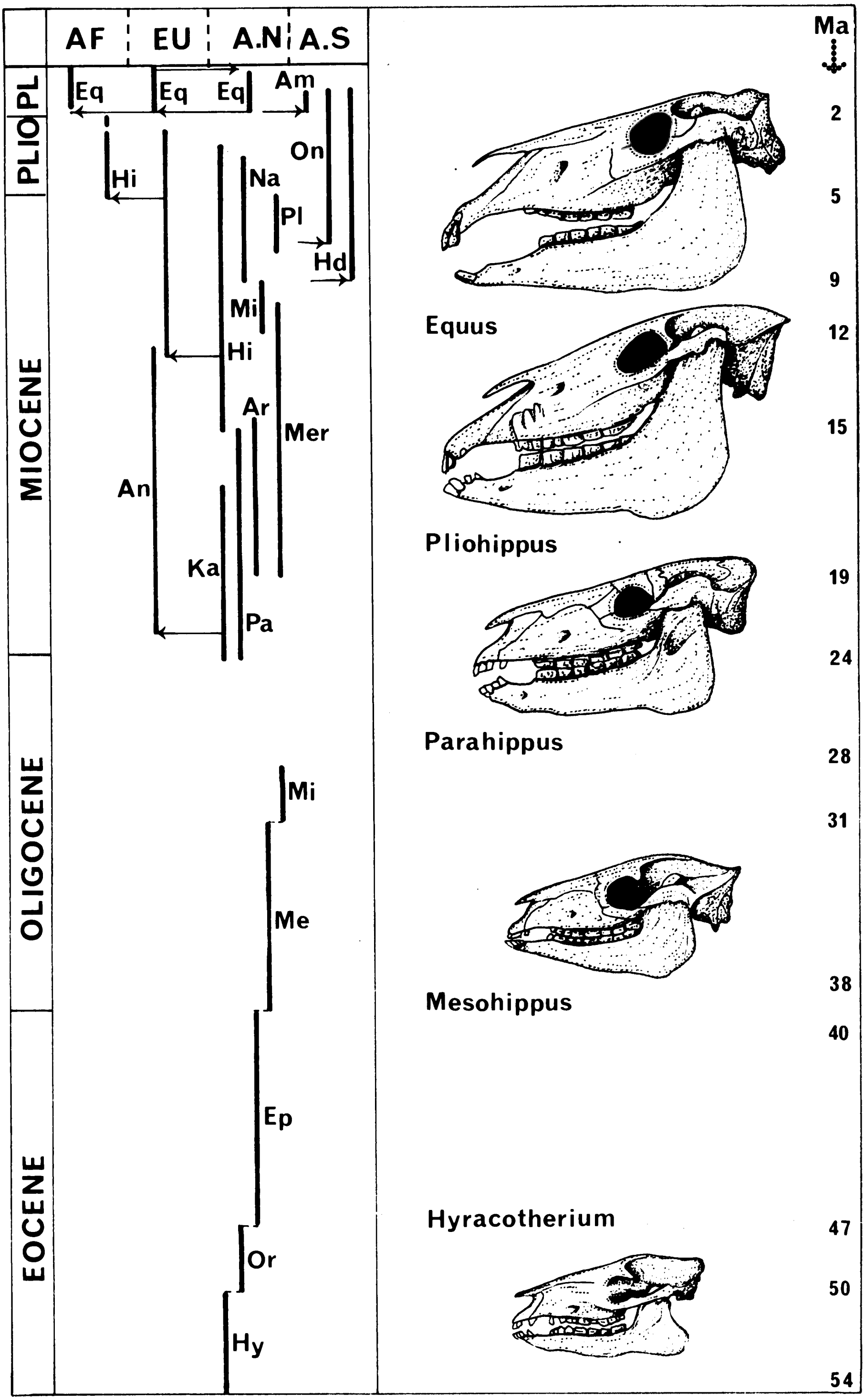
that the evolution of this group was characterized by a positive allometric relationship between the growth of the horns and that of the size of the body. He concluded that the evolutionary trend to form increasingly large horns was linked with the selection of an increasingly massive body. This mechanism of allometric change is to be explained in terms of developmental heterochrony by hypermorphosis (juvenile development identical with that of the ancestor, retardation of onset of sexual maturity, adult bigger than the ancestral adult; see Chap. 1.4) Reviewing the same data, McKinney and Schoch showed that the phenomena were more complex (Fig. 7.12). A discontinuity exists between the lines of development of the Eocene and Oligocene forms that may be interpreted as the result of a pre-displacement (morphologic development of an organ initiated earlier during ontogenesis). Moreover, the differences of slope between the axes of regression of the Oligocene genera *Allops, Brontotherium, Menodus,* and *Brontops* could result from changes in the rates of morphologic development in relation to their Eocene ancestors. *Brontops* and *Menodus* would have had a decreasing rate of development (neoteny), while that of *Allops* and *Brontotherium* would be accelerated (acceleration).

7.5.8.2 Equidae

This classic example (Simpson 1951) is in process of reinterpretation (Fig. 7.13 and 14). Emerging from a form close to *Tetraclaenodon, Hyracotherium* is known from the lower Eocene of North America and Europe. An animal with a height varying from 25 cm to that of a Shetland pony, *Hyracotherium* had fore-limbs with four digits and hind-limbs with three digits resting on pads. In Europe, *Hyracotherium* gave rise to the Paleotheriidae (*Pachynolophus*), which persisted to the end of the Oligocene.

In North America, *Hyracotherium* was to evolve following a trend marked by an increase of size, brachyodont teeth that became increasingly lophodont, and successive molarization of the premolars of *Orohippus* of the middle Eocene (P4, then P3, and P2), a phenomenon completed with *Epihippus* (terminal Eocene). The dental crests became more pronounced with *Mesohippus-Miohippus*. *Miohippus* gave rise to *Anchitherium, Hypohippus, Megahippus,* and *Archaeohippus*,

Fig. 7.13. Equidae: stratigraphic distribution and cranial evolution. *Left* stratigraphic distribution of the principal genera: Hy: *Hyracotherium*; Or: *Orohippus*; Ep: *Epihippus*; Me: *Mesohippus*; Mi: *Miohippus*; Pa: *Parahippus*; Ka: *Kalobatippus* (= *Anchitherium*, archaic); An: *Anchitherium*; Mer: *Merychippus*; Ar: *Archaeohippus*; Hi: *Hipparion*; Mi: *Miohippus*; Hd: *Hippidion*; Pl: *Plesippus*; Na: *Nannippus*; On: *Onohippidion*; Eq: *Equus*; Am: *Amerhippus*. While the kinship relations between *Hyracotherium* and *Miohippus* are evident, those of the Miocene and Pliocene forms are not well established. (The *transverse arrows* indicate dispersions between the continents. *AF* Africa; *EU* Eurasia; *N.A.* North America; *S.A.* South America). *Right* evolution of the cranium showing tendency to increase in size. (*Ma* millions of years; *PL* Pleistocene). (*Left* after unpublished data of C. Devillers; *right* after Matthes 1964)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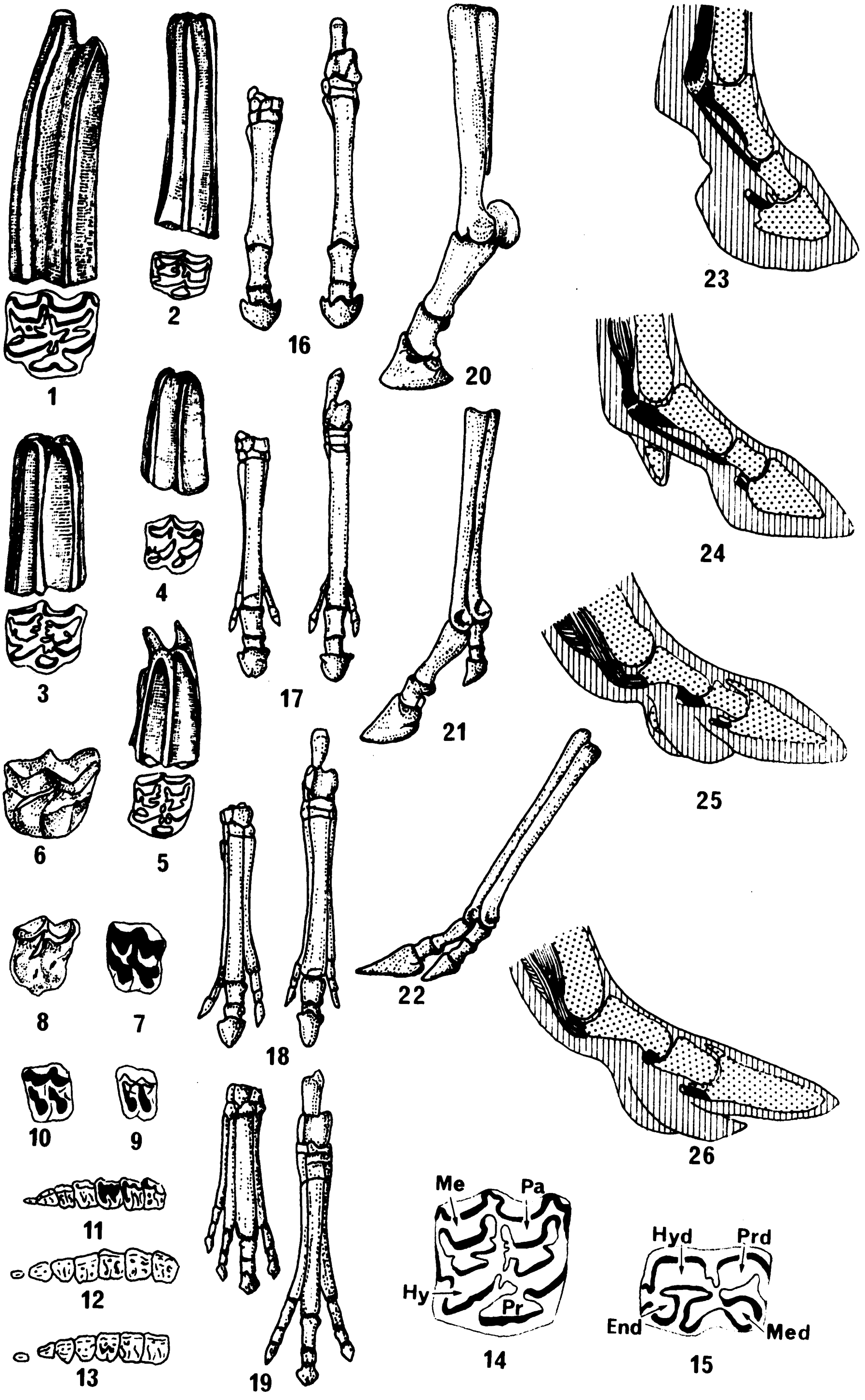
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conservative forms in which the increase in size is indicated by a relative augmentation of the brachyodonty. *Mesohippus* had all its tridactyl limbs resting on pads. The lateral digits touched the ground and were functional even at rest. This tridactyl type with lateral flexibility persisted in the Anchitheridae, which migrated into Eurasia or the end of the Oligocene. *Miohippus* was also the origin of *Parahippus*, a form characterized by increased hypsodonty and the appearance of dental cement. In *Merychippus*, represented by several species in the upper Miocene, the height of the teeth reached twice their length. The central phalanges of the foot elongated and the foot was raised above the ground and lost its pads which were replaced by hooves. This type of rigid tridactyl foot already had a pendular type of movement (Sondaar 1969). *Merychippus* gave rise in the upper Miocene to *Hipparion, Neohipparion*, and *Nannippus* (upper molars with a protocone separate from the protoconule). In the Pliocene *Hipparion* migrated into Eurasia and Africa, where it persisted until the Pleistocene as *Stylohipparion*. *Nannipus* was a form of very small size with very hypsodont teeth (H = 4L). *Merychippus* also gave rise to *Protohippus* and *Calippus*, a dwarf form morphologically close to *Pliohippus* (Pliocene), the ancestor of *Equus* (Pleistocene). In this line the teeth had a protocone confluent with the protoconule and in *Equus* the hypsodonty reached three times the dental length. The foot became monodactylar and suited for galloping and jumping by reduction of the lateral digits. The articulation of the foot was raised above the ground and its movement was pendular. At the end of the Pliocene, when the Panama isthmus emerged, evolved forms of *Pliohippus* reached South America, where they diversified into *Hippidion*, *Onohippidion*, and *Parahippidion*. In the upper Pliocene, *Equus* migrated into Eurasia and Africa, where it gave rise to several species of zebras. In Eurasia *Equus* was represented by several species, including *E.przewalski*, which was domesticated by man (*E. caballus*). *Equus* disappeared from North America at the beginning of the postglacial period and was reintroduced there by the conquistadors. The asses (*Asinus*) and hemiones constituted other differentiations of *Equus* in Eurasia in the Pleistocene.

Fig. 7.14. Equidae: evolution of teeth and limbs. **1** to **14** Upper molars with 1 to 5 occlusal and lateral views showing hypsodont dentition. **1** *Equus* (Pleistocene); **2** *Nannipus*, Pliocene dwarf form with most hypsodont teeth of group; **3** *Hipparion* (upper Miocene, Pliocene); **4** *Merychippus* (*Protohippus*), upper Miocene; **5** *Merychippus* (*Merychippus*), upper Miocene; **6** *Hypohippus*, Pliocene, giant brachyodont form; **7** *Parahippus* (Miocene); **8** *Anchitherium* (Miocene); **9** *Mesohippus* (Oligocene); **10** *Miohippus* (Oligocene); **11** *Epihippus* (Eocene); **12** *Orohipus* (Eocene); **13** *Hyracotherium* (Eocene); **14** *cusps of upper molars of Equus* (*Pr* protocone; *Pa* paracone; *Me* metacone; *Hy* hypocone); **15** *cusps of lower molars of Equus* (*Prd* protoconid; *Med* metaconid; *End* entoconid; *Hyd* hypoconid; see also Fig. 7.8.); **16** manus (*left*) and foot (*right*) of *Equus* (1 digit); **17** manus (*left*) and foot (*right*) of *Merychippus* (3 digits); **18** manus (*left*) and foot (*right*) of *Miohippus (3 digits);* **19** manus with 4 digits (*left*) and foot with 3 digits (*right*) of *Hyracotherium*; positions of the manus of *Equus* (**20**) *Hipparion* (**21**), and *Mesohippus* (**22**) showing the elongation of the central phalanx in *Hipparion*, then *Equus*; feet and sesamoid ligaments in *Equus* (**23**), *Hipparion* (**24**), *Mesohippus* (**25**), and *Hyracotherium* (**26**). (**1** to **10** after Simpson 1951; **20** to **26** after Sondaar 1968)

This history of the Equidae is characterized by major evolutionary changes in size, the shape of the skull, the teeth, and the structure of the feet (Figs. 7.13 and 14).

While, during the course of their history, often major global increase in size is observed between *Hyracotherium* and *Equus*, there are also lines of reversion of size towards dwarfism (*Archaeohippus, Calippus, Nannippus*) and others exhibiting a tendency to gigantism (*Dolichohippus, Hippidion, Onohippidium*). Devillers et al. (1984) have shown that the increase in length of the muzzle, an important character of skull morphology, evolved independently of increase in body size. It often accompanied it, but was not strictly determined by it. For example, *Calippus* had a muzzle as long as the large contemporary *Pliohippus*, whereas its absolute size was of the order of that of the Oligocene *Miohippus*!

From the dental aspect, a brachyodont phase can be distinguished from *Hyracotherium* to *Hypohippus* and *Anchitherium*. Besides the molarization of the premolars already mentioned, there can be noted with the increase of these animals in size an increase in dental height which remains, however, within the bounds of brachyodonty (height less than length). From *Parahippus* to *Merychippus* there developed dental crests which came to enclose small fossae that filled with cement. The increase in height of the stem of the teeth attained twice the dental length in *Merychippus*, three times the length in *Equus*, and four times in *Nannippus*, the most hypsodont, though dwarf, form. For the evolution of the structure of the limbs, Sondaar (1969) has demonstrated four morpho-functional types of locomotion (Fig. 7.14). The hyracotherian type (26), with four digits on the fore-foot and three on the hind-foot left great freedom of movement to the metapodials. The feet made an angle with the ground and rested on pads. The tridactyl type (25) with lateral flexibility (*Mesohippus, Anchitherium,* and *Hypohippus*) relied on a functionally tridactylar foot where the lateral metapodials were narrowly reduced and attached by their upper ends to the central digit, leaving a single bony element resting on the ground by means of a hood. The monodactylar type (23) of *Pliohippus* and *Equus* (gallop-jump) was characterized by the disappearance of the lateral digits and elongation of the phalanges, which made an angle of 90° with the ground. The motor tendons of the phalanges of the third digit (perforating and perforated tendons) were very developed and allowed pendular movement.

These modifications may be explicable in terms of adaptation to different ecologic niches. The first phase from *Hyracotherium* to *Hypohippus*, characterized by locomotion with lateral flexibility and brachyodont dentition, corresponds to the occupation of a forest environment, while the second phase starting in the upper Miocene was that of a pendular type of locomotion and a hypsodont dentition associated with conquest of open spaces and savannas.

7.5.8.3 Rhinoceroses

These appeared in the Eocene (Hyracodonts), reached their apogee in the Oligocene-Miocene, and are currently in process of disappearing. Their diversification into numerous lines with parallel evolution makes reconstruction of their phyletic history difficult. Trends can be noted to an increase in size which ended in the line of the *Baluchitherium* of the Oligocene-Miocene, the largest terrestrial mammals known (5 m tall at the withers and 7 to 8 m long).

7.5.8.4 Tapirs

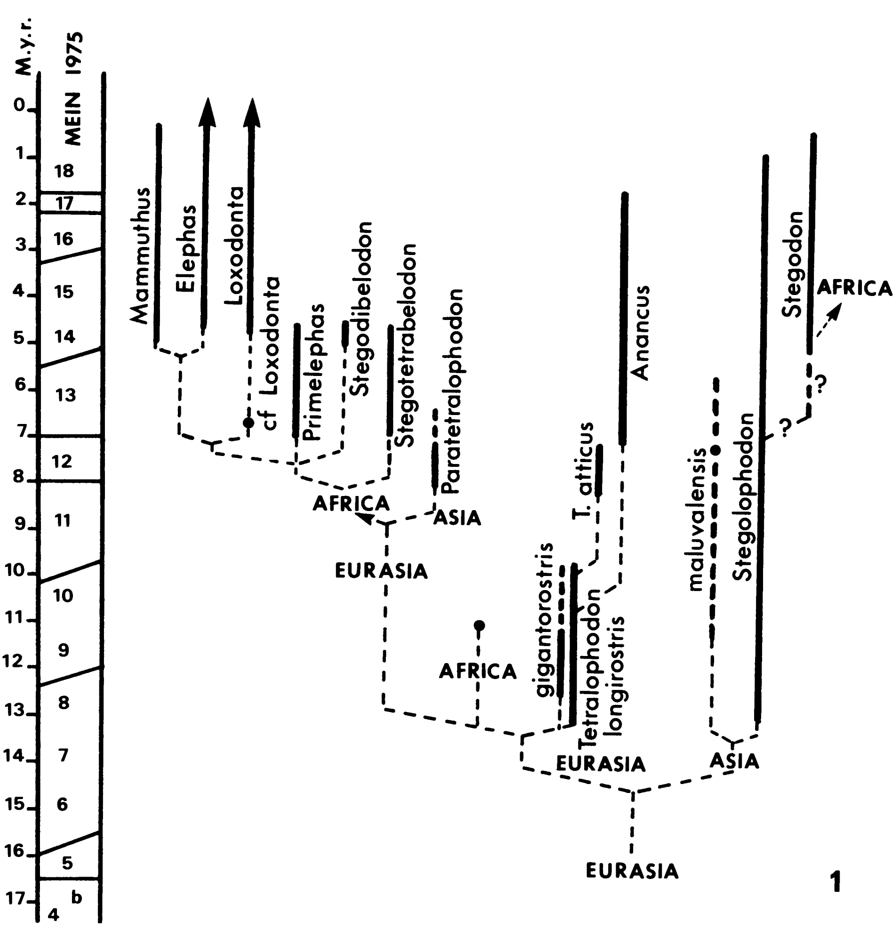
Rapidly differentiated at the Eocene, most of their lines disappeared in the Oligocene. They currently survive in a vestigial state in the humid tropical forests.

7.5.9 Artiodactyli

Characterized by feet with two to four digits whose axis passes between the third and fourth digits and an astragalus with two pulleys, the artiodactyls also have a cannon-bone corresponding to the metapodials of the fused third and fourth digits. The jaws, with a diastema, have brachyodont to bunodont molars, becoming selenodont to hypsodont. Many had horns or antlers. Their evolutionary success lay in the acquisition of the novel function of rumination which allowed them to supplant the perissodactyls. They underwent a very great diversification into Suidae (pigs), Tilopoda (camels), Cervidae, Giraffidae and Bovidae.

7.5.10 Proboscidea

The earliest known proboscidean remains have been found at El Kohol (Algeria) in a form akin to *Barytherium* (Mahboudi et al. 1984). The characters shared with modern representatives of Elephantoidea and Dinotheriidae suggest a close phylogenetic relationship and demonstrate the great antiquity of differentiation of modern proboscideans in Africa (Fig. 7.15.). Compared to *Barytherium* and *Moeritherium,* the Proboscidea constitute a poorly diversified group, split into two major branches, the Deinotheriidae and Elephantoidea. The elephantoidea are a monophyletic group of Neogene age characterized by a functional sequence of the dentition refered to as "horizontal". These animals lose their premolars prior to M3 becoming functional. Then M1 is shifted in front of the dental arch by a combination of dental drift and remodelling of the skull. This development is combined with a continued increase in size, and represents a real innovation resulting in the diversification into 38 genera of proboscideans (Tassy 1985). The ancestral relationship and a phylogenetic chart of the gomphotheria, elephantides, and stegodontides is presented in Fig. 7.15. Their large skull with pneumatized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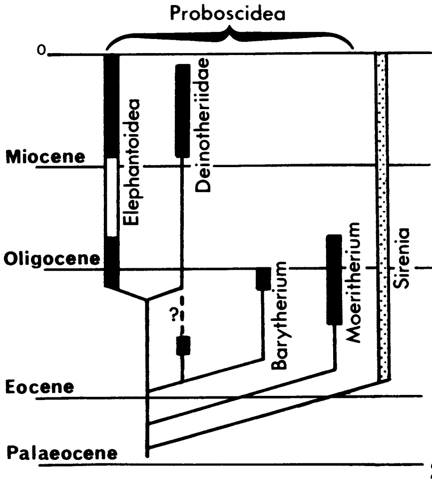
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bones carries a particular dentition. In the elephants of today only the incisors (i2), converted into defenses, remain of the front teeth and the molars succeed one another on the jaws. The Mastodontidae that appeared in the Oligocene gave rise to the Stegodontidae and Elephantidae. Apart from the development of defenses, they were characterized by a general tendency of the dentition to pass from brachyodont and bunodont to hypsodont and lophodont teeth with cement, and by an increase in size. The Hyracoidea (hyraxes) and Sirenia (dugongs and manatees) exhibit phylogenetic relationship with the Proboscidea. The Sirenia (*Halitherium*) were aquatic forms abundant in the Tertiary.

7.5.11 Carnivora

A special feature of the carnivores was the possession of carnassials, cutting and grinding teeth on the upper jaws (last premolar) and lower jaws (first molar). The most numerous forms are terrestrial, but some Mustelidae and Canoidae have become secondarily subaquatic.

7.5.11.1 Terrestrial Carnivora

The oldest, from the lower Paleocene of the northern hemisphere, were the Miacidae, which gave rise to numerous groups: Amphicyonidae (Eocene-Miocene), Ursidae, Canidae, Felidae, Viverridae, Hyaenidae, Ailuridae, and Mustelidae. Among evolutionary trends, the Felidae are notable for the reduced number of molars and the considerable development of the canine in the so-called sable-toothed cats (machaerodont forms) (e.g., *Smilodon, Barbourofelis)*. In North America, the succession of the species *Barbourofelis witfordi-morrisi-lovei* and *fricki* (Fig. 7.16) constitutes an excellent example of evolutionary tendencies characterized by: lengthening of the upper canines, reduction of the third premolars, the occipital region becoming inclined against the vertical in combination with morphological and functional modifications of the mastication, a reduction of the posterior part of the mandible, a ventral extension of the mandible at the position of the expansion of the upper canine, and all this accompanied with a pronounced general increase in size (Martin 1984). This evolutionary tendency is taking place in steps corresponding to successive speciations, reinforcing the tendencies of the ancestral forms within a development programme like that of *Barbourofelis*.

Fig. 7.15. Evolution of proboscideans. **1** Phylogenetic tree of tetralophodont gomphothers, elephantids, and stegodontids in the stratigraphical framework of the same groups. **2** Supposed phylogenetic relationships between the proboscideans. The sirenians, aquatic mammals, are closely related to proboscideans. (**1** after Tassy 1985; **3** after Mahboubi et al. 1984)

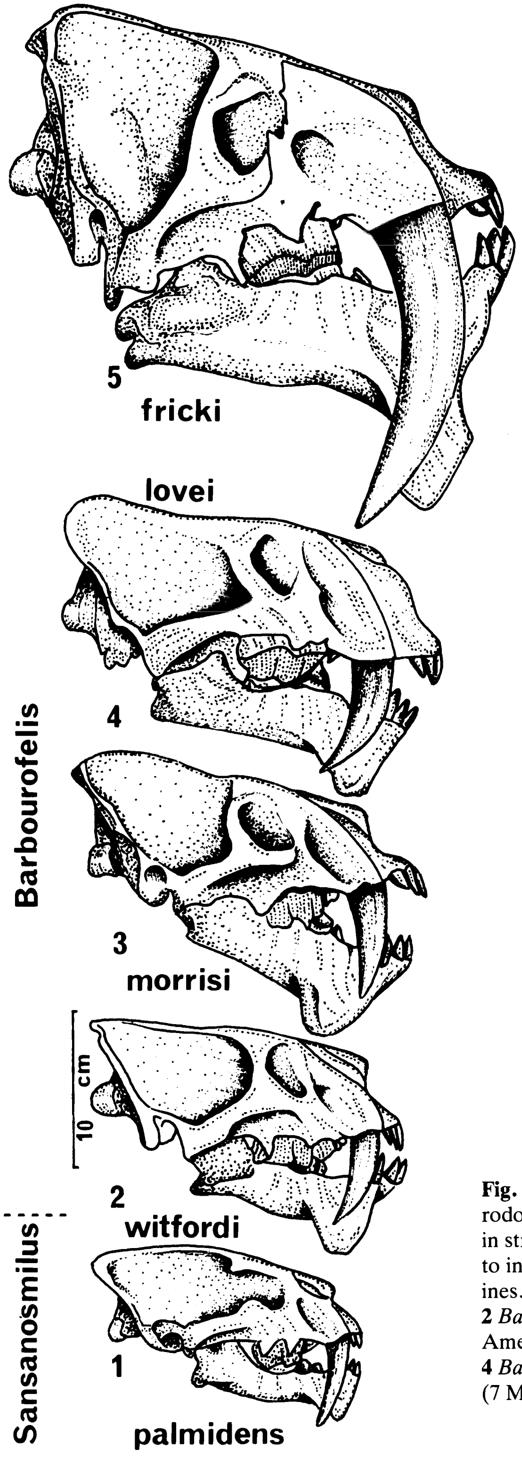


Fig. 7.16. Evolutionary trends in the machaerodonts (Barbourofelines). This group shows in stratigraphic sequence a general tendency to increase in size and elongation of the canines. **1** *Sansanosmilus palmidens* (Europe); **2** *Barbourofelis witfordi*, first form in North America (11 Ma); **3** *Barbourofelis morrisi*; **4** *Barbourofelis lovei*; **5** *Barbourofelis fricki* (7 Ma) (after Martin 1984)

7.5.11.2 Aquatic Carnivora

The Pinnipedia are Carnivora adapted to aquatic life. They include the seals (Phocidae), sea lions (Otariidae) and walruses (Odobenidae). There is some controversy, as to whether their origin is monophyletic or diphyletic. The diphyletic hypothesis proposes that seals originated from weasels (Musteloidea), and sea lions and walruses from the Ursoidea. This origin was initially accepted on the basis of fossils representing an intermediate stage between musteloids and seals, and between ursoids and "otarioids". Paleogeographical data suggest that the phocids originated in the Atlantic, and the "otarioids" in the Pacific. However, *Monachus schauinslandi,* the basal and most conservative fossil found in Hawaii (Pacific), refutes the notion of an Atlantic origin of the phocids. Furthermore, biochemical evidence only supported the morphology: cranial and skeletal specializations are not convergent adaptations, but are better explained by a common ancestral heritage. Thus the enaliarctids represent basal pinnipeds, followed in differentiation by Otariids. In contrast to this, walruses, fossil desmatophocids, and phocids are more closely related to each other (Flynn 1988).

Known since the Miocene (*Potamotherium*), they have shortened limbs but elongated hands and feet (e.g., *Acrophoca longirostris*) (Fig. 7.17).

7.5.12 Cetacea

Derived from the Condylarthra, these are known by the Archeoceti of the middle Eocene. They were aquatic and diversified into two main groups: the whales or cetacea with whalebone (Mysticeti) and the toothed whales (Odontoceti: cachalots, dolphins) which exhibit convergences with the ichthyosaurs (see Chap. 5.7). Possessing a very large skull, recessed nostrils, and very small eyes, they have converted limbs, in particular with hyperphalangism of the digits and a horizontal caudal fin. They include the largest vertebrates of all time, such as the blue whale (30 m and 120 tons).

7.5.13 Xenarthra

This South American group is characterized by the structure of the posterior vertebrae of the trunk, which interarticulate by the normal zygapophyses and by supplementary apophyses (xenapophyses), by a pelvis attached to the sacrum by the ilia and ischis, and by dental regression (Edentata). The upper Cretaceous mammal (Campanian) found in Patagonia *Gondwanatherium patagonicum* possess hypsodont molars with flat occlusal surface. This hypsodonty, a characteristic of Xenarthra (Edentata), suggests to Bonaparte (1986) that this derived character may be inherited from Cretaceous ancestors of *Gondwanatherium* type. But the phylogenetic relationships of this archaic mammal are very uncertain. The armadillos, which appeared in the Paleocene, possess an armor, an elongated snout

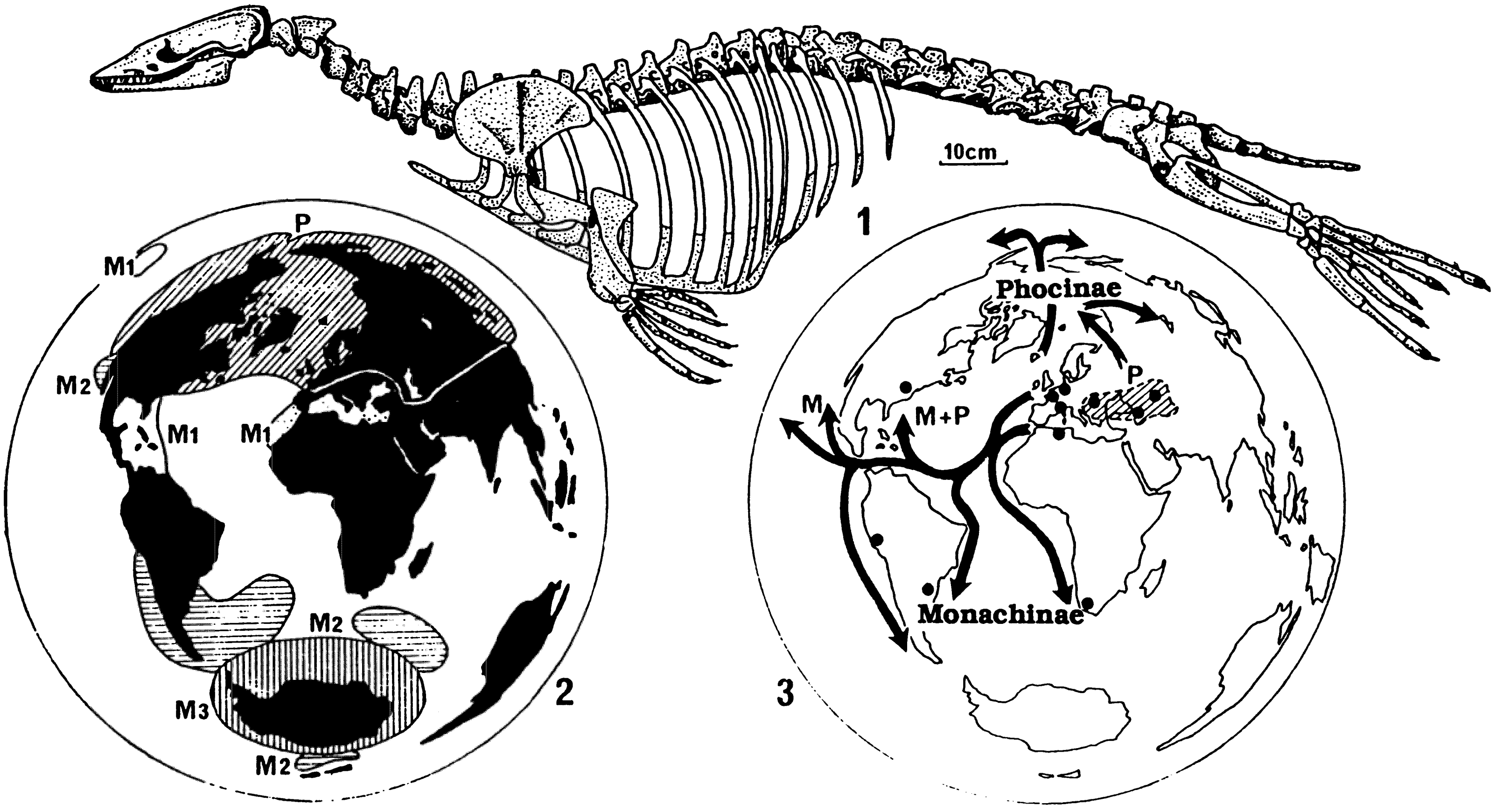


Fig. 7.17. Seals. **1** Reconstruction of skeleton of *Acrophoca longirostris*; **2** distribution of existing seals (*P* Phocinae; *M* Monachinae; *M1* monk seals; *M2* sea elephants; *M3* Antarctic seals); **3** dispersion of seals throughout the world. Probably originating in Europe (Parathetys – 20 Ma), they colonized the coasts of North America and entered the Pacific before the emergence of the isthmus of Panama. The *dots* indicate the deposits; Parathetys *obliquely hatched*. (**1, 2, 3** after de Muizon 1981)

with cylindrical teeth and powerful fore-limbs with claws. They reached a large size in the Pliocene and Quaternary (*Priodontes*). The Glyptodontidae, not very abundant from the Eocene to the Miocene, underwent a great development in the old Quaternary. At this epoch, *Glyptodon* had a carapace formed of fused polygonal plates, a raised skull and trilobed teeth. The weight of the carapace is correlated with the development of the pelvic girdle and hind-limbs. The Gravigradae were devoid of a carapace but bore dermal ossifications; among these the Megalonychidae became abundant in the Oligocene to the Quaternary when they migrated to North America (*Megalonyx*). The Megatheriidae, which appeared in the Miocene, gave the Quaternary the giant of the group, *Megatherium*, the size of an elephant with modified hands. The ant-eaters (Myrmecophagidae) are known from the Miocene as insectivorous forms devoid of teeth, and support themselves on the sides of their hands. The sloths (Bradypodidae) are assigned to the Xenarthra; they are unknown in the fossil state because their tropical forest habitat made fossilization difficult.

7.5.14 Lagomorpha

A sister-group of the rodents, these had continuously growing incisors, a diastema in place of the canine, and hypsodont premolars and molars. The earliest fossil lagomorphs are known from the late Eocene of Mongolia, China, and North America. They are related to Mimotonids, *Mimotona* from late Paleocene and *Mimolagus* from the Oligocene of China. The Mimotonids of the upper Paleocene preceded the very diversified Leporidae (Dawson 1967).

7.5.15 Rodents

The rodents, are a group which by itself includes as many species as all the other orders of mammals put together: 50 families of extant and fossil forms (Carleton 1984). Recent discussions about origin and phylogenetic relationships of rodents (Luckett and Hartenberger 1985) supported the hypothesis of close evolutionary relationships among Rodentia, Lagomorpha and Eurymyloidea suggested by Li and Ting (1985); Eurymylidae and Rodentia being more closely related as well as Mimotonidae and Lagomorpha.

Eurymylids (*Eurymylus*) and particularly *Heomys* from the middle and late Paleocene of China seems to be very close to the ancestry of Rodentia. The age of divergence of Eurymylids from asiatic protherian is earlier than middle Campanian, the age of origin of rodents is at least as early as Cretaceous.

They became diversified into a great variety of groups: dormice, squirrels, hamsters, rats, mice, voles, lemmings, beavers, porcupines, jerboas, chinchillas, pouched gophers, etc. Figure 7.18 proposes a working hypothesis of possible evolutionary relationships among major rodent taxa based from paleontological to molecular data (Luckett and Hartenberger 1985). We cannot analyse their

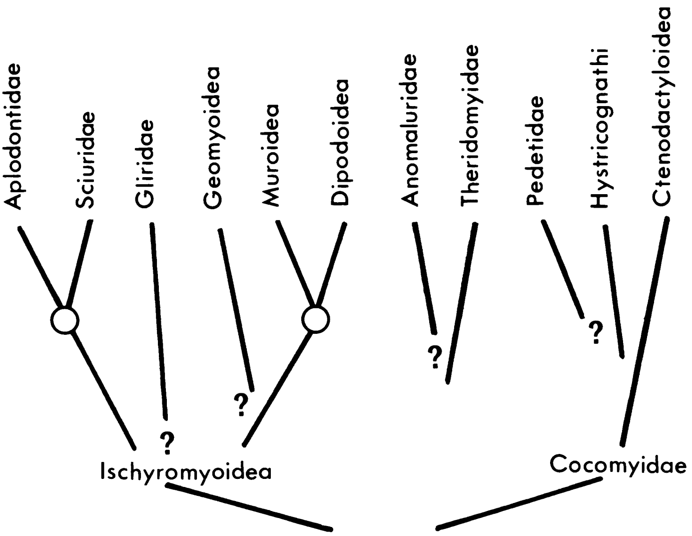
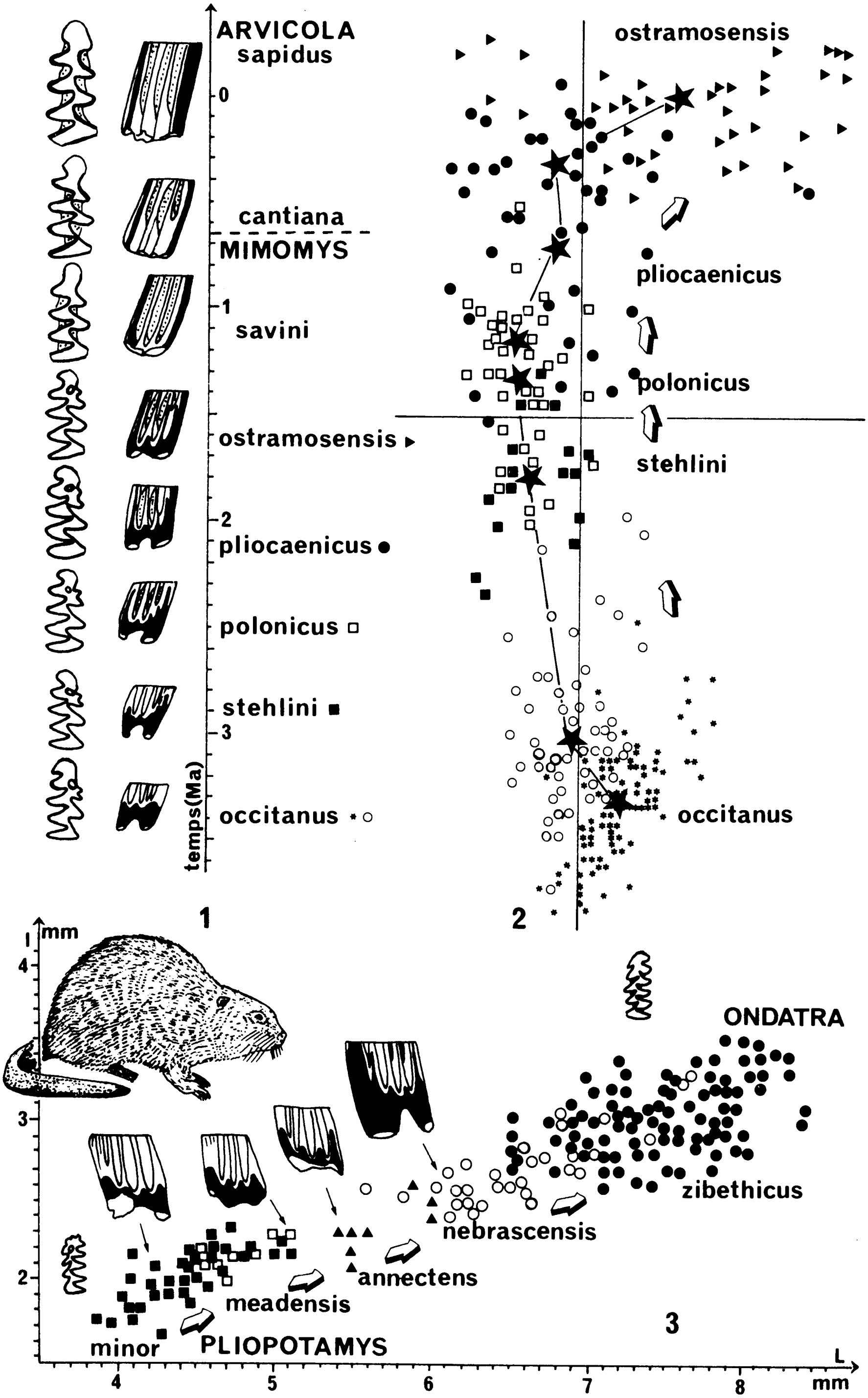


Fig. 7.18. Phylogenetic relationships of rodents. (After Luckett and Hartenberger 1985)

evolutionary history here – this has been done elsewhere in detail (see Chaline and Mein 1979) – but they provide examples demonstrating some very debated evolutionary problems, such as the existence of phyletic gradualism and its relative importance in morphological evolution. The voles (Arvicolidae) will be taken as an example.

Fig. 7.19. Phyletic gradualism in the voles. **1** Line leading from *Mimomys occitanus* (Pliocene) to *Arvicola sapidus* in Eurasia, the present mole-rat: the gradual evolution of the lower M1 teeth is indicated by some modifications of the wearing surface (*left* disappearance of fossette of the anterior curve) but especially in lateral view (*right*) by the development of indentations of the line of interruption of enamel (*black*), the progressive disappearance of the roots between *Mimomys occitanus* and *Mimomys savini*, the acquisition of continuous growth in *Arvicola cantiana*, the appearance of cement in the re-entrant angles in *Mimomys polonicus*. The evolution of the line is also characterized by a gradual increase in size and dental hypsodonty at a variable rhythm; **2** analysis of the modifications of 18 parameters of the M1 teeth by factorial analysis of correspondances of the same line *Mimomys occitanus – stehlini – polonicus – pliocaenus – ostramosensis* showing the overlapping of variations of successive populations and demonstrating the existence of phyletic gradualism (the *black stars* indicate the centers of gravity of the principal populations); line leading from *Pliopotamys minor* to *Ondatra zibethicus* in North America. The gradual evolution of the lower M1 teeth is indicated by an increase in size, the development of indentations of the lateral line of interruption of enamel (*black*) and dental hypsodonty. **1, 2** after Chaline and Laurin 1986; **3** after Martin 1979)


ARVICOLA
sapidus
0
cantiana
MIMOMYS
1
savini
ostramosensis ▸
2
pliocaenicus ●
polonicus □
stehlini ■
3
occitanus * ○
temps(Ma)
1
ostramosensis
pliocaenicus
polonicus
stehlini
occitanus
2
mm
4
3
2
ONDATRA
zibethicus
nebrascensis
annectens
meadensis
minor
PLIOPOTAMYS
3
4
5
6
7
8
L
mm

7.5.15.1 Phyletic Gradualism in the Voles

Demonstrated examples of phyletic gradualism are rare in the fossil record because they need to be documented over the total range of geographical and temporal range of a species lineage. The vole (Arvicolidae or field mouse) *Mimomys-Arvicola* example presented here (Chaline and Laurin 1986) brings about a reconciliation between paleobiological and cladistic approaches and the stratophenetic method. The total lineage is to be considered as a single spatio-temporal species (paleobiological and cladistic point of view) and the successive paleontological species distinguished in the lineages represent only evolutionary degrees within it (stratophenetic approach). The lineage which leads from *Mimomys occitanus* to *Arvicola sapidus* via the intermediate species: *Mimomys stehlini – polonicus – pliocaenicus – ostramosensis – savini – Arvicola cantiana – sapidus* between 3.5 Ma and the present day is characterized by the gradual modification of several variables (Fig. 7.19). The dental roots, which closed very early and prevented the teeth from growing in the older forms, closed increasingly later in the course of ontogenetic development, to the point of not closing at all in the later *M. savini* and thus ending in continuous growth (*Arvicola cantiana*). There resulted a gradual increase in dental height (hypsodonty), shown in the lateral view of the teeth by the development of a line of interruption of the enamel with more or less indentation. The morphology of the wearing surface of the tooth was also modified by the progressive disappearance of a small enamel pit situated in the anterior loop of the tooth and the acquisition of cement in the reentrant angles in *Mimomys polonicus*. The dental measurements of successive populations overlapped in a continuum in what is called a chronomorphocline (Fig. 7.19), where there is no interruption. As this evolution unfolded throughout Europe during an alternation of glacial and interglacial phases, it gives an opportunity to assess the role of the environment. It emerges that similar environmental conditions may trigger different modifications (acquisition of cement or increase of hypsodonty) and, that the same type of change (increase of hypsodonty) may be accelerated by a cold or warm phase. The environment acts rather as a stimulus releasing various evolutionary processes (Chaline and Laurin 1984, 1986).

Another example is found in North America in the gradual evolution of *Pliopotamys minor* into *Ondatra zibethicus* via the intermediate forms *P. meadensis – O. idahoensis – O. annectens – O. nebrascensis* between 3.5 Ma and the present (Fig. 7.19). This evolution is marked by an increase of hypsodonty and great increase in size, but did not result in continuous growth (Schultz et al. 1972).

7.5.15.2 Phyletic Gradualism and Stasis in Voles

The abundance of European material makes it possible, in the morphological evolution of the voles, to assess what is due to allopatric speciation (formation of new species lineage), what to phyletic gradualism, and what to stasis. In this group morphologic stases are not very numerous (26%), but in morphological differentiation it is phyletic gradualism that plays a great part, with 52% of changes as against 48% due to allopatric speciation.

These vole data lead to a reconsideration of the species and speciation concept into a more global spatio-temporal evolutionary model including stasis and phyletic gradualism as late speciation phases. Furthermore, these data refute punctuated equilibria lessening the role of phyletic gradualism. They suggest a punctuated equilibria/disequilibria model (Chaline 1987; see Chap. 9.4).

CHAPTER 8

The Primates and Hominization

8.1. Characteristics and Phylogenetic Relationships

8.1.1 Characteristics

The primates are animals with a snout of variable form, characterized by a tendency to an increase in cranial capacity and posterior closure of the orbits. The reduction of the nasal region allowed the development of stereoscopic vision. The hands and feet are often prehensile, the thumb and great toe being opposable to the other digits and the claws replaced by nails.

8.1.2 Phylogenetic Relationships

The fossil record of primates is incomplete because many arboreal forms are scarcely fossilized. The phylogenetic relationships are debatable (Fig. 8.1). According to Hoffstetter (1977), the *Tupaia,* close to the Insectivora, constitute the sister-group of all the other primates, which are divided into two major aggregates, depending on whether they possess a broad flattened nose (Strepsirhini) or a more pointed nose (Haplorhini). The Strepsirhini comprise the plesiadapiforms of the Paleocene, the adapiforms of the Eocene, the lemuriforms, loris and bush-babies. The Haplorhini group, the present-day *Tarsius* and the Simiiforms, include the monkeys of South America (Platyrrhini) and those of the Old World (Catarrhini: Cercopithecidae, Pongidae, and Hominidae).

8.2 Strepsirhini

The oldest primate, *Purgatorius*, dating from the upper Cretaceous of Montana (USA), is very close to the Insectivora, but its origin is to be sought in the Old World.

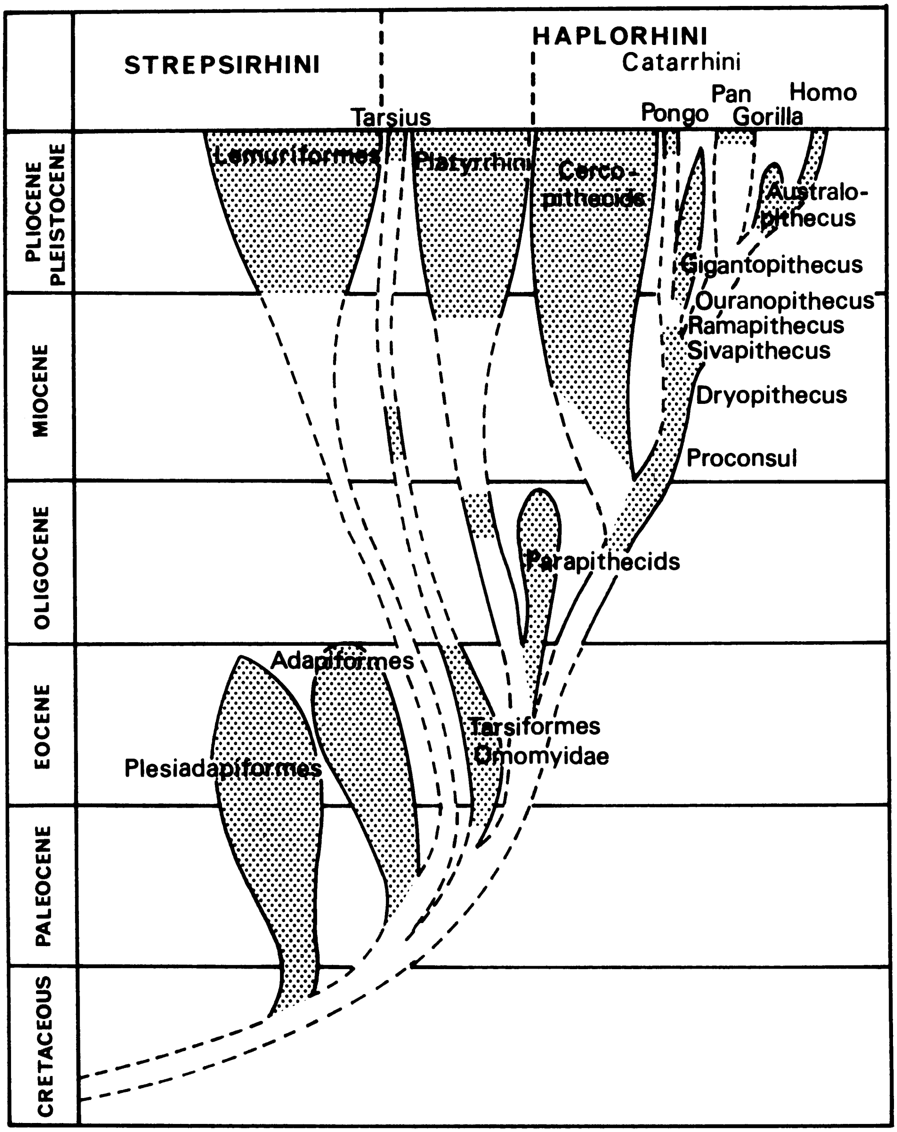


Fig. 8.1. Phylogenetic relationships of the primates

8.2.1 Plesiadapiformes, Adapiformes and Omomyids

Plesiadapiforms include two groups, Microsyopoidea (*Palaechton*) and Plesiadapoidea derived from *Purgatorius* ancestor. *Plesiadapis* was predominantly terrestrial and herbivorous (Gingerich 1984).

Primates of modern aspect appeared in the early Eocene of Asia, Europe and North America, where they are represented by two groups, Omomyidae and Adapidae. Omomyids are represented by *Altanius* and *Kohatius* in the early Eocene of Asia, but Adapids are not known with certainty. Early Eocene Omomyids (*Teilhardina*) and Adapids (*Cantius*) are better known in Europe and North America. They appear to be part of Holarctic mammalian fauna and the discovery of Adapids in the middle Eocene of Pakistan (*Panobius, Agerina*), and in southern Thailand (Suteehorn et al. 1988) show that faunal exchanges may have occurred between the Indian subcontinent and Europe at a time when it was supposed to be isolated by the sea (Russell and Gingerich 1987). According to Gingerich (1984), *Teilhardina*-like form gave rise to Microchoerinae in Europe (*Necrolemur*), and Anaptomorphinae and Omomyinae in North America (*Tetonius*). *Cantius* developed in Adapinae (*Adapis*) in Europe and Notharctinae in North America (*Notharctus*). The last record of Omomyids are in Oligocene (*Rooneyia* and *Ekgmowechashala*). Adapids survived in the late Miocene of India with *Sivaladapis*, and became extinct near the end of Miocene, when the distribution of forest was restricted and Cercopithecoids monkeys invaded South Asia.

Adapids exibit numerous characteristics in common with present-day Lemurids of Madagascar (lateral orbit closed behind). However, it is not possible to reconstruct their history because of the absence of fossils between Eocene and Quaternary. The existing lemurids are mainly nocturnal and fruit-eating tree-dwellers. The Aye-aye (*Daubentonia*) has continuously growing incisors like the rodents.

8.3 Haplorhini

8.3.1 Tarsids

The tarsids (*Tarsius* of Indonesia), which are related to the Necrolemuridae of the Eocene, have orbits of very great size, closed behind, and very elongated digits enabling them to make great leaps. The date of the loss of the tarsial rhinarium is also not known. Ginsburg and Mein (1987) discovered the oldest tarsiid fossil (*Tarsius thailandica*) in lower Miocene rocks of Li (Thailand). *Afrotarsius chatrathi* from the Oligocene of Fayum (Egypt) is not a tarsiid, but still related to the Simiiformes prior to their dichotomy into Platyrrhinians and Catarrhinians.

8.3.2 Platyrrhini

The Platyrrhini of South America are characterized by eyes far apart, three premolars per half-jaw, and a prehensile tail. They are represented from the late Oligocene by *Branisella* and have become diversified into the marmosets, spider-monkeys, howler monkeys, and woolly monkeys (*Lagothrix*).

8.3.3 Catarrhini

These are monkeys with nostrils approximated and two premolars per half-jaw, and resemble the Old World monkeys. A molar of an Eocene Catarrhinian (*Biretia piveteaui*) recently discovered in Algeria (De Bonis et al. 1988), reinforces the hypothesis of an African origin of the Catarrhini as opposed to a late Eocene migration from Asia. Except for *Amphipithecus* and *Podaungia* from the late Eocene of Burma which could represent either advanced adapids or early Simiiformes, the paleontological history of the Simiiformes is documented from the lower Oligocene (33 Ma) of Fayum (Egypt). The lower level has yielded *Oligopithecus* which is regarded either as an adapid or a primitive anthropoid. In the upper levels at Fayum the Parapithecids *Parapithecus, Apidium,* and *Quatrania* have been found. The presence of three premolars and the structure of the auditive region suggest similarities to the Platyrrhinians (Gingerich 1973; Hoffstetter 1974), but these result only from the separation of primitive characteristics (symplesiomorphies) without indicative value for ancestral relationships. Thus the Parapithecids could represent either a relict branch of the Simiiformes or a group closer to primitive catarrhinians, the latter, according to de Bonis (1987), being the more probable hypothesis.

Together with the Parapithecids, the Propliopithecids, *Propliopithecus* and *Aegyptopithecus*, which possess a dental formula typical of the catarrhinians with two premolars. *Aegyptopithecus* which undoubtedly was a quadruped frugivore tree-dweller, had a skull in which the face occupied an important place.

Between the Fayum beds (30 Ma) and the lower Miocene of East Africa there is a large gap in the fossil record. The Simiiformes are then found again in various regions of the old world where the migrations were made possible by the collision between the African and the Eurasian plates.

The Pliopithecids *Pliopithecus, Crouzelia, Plesiopliopithecus,* and *Anapithecus* of Europe between 20 and 10 Ma, for example, preserved the archaic characteristics of the Propliopithecids (Ginsburg and Mein 1980).

Two forms have been found at the end of the lower Miocene in Kenya: *Prohylobates* and *Victoriapithecus* with a bilophodont structure reminiscent of the Cercopithecids which are still extant in Africa and Asia. The Cercopithecids are subdivided into two groups: the first containing the Cerçopithecinae (*Dinopithecus, Dolichopithecus, Papio*) and the macaques (*Macaca:* from latest Miocene to the present) living in various environments from forests to open spaces, the second one containing the Colobinae (*Mesopithecus, Libypithecus, Colobus*) which are essentially terrestrial (Delson 1975). The Cercopithecids exhibit pronounced sexual dimorphism.

Dendropithecus appears to be an ancestral form of the gibbons (Hylobatidae) on the basis of its humerus, but its phylogenetic relationship is still under discussion. *Dyonysopithecus* from the upper Miocene of China clearly is a Hylobatid.

Proconsul from the lower to middle Miocene of Kenya was a generally tree-dwelling quadruped which had already acquired certain characteristics of the Catarrhinians, connecting them to the Pongidae (orang utans, chimpanzees, and gorillas) and to the Hominidae (*Australopithecus* and *Homo*).

Rangwapithecus, Mabokopithecus from the early Miocene of Kenya, and *Nyanzapithecus* of the mid-Miocene (15–16 Ma) appear to be related to *Oreopithecus* from the late Miocene of Europe (Harrison 1986). The latter previously was associated with the hominids because of certain morphological similarities of the mandible and pelvis (Hürzeler 1962) or even to the cercopithecids.

Dryopithecus, a form from the middle to upper Miocene of Eurasia (14–9 Ma), shows certain characteristics such as teeth covered by a thin layer of enamel, dentition, and height very similar to those of chimpanzees and gorillas. Pilbeam and Simons (1971) interpreted them as intermediaries between *Proconsul* and the recent chimpanzees and gorillas. They are now regarded as an original Miocene group exhibiting convergences with existing animals, but not with their direct ancestor, as its skull does not have the superstructure of the latter.

Some other related primates are rather interesting: *Ramapithecus, Sivapithecus,* and *Ouranopithecus.*

The sivapithecids are regarded as relatives of the orang utans and of the gigantopithecids, a group of giant Asian anthropomorphs, that became extinct during the Quaternary. The ramapithecids possessed certain hominid dental characteristics (vertically implanted incisors, reduced canine, molar enamel) which in the 1970's caused them to be considered as the potential ancestors to chimpanzee and man (Simons 1961, 1979). Actually, sivapithecids and ramapithecids lived between 14–10 Ma in the same regions and often at the same sites, differing mainly in size. These finds are more suggestive of sexual dimorphism, important in anthropomorph primates, than of different genera (de Bonis 1982). The recent discovery of the face of a *Sivapithecus* in Pakistan (Pilbeam 1982) has confirmed its close relationships with the orang utan. As the female of an orang utan ancestor, *Ramapithecus* has this last ist prestigious position.

With his thick molar enamel and the reduction of the premolars, *Ouranopithecus* from the upper Miocene of Greece presents characteristics connecting him to the gigantopithecids and to the australopithecids (de Bonis 1987 a, b) a hypothesis which, however, has not been generally accepted.

8.4. Relationships Between Pongidae and Hominidae

8.4.1. Comparisons and Consequences

While the data of comparative anatomy have shown that the common chimpanzee is the closest relative of man, investigations into their biochemical make-up have revealed an identity of composition exceeding 99% (King and Wilson 1975; Miyamoto et al. 1988). This is a surprising result since such identities are found in the animal world only in twin species. Chromosomal study (Dutrillaux and Couturier 1986) shows that in their evolution the orang-utan (*Pongo*) was the first to separate, and that then the line: chimpanzees (*Pan*) – gorillas (*Gorilla*) diverged from that of the Hominidae (*Homo*). The biochemical identity of *Pan* and *Homo* and their chromosomal proximity (they differ by a chromosomal fusion and some rearrangements) *imply a common origin*, a common ancestor located by the geneticists at 5 or 6 Ma. This is a paradoxical resemblance, since there are major differences from the morphologic aspect: acquisition of biped habit in the Australopithecids and of a large cranial capacity in the line *Homo*. These differences suggest that, *starting from a common ancestor, there were major morpho-functional divergences* not involving any considerable genetic differentiation.

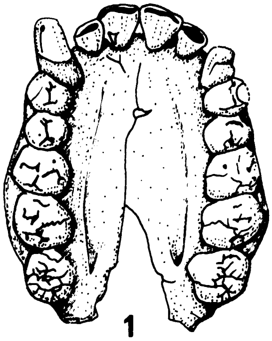
The absence of significant fossils in the deposits of the upper Miocene and the Pliocene means that the presumed ancestor has not yet been discovered.

8.4.2. Australopithecids

Discovered in southern and eastern Africa in deposits dated between 4 and 1 Ma, the Australopithecids have a cranial structure identical with that of the chimpanzees and gorillas. Certain specimens possessed a sagittal crest, a marked occipital

→

Fig. 8.2. Australopithecines and fossil men. **1** *Australopithecus afarensis* (Hadar AL. 200-1), maxilla differing from that of chimpanzee by the smaller second incisor; **2** *Australopithecus africanus* (Sterkfontein 5, South Africa), lateral view of cranium; **3** same, dorsal view showing absence of sagittal crest (female); **4** *Australopithecus africanus* (Taung, South Africa), holotype, juvenile form; **5** *Australopithecus robustus* (East Turkana, Kenya, 406), frontal view of cranium with sagittal crest (male); **6** same, dorsal view with sagittal crest and marked retro-orbital constriction (male); **7** *Homo habilis* (East Turkana, Kenya, 3733), lateral view of cranium; **8** same in dorsal view. Comparison with **6** *Homo habilis* has a larger cranium, a minor retro-orbital constriction and no sagittal crest but parietal crests (male); **9** *Homo erectus* (Chou-Kou-Tien, China), lateral view of cranium; **10** *Homo erectus* (Steinheim, Germany), cranium very rounded in posterior part; **11** *Homo sapiens neandertalensis* (La Chapelle-aux-Saints, Corrèze), lateral view of cranium; **12** *Homo sapiens sapiens* (Cro-Magnon, les Eyzies, Dordogne), lateral view of cranium. The mandible has a chin, the cranium no longer has a supraorbital ridge; **13** pelvis of *Homo sapiens* (Pygmy); **14** pelvis of *Australopithecus afarensis* (Lucy, AL. 288); **15** pelvis of common chimpanzee (*Pan troglodytes*). (**1, 2, 3, 4, 9, 10, 11, 12** after Chaline 1985; **5, 6, 7, 8** after Walker and Leakey 1978; **13, 15** after Chaline et al. 1986; **14** after Berge and et al. 1984)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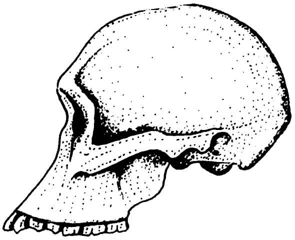
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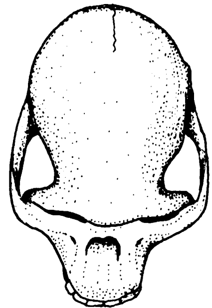
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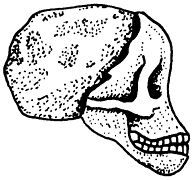
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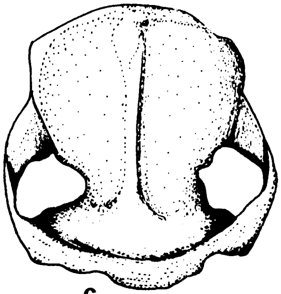
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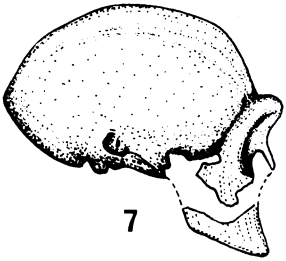
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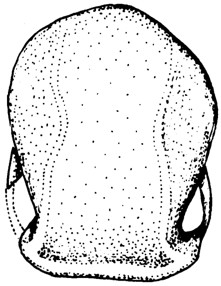
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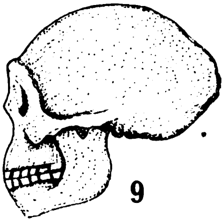
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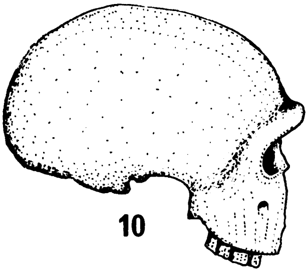
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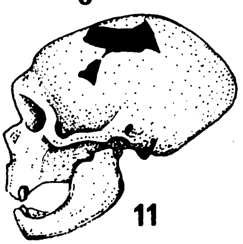
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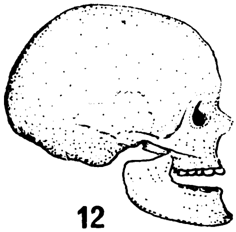
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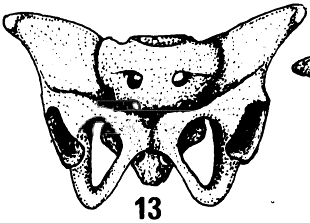
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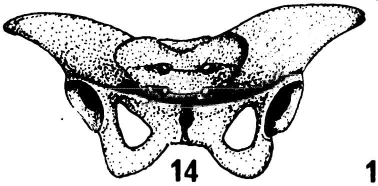
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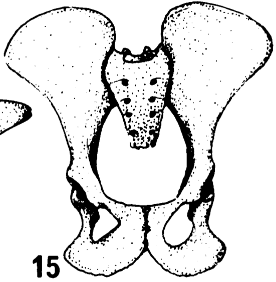
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rim, a marked supra-orbital prominence and a marked retro-orbital constriction; in those others devoid of a sagittal crest the other characteristics are less distinct (Fig. 8.2). These two types were successively interpreted, first as two distinct genera: *Australopithecus* and *Paranthropus*, then as two distinct species: *africanus* and *robustus* (Coppens 1986). In fact, the features mentioned are those which characterize the males and females respectively of present-day gorillas and chimpanzees (Chaline and Marchand 1976). This conception is now generally admitted for the Australopithecids of East Africa, but is still debatable for some of Southern Africa. The Australopithecids are here considered as constituting a single specific line with males and females in which, at a pinch, one can distinguish three successive evolutionary stages: *Australopithecus afarensis* (4 to 3 Ma) – *A.africanus* (3 to 2 Ma) – *A.robustus* (2 to 1 Ma) (Fig. 8.3).

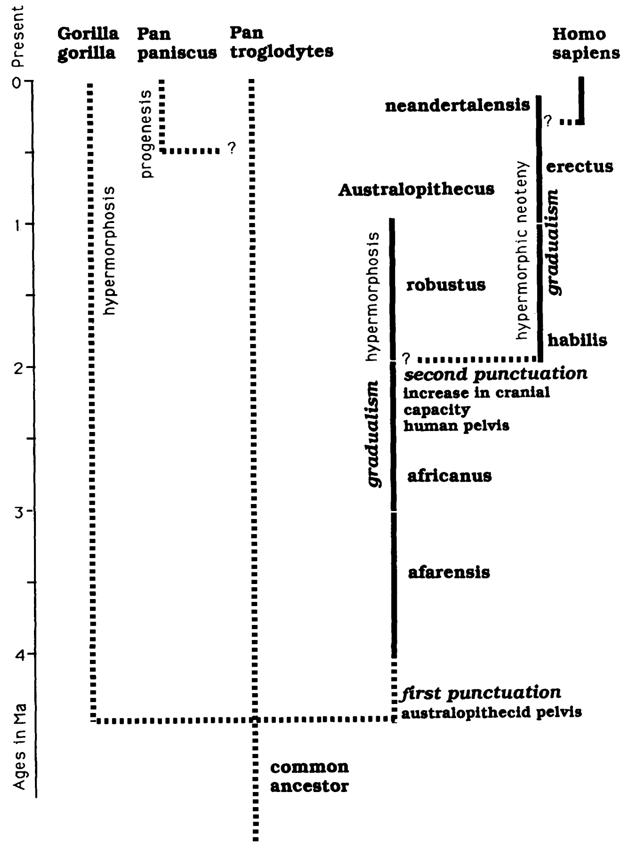


Fig. 8.3. Phylogenetic relationships of Hominids and anthropoid monkeys and developmental heterochronies. The appearance of bipedality in the Australopithecines seems to have resulted from a precocious innovation in the development of the pelvis and the increase in cranial capacity in *Homo* by hypermorphic neoteny. Interpretation of the evolution of lines at the term of development allows an understanding of the existence of phases of punctuation and of phyletic gradualism. (After Chaline et al. 1986)

The most important characteristic of the Australopithecids concerns the morphology of the pelvis, which allowed them to acquire the function of australopithecine bipedality. This resembles that of man and is spectacularly attested by two fossilized tracks of biped hominids in the volcanic ash of Laetoli (Tanzania) dating back 3.6 Ma. Still, resemblance does not amount to identity, and australopithecan bipedality had not attained the perfection of human bipedality (Berge *et al.* 1984). Thus the Australopithecids appear as a very special group, still anthropomorphs as far as their cranial structure is concerned, but already established on the path to hominization by the morphology of their pelvis, which permitted the biped state. During their evolution a slight increase of the size of the skull and teeth (megadonts) is to be noted, but they exhibit only one type of pelvis (Day 1982).

8.4.3. The Human Lineage

This appeared at about 2 Ma in East Africa as forms which had from the outset a human skull structure with a capacity varying from an average of 650 cm^3 to 800 cm^3. These archaic forms of *Homo*, called *H.habilis*, evolved by a progressive increase of cranial capacity, which reached 900 to 1200 cm^3 in *H.erectus*, and was to reach a capacity varying from 1100 to 2000 cm^3 in present-day *H.sapiens* (Fig. 8.2). In *H.habilis* and *erectus* the males lost the sagittal crest and were characterized by more marked parietal crests, a supraorbital prominence and an equally more marked retro-orbital constriction. The human line was further characterized by a perfectioning of the erect posture as indicated by forward displacement of the occipital foramen and a remodeling of the pelvis by a rotation of the ilium permitting enlargement of the pelvic cavity. Once this remodeling had been acquired, the pelvis remained stable in the human line.

About 800,000 years ago, the *H.erectus* that originated in Africa dispersed into Europe and Asia to undergo there a divergent evolution. In Europe the evolution was into *H.sapiens neandertalensis* (Neandertal Man), and in Asia it gave rise to *H.sapiens sapiens*, modern man. Thirty thousand years ago the Neanderthals mysteriously disappeared from Europe and were rapidly replaced by the modern *sapiens*, who colonized the entire world.

8.4.4. A New Explanatory Theory (Fig. 8.3)

Initially, comprehension of human evolution passed from a typologic conception of the species (1 specimen = 1 genus – 1 species) to a populational concept allowing for wide intraspecific variability. If we take into account sexual dimorphism and geopraphic variations, we arrive at the concepts of Fig. 8.3. However, one can conceive of passing from the descriptive to modalities, and then to processes, by analyzing this evolution in terms of development and growth. The paradoxical difference between the biochemical-chromosomal identity and the morphologic divergence between chimpanzee and man could be explained by modifications of ontogenetic pathways. In the absence of an identified common ancestor, the chimpanzee, a quadripedal form, can be taken as a reference standard. *Australopithecus* differs from the chimpanzee mainly in the shape of the pelvis: a long ilium in *Pan*, a short one in *Australopithecus*. Chaline *et al.* (1986) have suggested that the passage from a pelvic morphology of quadrupedal type to that of the australopithecine pelvis may have been by a precocious modification of the ontogenetic pathway of *Australopithecus* (*innovations*?). This new morphology allowed the function of australopithecine bipedality. Coppens (1986) has proposed another hypothesis according to which the divergence of the large African anthropomorphs and the Hominidae resulted from reactivation of the Rift Valley, which had divided the peri-equatorial regions of forest and wooded savanna of Africa. The chimpanzees and gorillas in the western part exposed to rains and the Hominidae in the eastern part in more open settings would then be the descendants of these common ancestors (East Side story). This postulates the inductor role of climatic change and geographic isolation, whereas in the preceding theory speciation results from internal modifications of the genome and of ontogeny (Inside story). Such a process could only have been rapid and corresponds to a punctuation. Subsequently, the gradual increase in size of the australopithecine lineage would be explained by *hypermorphosis*. The origin of the human line is characterized by a very rapid increase in cranial capacity (650 to 800 cm^3) and corresponds to a punctuation. Now, Bolk (1926) and Gould (1977) have shown that the shape of the human skull was *neotenic* in relation to that of a chimpanzee or of an adult Australopothecid. But while neoteny may explain the shape of the skull, it does not account for the marked increase in cranial capacity in *Homo sapiens* (×3), the possible outcome of a *hypermorphosis* gradually extending in time (Chaline *et al.* 1986). This *hypermorphic neoteny* also has implications for parturition. The widening of the pelvic cavity necessary to allow the passage of the more rounded cranium of *Homo* and the reinforcement of the vertebral axis associated with the constantly ventral position of the occipital foramen of the skull led to a remodeling of the australopithecine pelvis by rotation of the ilium and antero-posterior enlargement of the pelvic cavity. This precocious remodeling, which occurs in the first few months of fetal life, allowed the acquisition of human bipedality, different from that of the australopithecids.

Dambricourt-Malassé (1987) has confirmed this approach by showing that the evolution of the primates resulted in numerous chronologic shifts of successive ontogenies with an overall trend. The heterochronies are the results of an extension of the development phases of the brain such as cranio-facial contraction becoming more and more pronounced, more complex telencephalium, occipital leverage. The acquisition of the bipedal gait could thus just as well be only the secondary consequence of these changes in the cranial ontogenesis. In the same way, related to the chimpanzee taken as standard, the gorilla appears as the result of processes of *hypermorphosis* and the pygmy chimpanzee as that of *progenesis* or *neoteny* (Shea 1984). Figure 8.3 synthesizes this new interpretation of human evolution, allowing for both punctualism and gradualism.

CHAPTER 9

From Fossils to Explanatory Theories

9.1 Paleontology, the Science of Time

Paleontology is a science of time. By means of the fossils it extracts from the Earth's archives it is able to establish the stratigraphic distribution of the diverse species that have succeeded one another during the history of the Earth. This fossil record, incomplete witnesses as they are of the extraordinary diversification of life, are irreplaceable for an understanding of the composition of the existing biosphere. This may be compared to a transverse section of a cable diversified into 1 or 2 million strands (species) and 2.7 billion years long! While the present-day biosphere is the object of study of biologists working on a generational scale, the task of the paleontologist is carried out on a geological scale or a minimum of some 1000 to 1.000.000 generations.

Contrary to what might be thought, a reading of the fossil record does not immediately supply the history of life: a key is necessary. For the old poorly documented groups, cladistic analysis makes it possible to propose phylogenetic hypotheses; but as one approaches the present day, the documentation grows and the explanatory theories advanced are becoming increasingly complete.

9.2 The Lessons of the Fossils

Data from the fossil records make it possible to outline the general characteristics of vertebrate history.

- From the oldest to the most recent vertebrates, there is a global trend towards a greater complexity.
- This is manifested as a succession of increasingly complex groups characterized by the appearance of new features: the jaws of the Gnathostomes, the feet of the Tetrapoda, the egg of the Amniota, the mandibulo-otic structure of mammals, the placenta of the placentals.
- The origin of groups is always an unknown because of the imperfection of the fossil record and the problems of fossilization of the isolated pioneer populations with their small numbers, which give rise to new lineages.
- Thus groups appear suddenly and well characterized, and it is at this level that *innovations* are manifested. It is here that *possibilities* are realized by a true

»tinkering« of previous structures, as Jacob (1977;1981) has expressed it. The first representatives of groups are usually forms of small size.

– The groups very rapidly undergo a major diversification which exploits the potential and possible morphological variation of the structure of the group (organization plan): this is what is called a *radiation*. For example, in the placentals which appeared in the upper Cretaceous, almost all the main groups were differentiated at the Paleocene-Eocene boundary.

– Once diversified, the groups exhibit a maximum expansion, then a certain stability which lasts for at least a hundred million years. Their future is sometimes one of total extinction (placoderms, dinosaurs, pterosaurs), but often they persist as vestigial forms (hagfish, lampreys, sphenodonts, coelacanths, lungfishes), often qualified as *living fossils*.

– Within the groups there is noted the existence of *morphological evolutionary tendencies* which become more marked and are usually accompanied by an increase in size. Examples of this are numerous in the dinosaurs (Ceratopsia), pterosaurs, therapsids, and mammals (Titanothera, Equidae, Rhinoceroses, Carnivores, etc.). Here there is a real *evolutionary canalization* linked with the exploitation of the possibilities of ontogenies.

– Within the main groups, in the midst of their numerous lines, major morphological convergences can be observed: apody in the amphibians and snakes, ichthyosaur morphologies in the dolphins, the wings of pterosaurs, birds, and bats, skulls with large canines in *Thylacosmilus* (marsupial), *Barbourofelis* (Felidae) (Fig. 7.11), the feet of the Equidae and the liptoternes, the kangoroo-mouse form in *Antechinomys* (marsupial), *Elephantulus* (elephant shrew), *Argyrolagus* (marsupial) and *Dipodomys* (dipodideal rodent). These convergences seem closely linked with a habitat and a particular mode of life and are witnesses to the role of the environment on the possibilities existing in the genetic structure of the group.

– As for the species, their appearance is usually sudden in the fossil record and they seem to have two possible futures. They may remain in *morphological stasis* or globally stable, exhibiting *ecophenotypic variations* (*Clethrionomys*, a vole) or, in other cases, they are gradually modified according to a cumulative and irreversible trend (phyletic gradualism) which may last for some thousands to millions of years (*Mimomys – Arvicola*; *Pliopotamys – Ondatra*, voles: Fig. 7.19).

– Finally, the evolution of life appears as a historical phenomenon, *contingent* and unforeseeable, in which the chance of circumstances of terrestrial history plays an important part. The history of life is characterized by a series of unique and irreversible events and follows no laws (Tintant 1986).

9.3 From Fossils to Theories

The theory of descent with transformations or theory of evolution provides an explanation of the history of life. The various paleontological and biological aspects of the evolution of the living have been, and will be, progressively discovered in accord with the development of research and technique. Each new observation has been the point of anchorage for a new idea or concept, which, when it allows a reinterpretation of all the previously known facts, is expressed in the shape of a theory. Without intending a history of theories explaining evolution, it may be useful to take stock at this point by making a non-exhaustive summary of the accumulation of concepts marking:

- the increasing complexity of life (Lamarck 1809)
- the idea of transformism (Lamarck 1809)
- the role of the environment (Geoffroy-Saint-Hilaire 1830)
- natural selection (Darwin 1859)
- the formation of species by gradualism (Darwin 1859)
- relations between ontogeny and phylogeny (Meckel 1821, von Baer 1828, Haeckel 1856, Garstang 1922, de Beer 1930)
- the dissociation of characters in reproductive crosses (Mendel 1866)
- separation of germ-plasm and soma (Weismann 1892)
- mutations (de Vries 1906, Morgan 1926)
- systematics of populations (Fischer 1958, Haldane 1932, Wright 1978, Chetverikov 1926)
- progressive variations of the frequencies of alleles (Dobhzansky 1937)
- phyletic gradualism – different evolutionary rates – quantic evolution – adaptive radiation (Simpson 1953)
- the biologic concept of species – allopatric speciation (Mayr 1942, 1982)
- the »hopeful monster« (Goldschmidt 1940)
- structure of DNA (Watson and Crick 1953)
- model of control of genic expression of bacteria (Jacob and Monod 1961)
- chromosomal mutations (Mathey 1949 and White 1978)
- balanced polymorphism (Dobhzansky 1970, Lewontin 1974)
- stasis – punctuated equilibria (Eldredge and Gould 1972)
- regulatory genes (Davidson and Britten 1973)
- developmental heterochronies (Gould 1977, Alberch et al. 1979, McNamara 1988, Dommergues et al. 1986)

Over two centuries of research, after the transformist theory of Lamarckism, Darwin's theory of descent by natural selection and the mutationist theory, it was not until the 1940's that there arose the synthetic theory of evolution which gathered together the findings of genetics, biology, and paleontology. Many of the concepts of the synthetic theory have been questioned and replaced by others which are in the process of constituting a new stage of the theory of evolution.

9.4 Towards a Unifying Theory of Evolution

Since the elaboration of the synthetic theory, the development of the biological and paleontological sciences has occurred independently because of the necessary specializations. Now, in the study of evolution, while the historical approach of paleontology reveals the *modes, evolutionary rhythms*, and *results*, biology puts forward explanatory *processes* and *mechanisms*. We must therefore envisage a *unifying theory*. This unifying theory of evolution (Devillers and Chaline 1989) will have to integrate a number of biological and paleontological concepts which can be summed up under the following six statements:

– **The new genome** is made up by genes which are structured and ordered in such a way that they economize information (Jacob and Monod 1961; Davidson and Britten 1973). The importance of the genetic environment and of the physical factors of the environment in which the organism flourishes, underlines existence of a considerable epigenetic component in its development.

– **The hierachy of the organizational levels** is another essential point extending the case in question. This implies that on each level of organization properties are encountered which cannot be predicted only from the analysis of the underlying levels. It thus invalidates any strict reductionist approach. From the lowest right up to the highest level, the following, non-exhaustive hierachy can be visualized as being made up of two major steps. The first one characterizes individuals, populations, and species, encompassing what is usually refered to as *microevolution*, the main object of biological research: various stages of structure and ordering in genes, levels and defined by biochemistry, physiology, ontogeny, phenotype, ecology, and ethology. There is however, beyond the mere species, a second sequence of levels of integration, incorporating the factor »time«. This is the exclusive object of paleontological studies, resulting in the modes and tempos of evolutionary processes of *macroevolution*.

The *evolutionary trends* correspond to a strengthening of morphological characteristics which are maintained as one line, or a limited group of apparent lines over a succession of several species, despite an interruption of the speciation in certain cases (cf. Chapter 7.5.10.1, sabre-toothed carnivores).

The *adaptive radiations* correspond, via multiple early speciations, to the exploitation of a large number of possibles in an appearing new organizational pattern in, e. g., the differentiation of mammals taking place at the onset of the Tertiary.

The *appearance of major organizational »types«*, representing one of the most important phenomena of evolution, is frequently referred to as *macro-* or even *megaevolution*. It is difficult to explain as the result of the gradual accumulation of small mutations under the guiding influence of natural selection as postulated by the synthetic theory. In fact, it is not necessary to take recourse to such hypothetic processes of macroevolution. One should rather take into account the key role played by time-dependant changes of development.

– **The integration of ontogeny, chronological disordering (heterochronies), and their phylogenetic extensions.** This is the main short-coming of the synthetic theory, despite the important insights gained through studies since the beginning of the 19th century. Such an integration will eventually permit the correlation of a genotype with a phenotype. The phylogenetic extension of ontogeny leads to phylogeny (cf. Chapter 1.4). When passing from speciation or the origin of major organizational types through rapid environmental changes, ontogeny and its chronological irregularities (onto which innovations implant themselves) constitute simple mechanisms allowing nature to exploit the potential accumulated in the genetic programmes as a result of the gamble of the mutations. These mechanisms allow the passage from a preexisting structure in the embryonic or adult stage to other adult structures, without the necessity for pronounced genetic changes, solely through modulations (regulating genes ?) (cf. Chapter 8.4.4: hominid evolution).

The origin of the vertebrates, for example, appears to be explicable by a modification of a preexisting development pattern in which adult primitive vertebrates preserve throughout their lives the larval morphology of the ancestral forms (paedomorphosis), probably of non-skeletal echinoderms. Similarly, the change from the articulate structure of the therapsid jaws (mammal-like reptiles) to that of the mammals with corresponding modifications of the middle-ear appears to be the result of complex heterochronous processes. This is also suggested by the development of marsupial embryos in which one can still recognize a therapsid structure which disappears in the later stages (cf. Chapter 7.2.1). It was preponderant, for example, in the secondary adaptation of the Tetrapoda to the aquatic environment (de Ricqlès 1989). The existence of transformations resulting from paedomorphosis by neoteny in numerous unrelated groups (amphibians, urodeles, mesosaurs, nothosaurs, ichthyosaurs, sirenia) constitutes convergences and suggested to de Ricqlès (1989) the presence of the same hierarchized functional complex (structural and regulatory) in all Tetrapoda. This functional complex of the vertebrate genome, linked to internal and external factors, may be brought into play in certain ecologic situations. It dates back at least to the sarcopterygian stage of their evolution, since it is already manifest in the lungfishes (Bemis 1984). Especially when combined with innovations, it could explain certain structural leaps which hitherto have been incomprehensible. These mechanisms take place within a limited range of possibilities (Jacob 1977) governed by structural and functional constraints of the organisms concerned. Even considering the vast spans of time available, not everything is possible in evolution.

– **A new time-space concept of species and their formation.** The biological species which is defined as »a group of natural populations capable of interbreeding, but reproductively isolated from other similar groups«, appears static to the biologist at any given point in time. Through integration of the time dimension, it acquires a dynamic aspect in the time-space continuum or, as stated by Chaline (1987), »a spatio-temporal continuum between groups of natural populations which, at any point in this continuum, are interbreeding wich each other, but are isolated, from a reproductive point of view, from all other analogous groups«.

Research results underline the fundamental role played by very small isolated populations in the origin of species. Peripheral niches present particularities which are highly favourable to the establishment of new species. As they are situated along the edge of the area of partitionning of the species, they are frequently found in environments limited to the species and therefore exhibit extreme variations. The restricted number of individuals in isolates which posses only a small part of the genetic pool of the species, may lead to the interaction of particular processes (genetic drift) which favour the establishment of modifications at whatever level of integration of the living organism. The dispersal or disappearance of such a character can be fixed rapidly by consanguinity through transmittal to the homozygote stage.

These modifications are secondary consequences, especially those which are opposed to crossing with the bulk of the species when the niche becomes again sympatric with it. The reproductive isolation between two apparent species is frequently highly variable as a function of the levels connected by the restructuring, and of its more or less pronounced efficiency. These phenomena correspond to those referred to by the neontologists as »speciation«. However, these processes which started in the weak isolated populations, will not stop when reproductive isolation has been achieved and a new species established. They evade analysis by the biologist who considers the present point in time only, but become the privileged object of the paleontologist's interest who has at his disposal the factor »time«, the essential dimension of evolution.

Paleontological data suggest that the modifications occurring after reproductive isolation, morphological stasis, the reversible (ecophenotypic variations) and irreversible morphological variations (phyletic gradualism; see Chapter 7.5.14.1: voles example) may be considered as late phases of speciation after reproductive isolation has been achived.

One consequence of this space-time concept and the polyphased nature of speciation (Fig. 9.1; Chaline 1987) is, that anagenesis and cladogenesis which in the synthetic theory are considered as the two sole modes of evolution, are in fact only the result of the various processes and mechanisms of speciation.

– **The role of natural selection and adaptation is precisely defined.** These changes are not all adaptive right from the start. Many new structures resulting from changes in development with time and intervening more or less early, the ontogenetic path, are not necessarily adaptive in nature. Depending on the circumstances, eventually these changes can become adaptations indeed, but as a secondary response. Adaptation, just as extinction, is the result of interaction between internal structural and functional constraints and the external environmental constraints. Internal and external constraints thus are the two essential factors for natural selection, but a third one has to be taken into account additionally, namely hazard.

– **The necessary role of hazards**. Considered as the encounter between two mutually independant sequences of events, hazard plays an important role, intervening at all organizational levels of the living organism considered above: the encounter of the partners, formation of gametes, fertilization, recombination of characteristics, mutation of genomes. It works by playing a stimulating role for the various processes and mechanisms perturbing the programmes (e. g. erroneous replication of DNA) as well as the expression of the development programmes (innovations and heterochronies). Furthermore, due to its random nature, it introduces to evolution element of contingency imparting to it in parts an unforeseeable nature. Hazard appears to represent a necessary element of biological evolution constantly modifying the initial conditions. This explain why evolution

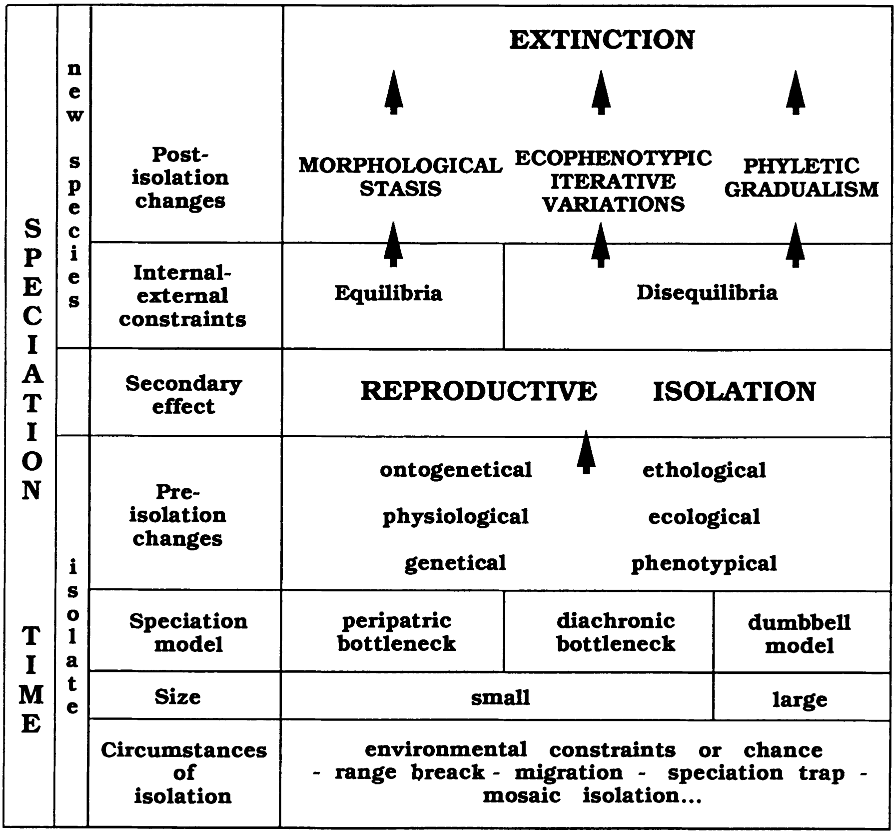


Fig. 9.1. Chronology of spatio-temporal speciation. This diagram shows that the speciation of the biologists which arrives at reproductive isolation and that of the paleontologists (phyletic speciation) are undoubtedly two successive phases of one and the same spatio-temporal phenomenon. (After Chaline 1987)

responds to state of statistical indetermination like the one known from quantum theory.

From an epistemological point of view, evolution demonstrates that some of the events characterized by punctuated innovations at the formation of the lineage of a new species as a response to internal and external constraints and hazard occurences, introduce to evolution an element of chance. Moreover, there are sequential stages in development, such as stasis when in equilibrium, or reversible and/or irreversible phyletic gradualism within a lineage when disequilibrium leads to adaptions. These are more deterministic and thus in part predictable. The general scheme of evolution is not a punctuated equilibrium model (Eldredge and Gould 1972), but a **punctuated equilibrium/disequilibrium model.**

CHAPTER 10

Applied Paleontology

10.1 Biostratigraphy

10.1.1 Principles

The demonstration by Cuvier of successions of associations of fauna, and the concept of evolutionary degree put forward by Gaudry, have enabled paleontologists to establish a stratigraphy of life (biostratigraphy) in which each period is characterized by a collection of particular species. Correspondingly, the presence of a particular fossil makes it possible to give a date to a geologic layer. The method has been so successful that paleontology has very nearly become its own victim, for the developments of the various disciplines of the earth sciences required increasingly more numerous datings than the fossils could usually supply. So much so that the paleontologist has too often found himself a mere enquiry agent, not devoting himself to the specific problems of his discipline. Biostratigraphy is a method of relative dating that utilizes the *irreversible phenomenon of biological evolution*; and it is perfectly clear that the reliability of its biostratigraphic applications is conditioned by a precise knowledge of the evolutionary modalities.

10.1.2 High-Resolution Biostratigraphy

The lessons of paleontology have shown that lines, once differentiated, may undergo different evolutions.

10.1.2.1 The Use of Morphological Stasis

Species which remain in morphological stasis during thousands or even millions of years can be utilized only in groupings of species in which only their first and last appearances are significant.

10.1.2.2 The Use of Ecophenotypic Variations

Globally stable species capable of exhibiting iterative ecophenotypic variations are of essentially ecologic or paleoclimatic significance, but from the biostratigraphic viewpoint they have the same importance as species in morphological stasis.

10.1.2.3 Phyletic Gradualism and Biostratigraphy

Only those lines in gradual evolution permit precise dating. In effect, the continuum of the chronomorphoclines is the only one that can be cut up into an infinity of successive and irreversible states. The continuum of the specific lineage begins with its reproductive isolation and ends with its extinction. This continuum may be considered as a chronospecies and sectioned by distinguishing degrees of evolution corresponding to transients, morphospecies, or paleospecies. It follows from this that such sectioning is a heritage from the historical development of the nomenclature of the group under consideration, that it is conventional and may be more or less arbitrary. Thanks to the utilization of statistical methods and data processing, it should become possible to define evolutionary degrees by quantitative parameters underlining the otherwise variable rhythms of gradualism, and to achieve a high-resolution biostratigraphy. This method often competes with physical dating that may be difficult to initiate.

10.1.3 Biostratigraphies of Vertebrates

It is quite clear that, among all the groups of vertebrates mentioned during this history, not all have the same impact in this field. In general terms, the larger mammals, usually only partly fossilized, do not make it possible to put a ring around the subjacent biologic species and give very relative, and rarely precise, stratigraphic indications. It is the continental micromammals, notably the Tertiary (Mein 1975) and Quaternary (Chaline 1985) rodents abundantly represented in recent time zones, which provide a demonstration of the possible phases of gradualism and an approach to high resolution.

10.2 Reconstruction of Paleoenvironments and Climates

The arrangement and dispersal of vertebrates remains in the deposits may help to characterize the environment in which fossilization occurred; but the results are most important in connection with the analysis of associations.

10.2.1 The "Grande coupure" Obligocene

In 1964, Valverde showed that vertebrate communities were not structured at random, but that species were distributed in ecologic niches according to a gradient of size and body weight. On the basis of ecologic diagrams (or cenograms) of the distribution of existing species established in diverse communities in the tropical rainforest, wooded savanna, predesert and desert (Fig. 10.1), Legendre (1986) has analyzed the constitution of the communities on either side of what is called "la Grande coupure" at the Eocene-Oligocene boundary (Fig. 10.1). Thus, he was able to show that the change in fauna linked with a wave of immigration also corresponded to the replacement of societies of tropical rainforests or savanna by the populations of desert or semidesert zones.

10.2.2 Quaternary Environments and Climates

The rodents and insectivores fossilized in great abundance in the infills of Quaternary caves provide accumulations of the rejection pellets of bird of prey. Very narrowly adapted to particular biotopes and limited in their geographic distribution by climatic parameters, they provide excellent guides to paleoenvironments and climates. Thus, the incursions of societies of fauna derived from Siberia and the arctic zone into the south-west of France (3000 km) during the great ice ages of the Quaternary prove the existence of a cold steppe covering mountains and valleys transformed into vast marshes from spring to autumn, but locally sheltering residual wooded areas (see Chaline 1985).

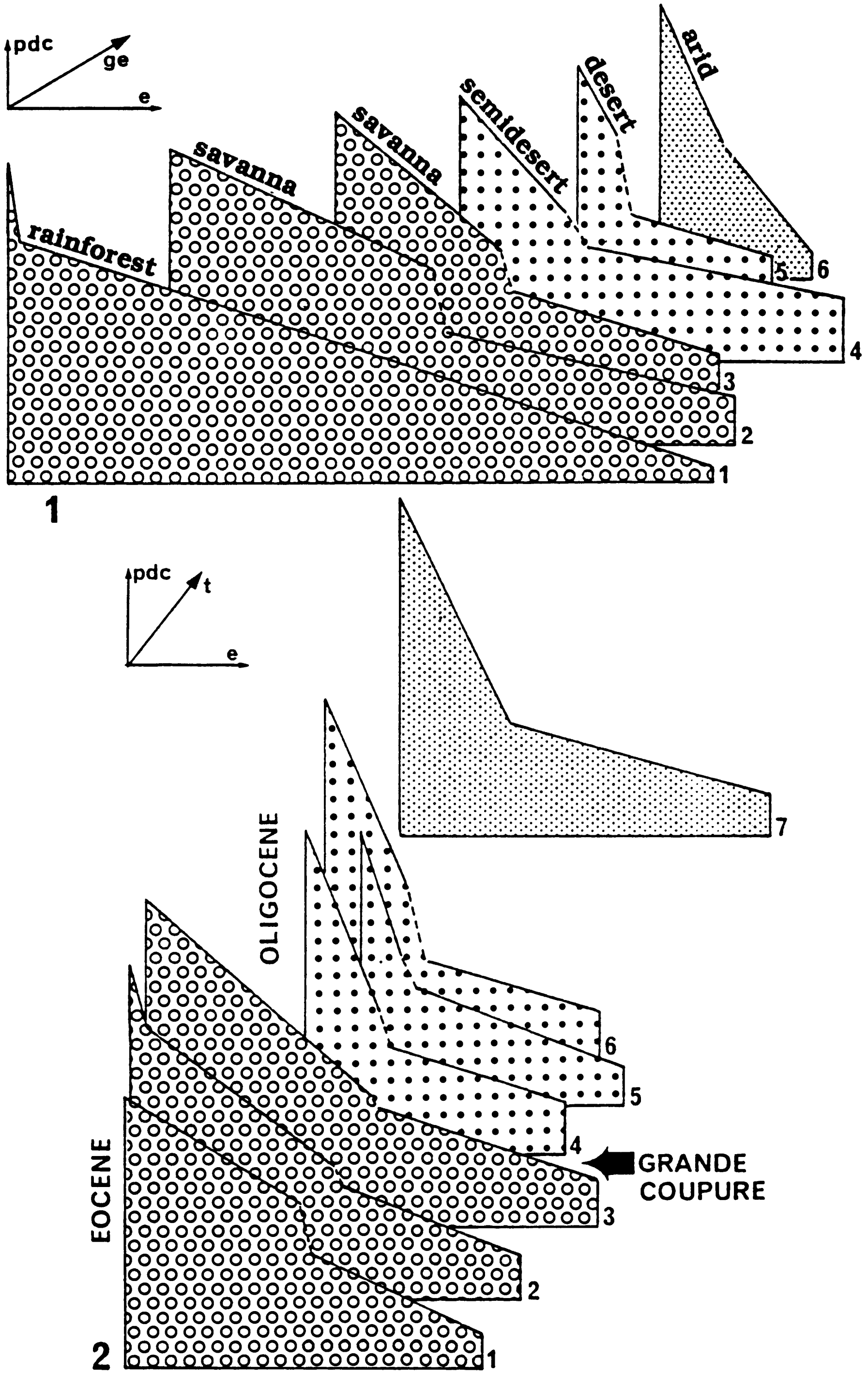
10.3 Contributions of Paleontology to Global Tectonics

The diversification of life has been greatly influenced by the paleogeopraphic history of the continents and oceans.

10.3.1 Influence of Paleogeography on Evolution

Intercontinental connections and the separations between plates have played a major part in the diversification and dispersion of groups. For example, the placentals originating from Asia and the marsupials of South America (Gondwana) had an entirely different evolution.

The history of the marsupials (see Chap. 7.4) began with a radiation spreading from South America, or the continent of Gondwana, towards Africa (*Garatherium*) and North America. This first dispersion took place before the definitive opening-up of the South Atlantic at 100 Ma, between the lower Cretaceous and the beginning of the upper Cretaceous. A second radiation in the lower Eocene into North America, Eurasia (*Peratherium*), and Africa (*Peratherium*, *Kasseri-*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notherium) could have resulted from a last passage between South America and Africa after the opening-up of the South Atlantic, via the ridge conneting the Rio Grande and Walvis (Crochet 1986) (see Chap. 7.4).

The placentals colonized Asia, Europe, Africa, and North America. The isolation of the South American plate allowed the placentals to develop several special lines of which some, like the Litopternes, exhibit remarkable convergences with the holarctic Equidae of North America and Eurasia. This isolation was to last for nearly 50 Ma; it was interrupted by the resumption of exchange of fauna with North America which began in the Messinian and increased in the Pliocene and Pleistocene following the emergence of the isthmus of Panama. The arrival of numerous placentals evolved in South America resulted in the massive elimination of the archaic marsupials and placentals. The history of the Equidae (see chap. 7.5.7.2) and numerous other groups of placentals was greatly conditioned by the frequent passage of fauna between North America and Eurasia in the Bering region. This also applies to passages between Eurasia and Africa.

10.3.2 Paleontology as a Test of Geodynamic Models

Conversely, the distribution of the populations of the different continents makes it possible to test the paleogeographic models proposed by geophysicists.

10.3.2.1 The South American Plate

According to the mobilist diagrams of the geophysicists, the South American plate remained isolated for about 50 Ma. However, the arrival in South America of two allochthonous groups is to be noted at the end of the Oligocene: the primates (*Branisella*) and the caviomorph rodents (*Platypittamys*). This supply of allochthonous forms of African origin implies the existence of a temporary and selective filter zone functioning at this epoch. Hoffstetter and Lavocat (1970) have suggested the existence of natural rafts derived from the African rivers and capable of transporting "shipwrecked" populations to South America as "founders" at an epoch when the Atlantic Ocean was still narrow and the marine currents different

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Fig. 10.1. Demonstration of environmental changes by societies of mammals: the "Grande Coupure" oligocene. **1** Cenograms of existing associations: *1* tropical rainforest (Gabon); *2* tropical wooded savanna (Ruanda); *3* tropical savanna (Congo); *4* predesert of northern Sahara (Algeria); *5* desert (Iran); *6* open arid Mediterranean environment (Spain); **2** Changes in fauna around the Grande Coupure oligocene which corresponds to the replacement of fauna of the tropical rainforest or savanna (Eocene) by those of desert or arid environments (Oligocene). *1* Le Bretou; *2* Perrière; *3* Escamps; *4* Aubrelong 1; *5* Mas de Got; *6* Pech Crabit; *7* Pech du Fraysse *bw* body weight; *eg* ecologic gradient; *s* species; *t* time. (After Legendre 1986)

from those of today. Hartenberger (1982) wonders whether the geophysical and paleontological data are adequate to allow any conclusions. Indeed, the paleogeography of the Caribbean remains rudimentary and the fauna of the old Tertiary of South America and Africa are still too little known.

10.3.2.2 The Collision of India and Asia

Another example concerns the attachment of India and Asia. According to the findings of plate tectonics (Audley et al. 1981), India remained isolated from the other continents between 80 and 40 Ma, the epoch at which it became fused with Asia. However, the paleontologic data refute this hypothesis. To begin with, such a long isolation would have been bound to bring about the development of an endemic Indian fauna based on archaic African elements, and there is no such fauna. Further, it has been discovered that the rodent fauna of the lower Eocene of India had common ancestors with those of Central Asia. The Eocene Artiodactyla and Brontotheridae are likewise Asiatic elements. Finally, in the Paleocene of Nagpur (65 Ma) there have recently been discovered Pelobatidae (amphibians) related to a laurasiatic group from Mongolia. As typical African elements (such as the Hyracoidae) are unknown in the Indian fauna, the absence of contact between Africa and India from the beginning of the Tertiary must likewise be conceded. The existence of Asiatic fauna on the Indian subcontinent suggests the existence of Tethysian land masses (an Iranian or Afghan plate?) just where there was supposed to be a sea. It is possible that there may have been continental masses or arcs of islands extending the Asiatic plate towards the south which disappeared during the collision or rather the collisions, with Asia, as shown by the investigations of the Franco-Chinese expedition in Tibet. The collision of India with Asia would have flung the Indo-Chinese block and the Indonesian platform westward after this collision, that is, during the Oligocene and the start of the Miocene. Unfortunately, it is impossible to reconstruct the paleogeography of those large parts of the crusts that disappeared by subduction and to determine whether they belonged to Laurasia or to India (Hartenberger 1982; Gayet et al. 1984; Rage 1986).

References

Alberch P, Alberch J (1981) Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical Salamander *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). J Morph 167: 249–264

Alberch P, Gould SJ, Oster F, Wake DB (1979) Size and shape in ontogeny and phylogeny. Paleobiology 5: 196–317

Aldridge RJ, Briggs DEG, Clarkson ENK, Smith MP (1986) The affinities of Conodonts, new evidence from the Carboniferous of Edinburgh, Scotland. Lethaia 19 (4): 279–291

Alvarez LW, Alvarez W, Asaro F, Michel HV (1980) Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science 208: 1095–1108

Audley-Charles MG, Hurley AM, Smith AG (1981) Continental movements in the Mesozoic and the Cenozoic. In: Whitmore C (ed.) Wallace's line and plate tectonics, Clarendon Press, Oxford: 9–23

Baer KE von (1828) Lungsgeschichte der Thiere: Beobachtung und Reflexion. Bornträger, Königsberg

Bardack D (1985) Les premiers fossiles de Myxines (Myxiniformes) et Enteropneustes (Hemichordata), dépôts de la faune pennsylvanienne du Mazon creek dans l'Illinois, USA. In: Heyler D (ed.) Le gisement stéphanien de Montceau-les-Mines. Bull Soc Hist Nat Autun 116: 97–99

Bardack D, Richardson ES (1977) New agnathous fishes from the Pennsylvanian of Illinois. Fieldiana, Geology 33 (26): 489–510.

Beatty J (1982) Classes and cladists. Syst Zool 31: 25–34

Beaumont A, Cassier P (1987) Biologie animale. Les Cordés, anatomie comparée des vertébrés. Dunod, Paris

Bemis WE (1984) Paedomorphosis and the evolution of the Dipnoi. Paleobiology 10: 293–307

Benton MJ (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linnean Soc, London 84: 97–164

Berge C, Orban-Segebarth R, Schmid P (1984) Obstetrical interpretation of the Australopithecine pelvic cavity. J human evol 13: 573–587

Bocherens H, Fizet M, Cuif JP, Jaeger JJ, Michaud JG, Mariotti A (1988) Premières mesures d'abondances isotopiques naturelles en ^{13}C et ^{15}N de la matière organique fossile de Dinosaure. Application à l'étude du régime alimentaire du genre *Anatosaurus* (Ornitischia, Hadrosauridae). C R Ac Sc, Paris 306 (II): 1521–1525

Bolk L (1926) Das Problem der Menschwerdung. Gustav Fischer, Iena

Bonaparte JF (1986) Specialized dentitions in two Cretaceous mammals from Patagonia. In: Russel DE, Santono JP, Sigogneau-Russel D (eds) Teeth revisited. Proc VII Int Symp Dental Morphology. Mem Mus Hist Nat, Paris 53: 207–215

Bonde N (1977) Cladistic classification as applied to vertebrates. In: Hecht MKH et al. (eds) Major patterns in vertebrate evolution. Plenum, New York, p 741

Bonde N (1981) Problems of species concepts in paleontology. Inter Symp Concept Meth Paleo Barcelona: 19–34

Boonstra LD (1969) The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo). Ann S Afr Mus 56: 1–73

Bossy KVH (1976) Morphology, paleoecology and evolutionary relationships of the Pennsylvanian urocordylid nectrideans (Subclass Lepospondyli, class Amphibia). Diss Abst : B37, 2731. Ph. D. Thesis Yale University

Brady RH (1984) On the independence of systematics. Cladistics 1(2): 113–126

Brink AS (1963) On *Bauria cynops* Broom. Palaeont afr 8: 39–56

Broom R (1924) Further evidence on the structure of the Eosuchia. Bull Am Mus Nat Hist 51: 67–76

Brown B, Schlaikjer EM (1940) The origin of ceratopsian horn cores. Amer Mus Nov: 1065

Buffetaut E (1979) L'évolution des Crocodiliens. Pour la Science 26: 18–26

Cain AJ (1954) Animal species and their evolution. Hutchison's Univ. Library, London

Campbell KE (1980) The world's largest flying bird. Terra 19 (2): 20–23

Cale GR, Balda RT, Willis WR (1983) The physics of leaping animals and the evolution of preflight. Amer Nat 121: 455–467

Carleton MD (1984) Introduction to rodents. In: Anderson S, Jones JK, Jr (eds) Orders and families of recent mammals of the world, J. Wiley and Sons, New York, p 255

Cassiliano ML, Clemens WA (1979) Symmetrodonta. In: Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds) Mesozoic mammals. Univ. California, Press, Berkeley, p 150

Chaline J (1972) Les rongeurs du Pléistocène moyen et supérieur de France. Cahiers de Paléontologie, CNRS, Paris

Chaline J (1985) Histoire de l'homme et des climats au Quaternaire. Doin, Paris

Chaline J (1987) Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. Evolutionary Biology 21: 237–310

Chaline J, Laurin B (1984) Le rôle du climat dans l'évolution graduelle de la lignée *Mimomys occitanus-ostramosensis* (Arvicolidae, Rodentia) au Pliocène supérieur. Géobios 8: 323–331

Chaline J, Laurin B (1986) Phyletic gradualism in a European plio-pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). Paleobiology 12 (2): 203–216

Chaline J, Marchand D (1976) Une solution biologique au problème des Australopithèques. Bull Mus Anthr Préhist Monaco 20: 5–26

Chaline J, Mein P (1979) Les rongeurs et l'évolution. Doin, Paris

Chaline J, Marchand D, Berge C (1986) L'évolution de l'homme: un modèle gradualiste ou ponctualiste? Bull Soc Royale Belge Anthr Prehist 97: 77–97

Chang MM, Yu X (1984) Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the Lower Devonian of eastern Yunnan, China. Proc Linn Soc New South Wales 107 (3): 171–184

Chetverikov SS (1926) On certain aspects of the evolutionary process from the standpoint of modern genetics. J Explt Biol (Russian) A2: 3–54 (English transl. 1961. Proc Amer Phil Soc 105: 167–195)

Clark J, Carroll RL (1973) Romeriid reptiles from the Lower Permian. Bull Mus Comp Zool 144 (5): 353–407

Clemens WA (1986) On Triassic and Jurassic mammals. In: Padian K (ed) The beginning of the age of dinosaurs. Cambridge Univ. Press, p 237

Cope ED (1887) The origin of the fittest. MacMillan, New York

Coppens Y (1986) Evolution de l'homme. Vie des Science, C R Ac Sc Paris, 3 (3): 227–243

Courtillot V, Besse J, Vandamme D, Montigny R, Jaeger JJ, Cappetta H (1986) Deccan flood basalts at the Cretaceous/Tertiary boundary? Earth Planet Sc Letters 80: 361–374

Cracraft J (1974) Phylogenetic models and classification. Syst Zool 23: 71–90

Cracraft J (1988) Early evolution of birds. Nature 331: 389–390

Crochet JY (1979) Diversité systématique des Didelphidae (Marsupialia) européens tertiaires. Géobios 12 (3): 365–378

Crochet JY (1984) *Garatherium mahboudi* nov. gen. nov. sp., Marsupial de l'Eocène inférieur d'El Kohol (Sud-Oranais, Algérie). Ann Paleont 70 (4): 275–294

Crochet JY (1986) Le berceau des Marsupiaux. La Recherche 17 (174): 274–274

Crompton AW (1958) The cranial morphology of a new genus and species of ictidosaurian. Proc Zool Soc London 130: 183–216

Crompton AW (1963) On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. Proc Zool Soc London 140: 697–753

Crompton AW, Jenkins FA (1968) Molar occlusion in late Triassic mammals. Biol Rev 43: 427–458

Dambricourt-Malassé A (1988) Hominisation et foetalisation (Bolk, 1926) C R Ac Sc Paris 307 (II): 199–204

Darwin C (1859) On the origin of species. John Murray, London

Davidson EH, Britten TJ (1973) Organization, transcription, and regulation in the animal genome. Quart Rev Biol 48: 565–613

Dawson MR (1967) Lagomorph history and the stratigraphic record. In: Moore RC Commemorative volume: Essays in paleontology and stratigraphy. Univ Kansas, Geology 2: 287–316

Day MH (1982) The *Homo erectus* pelvis: punctuation or gradualism. In: de Lumley H (ed) L'*Homo erectus* et la place de l'homme de Tautavel parmi les hominidés fossiles. 1st Congrès int Paléont humaine: 411–421

de Beer GR (1930) Embryology and evolution, Clarendon, Oxford

de Bonis L (1982) Réflexions sur la phylogénie et la classification des Hominoïdés. Géobios mém sp 6: 305–319

de Bonis L (1987a) L'origine des Hominidés. Anthropologie 91 (2): 433–454

de Bonis L (1987b) Les Primates de l'ancien monde du Paléocène au Miocène. In: Marois M (ed) L'évolution dans sa réalité et ses diverses modalités. Fondation Singer-Polignac, Masson, Paris: 93–131

de Bonis L, Jaeger JJ, Coiffait B, Coiffait PE (1988) Découverte du plus ancien primate Catarrhinien connu dans l'Eocène supérieur d'Afrique du Nord. C R Ac Sc Paris 306 (II): 929–934

Delson E (1975) Evolutionary history of the Cercopithecidae. In: Szalay FS (ed) Approaches to primate paleobiology. Contrib Primat 5: 167–217

de Muizon C, Marshall LG (1987) Le plus ancien Pantodonte (Mammalia), du Crétacé supérieur de Bolivie. C R Ac Sc Paris 304 (II) 5: 205–208

de Muizon C, Marshall LG (1987) Le plus ancien condylarthre (Mammalia) sud-américain (Crétacé supérieur, Bolivie). C R Ac Sc Paris 304 (II) 13: 771–774

de Muizon C, Marshall LG (1987) Deux nouveaux condylarthres (Mammalia) du Maastrichtien de Tiupampa (Bolivie). C R Ac Sc Paris 304 (II) 15: 947–950

Derek E, Briggs R, Aldridge J, Smith MP (1987) Conodonts are not aplacophoran molluscs. Lethaia 20: 381–382

de Ricqlès A (1979) Relations entre structures histologiques, ontogenèse, stratégies démographiques et modalités évolutives: le cas de Reptiles captorhinomorphes et des Stégocéphales temnospondyles. C R Ac Sc Paris D (288): 1147–1150

de Ricqlès A (1980) Croissance périodique, ontogenèse, phylogenèse et stratégies démographiques: le cas des reptiles captorhinomorphes. Soc Zool Fr 105 (2): 363–369

de Ricqlès A (1984) Remarques systématiques et méthodologiques pour servir à l'étude de la famille des Captorhinidés. Ann Paleont 70 (10): 1–39

de Ricqlès A (1989) Les mécanismes hétérochroniques dans le retour des tétrapodes au milieu aquatique. In: David B, Dommergues JL, Chaline J, Laurin B (eds) Ontogenèse et évolution, Colloq int CNRS Dijon, Géobios 12: 337–348

de Ricqlès A, Taquet P (1982) La faune de Vertébrés du Permien supérieur du Niger. 1 Le Captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria). Le crâne. Annales Paléont 68 (1): 33–106

Devillers C (1981) La genèse des mammifères. La Recherche 122 (12): 580–589

Devillers C, Clairambault P (1976) Précis de zoologie, vertébrés, anatomie comparée. Masson, Paris

Devillers C, Mahé J, Ambroise D, Bauchot R, Chatelain E (1984) Allometric studies on the skull of living and fossil equidae (Mammalia, Perissodactyla). J Vert Paleont 4 (3): 471–480

Devillers C, Chaline J (1989) La théorie de l'évolution. Etat de la question à la lumière des connaissances actuelles. Dunod Paris de Vries H (1906) Species and variety: their origin by mutation. 2nd ed, Open Court Pub Co, Chicago

Dobhzansky T (1937) Genetics and the Origin of species. Columbia Univ Press, New York

Dobhzansky T (1970) Evolutionary oscillations in *Drosophyla pseudoobscura*. In: Creed R (ed) Ecological genetics and evolution, Blackwell, Oxford

Dommergues JL, David B, Marchand D (1986) Les relations ontogenèse-phylogenèse: applications paléontologiques. Géobios 19: 335–356

Dutrillaux B, Couturier J (1986) Principe de l'analyse chromosomique appliquée à la phylogénie: l'exemple des Pongidae et des Hominidae. Mammalia 50: 22–37

Easton GF (1904) The characters of *Pteranodon*. Am J Sc 17 (91) 318–320

Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf T (ed) Models in Paleobiology. Freeman, Cooper, San Francisco, p 82

Estes R, Reig OA (1973) The early fossil record of frogs. In: Vial LJ (ed). Evolutionary biology of the anurans. Univ. Missouri Press, Columbia, Missouri, p 24

Fabre J (1980) La famille des Pleurosauridae (Rhynchocephalia). Exemple remarquable d'évolution par néoténie squelettique. C R Ac Sc Paris 291 (D): 929–932

Fabre J (1981) Les Rhynchocéphales et les Ptérosaures à crête pariétale. Le gisement de Canjuers (France). Fondation Singer-Polignac, Paris

Fischer RA (1958) The genetical theory of natural selection. 2e ed Dover Pub

Flynn JJ (1988) Ancestry of sea mammals. Nature 334 (4): 383–384

Forey P (1980) *Latimeria*: a paradoxal fish. Proc R Soc London B, 208: 369–384

Gaffney ES (1975) A phylogeny and classification of the higher categories of Turtles. Bull Amer Mus Nat Hist 155 (5): 389–436

Gaffney ES, Mc Kenna MC (1979) A late Permian captorhinid from Rhodesia. Am Mus Novit 2688: 1–15

Gagnier PY, Blieck A, Rodrigo G (1986) First Ordovician vertebrate from South America. Géobios 19(5): 629–634

Gardiner BG (1982) Tetrapod classification. Zool J Linn Soc 74: 207–232

Gardiner BG (1983) Gnathostome vertebrae and the classification of the amphibia. Zool. J. Linn Soc (79 (1): 44–59

Garstang W (1922) The theory of recapitulation: a critical restatement of the biogenetic law. Zool J Linn Soc 35: 80–101

Gaupp E (1913) Die Reichertsche Theorie (Hammer-Amboss- und Kieferfrage) Arch Anat Physiol Anat Abt Suppl bd 1912

Gauthier J (1984) A cladistic analysis of the higher systematic categories of the diapsida. Ph D Thesis, Univ California, Berkeley

Gauthier J, Padian K (1984) Phylogenetic, functional and aerodynamic analyses of the origin of birds and their flight. In: Hecht MK et al. (ed) Beginnings of birds, Eichstätt: 185–197

Gayet M, Rage JC, Rana RS (1984) Nouvelles ichthyofaunes et herpetofaunes de Gitti Khadan, le plus ancien gisement connu du Deccan (Crétacé/ Paléocène) à Microvertébrés. Implications paléogéographiques. Mém Soc Géol Fr NS (147): 55–65

Geoffroy-Saint-Hilaire I (1830) Principes de philosophie zoologique discutés en mars 1830. Pichon, Paris

Giard D (1887) La castration parasitaire et son influence sur les caractères du sexe mâle chez les crustacés décapodes. Bull Scient Départ Nord 18: 1–28

Gilmore CW (1920) Osteology of the carnivorous Dinosauria in the United States National Museum. Smith hist US Nat Hist 110

Gingerich P (1973) Anatomy of the temporal bone in the Oligocène anthropoid *Apidium* and the origine of Anthropoidea. Folia Primatol 19: 329–337

Gingerich P (1979) The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In: Cracraft J, Eldredge N (eds) Phylogenetic analysis and paleontology. Columbia Univ Press, New York, p 41

Gingerich PD (1984) Primate evolution. In: Gingerich PD, Bradley CE (eds) Mammals: notes for a short course. Univ. Tennessee Studies in Geol, 8: 167–184

Ginsburg L (1984) Théories scientifiques et extinction des Dinosaures. C R Ac Sc Paris 298 (II/7): 317–320

Ginsburg L, Mein P (1980) *Crouzelia rhodanica*, nouvelle espèce de Primate catarrhinien, et essai sur la position systématique des Pliopitheciadae. Bull Mus nat Hist nat Paris 4(2): 57–85

Ginsburg L, Mein P (1987) *Tarsius thailandica* nov sp, premier Tarsiidae (Primates, Mammalia) fossile d'Asie. C R Ac Sc, Paris 304 (II): 1213–1215

Goette A (1901) Über die Kiemen der Fische. Z Wiss Zool 69: 533–577

Goldschmidt R (1940) The material bases of evolution. Yale Univ Press, New Haven

Goujet D (1984a) Pladoderm interrelationships: a new interpretation with a short review of placoderm classifications. Proc Linn Soc NSW 107: 211–243

Goujet D (1984b) Les poissons placodermes du Spitzberg. Arthrodires dolichostraci de la formation de Wood Bay (Devonian inf). Cahiers de Paléontologie CNRS, Paris

Gould SJ (1977) Ontogeny and phylogeny. Belknap, Cambridge

Gaffney ES, McKenna M (1979) A late Permian Captorhinid from Rhodesia. Am Mus Novitates 2688: 1–15

Graham-Smith W, Westoll TS (1937) On a new long-headed dipnoan fish from the upper Devonian of Scaumenac Bay PQ Canada; Trans R Soc Edimb 59: 241–266

Grassé PP (1979) Vertébrés. Abrégé Zoologie, Masson, Paris

Grassé PP, Devillers C (1965) Zoologie Vertébrés. Masson, Paris

Gregory WK, Simpson GG (1926) Cretaceous mammal skulls from Mongolia. Amer Mus Nov New York, 225: 1–20

Gross W (1961) *Lunaspis broili* und *Lunaspis heroldi* aus dem Hunsrückschiefer (Unterdevon, Rheinland). Notzbl Hess Landesamt Bodenforsch Wiesbaden 89: 17–43

Gross W (1963) *Gemnuendina stuertzi* Traquair, Neuuntersuchung. Notizbl Hess Landesamt Bodenforsch Wiesbaden 91: 30–73

Haeckel E (1856) Natürliche Schöpfungsgeschichte. G. Reiner, Berlin

Harrisson T (1986) New fossil anthropoids from the Middle Miocene of east Africa and their bearing on the origin of the Oreopithecidae. Am J Phys Anthro 71: 265–284

Haldane JBS (1932) The causes of evolution. Longmans, Green, New York

Hartenberger JL (1982) Exemples de données géophysiques et paléontologiques antinomiques dans le Tertiaire ancien. Bull Soc Géol Fr 7 (24), 5–6: 927–933

Hatcher JB, Marsh O, Lull RS (1907) The Ceratopsia. Monogr US Geol Surv, 49

Heaton MJ (1980) The Cotyosauria: a reconsideration of a group of Archaic tetrapods. In: Panchen AL (ed) The terrestrial environment and the origin of land vertebrates. Acad Press, London, p 497

Hecht MK, Tarsitano S (1982) The paleobiology and phylogenetic position of *Archaeopteryx*. Géobios 6: 141–149

Heintz A (1939) Cephalaspida from the Downtonian of Norway. Skr norks Vidensk Akad Oslo Mat-Naturv KL: 1–119

Heintz A (1958) The head of the Anaspid *Birkenia elegans* Traquair. In: Watson DMS (ed) Studies on fossil vertebrates, Westoll, London, p 71

Heintz N (1960) The Downtonian and Devonian vertebrates of Spitzbergen 11. *Gigantaspis* a new genus of fam. Pteraspidae from Spitzbergen. Norsk Polarinst Arb: 22–27

Heilmann G (1926) Origin of birds. Witherby, London

Hennig W (1950) Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin

Hersh AH (1934) Evolutionary relative growth in the Titanotheres. Amer Natur 68: 537–561

Heyler D (1969) Vertébrés de l'Autunien de France. Cahiers de Paléontologie, CNRS, Paris

Hoffstetter R (1974) *Apidium* et l'origine des Simiiformes (=Anthropoidea) C R Ac Sc Paris 278: 1715–1717

Hoffstetter R (1975) Les marsupiaux et l'histoire des mammifères: aspects phylogénétiques et chronologiques. In: Lehman JP (ed) Evolution des Vertébrés, CNRS, Paris

Hoffstetter R (1976) Histoire des mammifères et dérive des continents. La Recherche 64 (7): 124–138

Hoffstetter T (1977) Phylogénie des Primates. Confrontation des résultats obtenus par les diverses voies d'approche du problème. Bull Mem Soc Anthr Paris 4 (XIII): 327–346

Hoffstetter R, Lavocat R (1970) Découverte dans le Déséadien de Bolivie de genres pentalophodontes appuyant les affinités africaines des Rongeurs Caviomorphes. C R Ac Sc Paris 271 (D): 172–175

Humphrey RR (1967) Albino axolotls from an albino tiger salamander through hybridization. J Heredity 58: 95–101

Hürzeler J (1968) Questions et réflexions sur l'histoire des anthropomorphes. Ann Pal Vertébrés 54: 195–233

Jaeckel O (1906) Neue Rekonstructionen von *Pleuracanthus sessilis* und *Polyacrodus (Hybodus) hauffianus*. Sber Ges Naturf Freund Berl: 155–159

Jacob F (1977) Evolution and tinkering. Science 196: 1161–1166

Jacob F (1981) Le jeu des possibles. Essai sur la diversité des vivants. Fayard, Paris

Jacob F, Monod J (1961) Genetic regulatory mechanisms in the synthesis of proteins. J Mol Biol 3: 318–322

Janensch W (1925) Ein neues aufgestelltes Skelett des Stegosauriens *Kentrurosaurus aethiopicus*. Palaeontographica suppl 7, I Reihe, H.I

Janvier P (1981) The phylogeny of the Craniata with particular reference to the significance of fossil "agnathans". Journ Vert Paleont 1(2): 121–159

Janvier P (1984) Cladistics: theory, purpose, and evolutionary implications. In: Pollard JW (ed) Evolutionary theory: paths into the future. John Wiley London, New York, p 39

Janvier P (1985) Les céphalaspidés du Spitzberg. Cahiers Paleont, CNRS, Paris,

Janvier P (1986) Les nouvelles conceptions de la phylogénie et de la classification des "Agnathes" et des Sarcoptérygiens. Oceanis 12(3): 123–138

Janvier P, Lund R (1983) *Hardiestiella montanensis* nov. gen., nov. sp. (Petromyzontida) from the lower Carboniferous of Montana, with remarks on the affinities of the Lampreys. Journ of Vert Pal 2(47): 407–413

Jarvik E (1952) On the fish-like tail in the ichothyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the upper Devonian of East Greenland. Medd Gronland 114: 1–90

Jarvik E (1954) On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. K Svenska Vetersk Adad Homdl 4(5): 1–104

Jarvik E (1955) The oldest tetrapod and their foreruners. Sci Monthly 80: 141–154

Jarvik E (1950) Théories de l'évolution des vertébrés, Masson, Paris

Jarvik E (1964) Specializations in early vertebrates. Annls Soc R Zool Belge 94: 11–95

Jefferies RPS (1968) The subphyllum Calcichordata (Jefferies, 1967) primitive fossil chordates with echinoderms affinities. Bull Brit Mus Nat Hist 16(6), 340 p

Jefferies RPS (1981) Le monde animal. Gründ, Paris

Kemp TS (1984) Mammal-like reptiles and the origin of mammals. Acad Press, London

Kermack DM, Kermack KA, Mussett F (1968) The Welsh pantothere *Kuehneotherium praecursoris*. Zool J Linn Soc 474: 407–423

Kermack KA, Mussett F, Rigney HW (1973) The lower jaw of *Morganucodon*. Zool J Linn Soc 53: 87–175

Kiaer J (1988) The structure of the mouth of the oldest known vertebrates, pteraspids and cephalaspids. Palaeobiologica 1: 117–134

Kielan-Jaworowska Z, Eaton JG, Bown TM (1979) Theria of metatherian-eutherian grade. In: Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds). Mesozoic mammals. Univ California, Press, Berkeley, p 182

King MC, Wilson AC (1975) Evolution at two levels in humans and chimpanzees. Science 188: 107–116

Kollman J (1885) Das Ueberwintern von europäischen Frosch- und Tritonlarven und die Umwandlung des mexikanischen Axolotl. Verhandl Naturf Gesell Basel 7: 3287–398

Krebs B (1971) Evolution of the mandible and lower dentition in dryolestids (Pantotheria, Mammalia). In: Kermack DM, Kermack KA (eds) Early mammals. Linn Soc Journ 50(1): 89–102

Kuhn-Schnyder E (1966) Das problem der Euryapsida. Colloque Int CNRS, Paris 163: 335–348

Kühne WG (1956) The Liassic Therapsid *Oligokyphus*. Brit Mus (Nat Hist), London

Lamarck JB (1809) Philosophie zoologique. Dentu, Paris

Lambert D, and the Diagram group (1983) Collin's guide to dinosaurs. Collins, London

Lauder GV, Liem KF (1983) The evolution and interrelationship of the actinopterygian fishes. Bull Mus Comp Zool 150 (3): 95–197

Langson W (1983) Les Ptésosaures. Pour la Science: 77–87

Lehman JP (1947) Description de quelques exemplaires de *Cheirolepis canadensis* (Whiteaves). K svenska Vetensk Akad Handl 3 (24): 1–40

Lehman JP (1966) Actinopterygii. In: Piveteau J (ed) Traité de Paléontologie, vol 4.3 Masson, Paris, p 1

Legendre S (1988) Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale. Thèse Univ, Montpellier

Lewontin RC (1974) The genetic basis of Evolutionary change. Columbia Univ. Press, New York

Li CK, Ting SY (1985) Possible phylogenetic relationship of asiatic Eurymylid and rodents, with comments on mimotonids. In: Luckett WP, Hartengerger JL (eds) Evolutionary Relationships among Rodents, A Multidisciplinary Analysis, Nato, vol 92, Plenum Press, New York, p 35

Lövtrup S (1977) The phylogeny of Vertebrata. Wiley, London

Luckett WP and Hartenberger JL (1985) Evolutionary relationships among rodents: comments and conclusion. In: Luckett WP, Hartenberger JL (eds) Evolutionary relationships among rodents, A multidisciplinary Analysis, Nato vol 92, Plenum Press, New York, p 685

Lull RS, Wright NE (1942) Hadrosaurian dinosaurs of North America. Geol Amer Spec Pap: 40

Mahboubi M, Ameur R, Crochet JY, Jaeger JJ (1983) Première découverte d'un Marsupial en Afrique. C R Ac Sc Paris 297 (II): 691–694

Mahboudi M, Ameur R, Crochet JY, Jaeger JJ (1984) Earliest known proboscidean from early Eocene of north-west Africa. Nature 308 (5949): 543–544

Maisey JG (1984) Chondrichthyan phylogeny: a look at the evidence. J Vert Pal 4 (3): 359–371

Mallatt J (1984) Early vertebrate evolution: pharyngeal structures and the origin of Gnathostomes. J Zool 204: 169–183

Marsch DC (1988) Notice of a new genus of Sauropoda and other new dinosaurs from the Potomac formation. Am J Sc 3(35): 12–48

Marshall LG, de Muizon C, Sigé B (1983) Late Cretaceous mammals (Marsupialia) from Bolivia. Géobios 16: 739–745

Marshall LG, de Muizon C (1988) The Dawn of the age of Mammals in south America. Nat Geogr Res 4 (1): 23–55

Martin LD (1979) The biostratigraphy of arvicoline rodents in North America. Trans Nebraska Acad Sc 7: 91–100

Martin LD (1984) Phyletic trends and evolutionary rates. In: Genoways H, Dawson MR (eds) Contributions in Quaternary vertebrate paleontology. Carnegy Mus Nat Hit Spec Publ 8: 526–538

Martin LD, Tate J Jr (1967) A *Hesperornis* from Pierre shale. Proc Nebraska Acad Sc: 49–50

Mathey R (1949) Les chromosomes des vertébrés. Lausanne, Rouge

Matthes HW (1964) Aus der Geschichte der Tiere. In: Kummer G, Germeinhardt M (eds) Beiträge zur Abstammungslehre. Volk u Wissen Berlin 1: 98–127

Matthew WD, Granger W (1917) The skeleton of *Diatryma*, a gigantic bird from the lower Wyoming. Bull Amer Mus Nat Hist

Mayr E (1942) Systematics and the origin of species. Columbia Univ Press, New York

Mayr E (1982) The growth of biological throught: Diversity, evolution, and inheritance. Harvard Univ Press, Cambridge

Mazin JM (1982) Affinités et phylogénie des Ichthyopterygids. Géobios 6: 85–98

Mazin JM (1985) Les Ichthyosaures. Pour la Science 4: 76–82

McKinney ML, Schoch RM (1985) Titanothere allometry, heterochrony, and biomechanics: revising an evolutionary classic. Evolution 39 (6): 1352–1363

McNamara KJ (1986) A guide to the nomenclature of heterochrony. J Paleontol 60: 4–13

McNamara KJ (1988) The abundance of heterochrony in the fossil record. In: McKinney ML (ed) Heterochrony in evolution. Plenum Pub Corp, New York, p 287

Meckel JF (1821) System der vergleichenden Anatomie. Rengersche Buchhandlung, Halle

Mein P (1975) Biozonation du Néogène méditerranéen à partir des mammifères. Report Activity Neogene Working group: 78–81

Mendel G (1866) Versuche über Pflanzenhybriden. Verh Natur Vereins Brünn 4: 3–57

Mickevich MF, Johnson MS (1976) Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst Zool 25: 260–270

Miles RS (1966) The acanthodian fishes of the Devonian Plattenkalk of the Palfrath Tough in the Rhineland, with an appendix containing a classification of the Acanthodii and a revision of the genus *Homolacanthus*. Ark Zool 18 (2): 94–147

Miles RS (1967) "Class Placodermi". In: Harland WB (ed) The fossil record. Geol Soc London, p. 640

Miles RS, Westoll TS (1968) The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle old red sandstone of Scotland. Descriptive morphology. Trans R Soc Edinb 67: 373–476

Millot J, Anthony J (1958) Anatomie de *Latimeria chalumnae*. Squelette et muscles. CNRS, Paris

Milner AC (1980) A Review of Nectridea (Amphibia). In: Panchen AL (ed) the Terrestrial environment and the origin of land vertebrates. Acad Press, London, p 377

Miner RW (1925) The pectoral limb of *Eryops* and other primitive Tetrapods. Bull Amer Mus Nat History: 51

Milner AR, Smithson TR, Milner AC, Coates MI, Rolfe WDI (1986) The search for early Tetrapods. Modern Geology 10: 1–28

Miyamoto MM, Koop BF, Slighton JL, Goodman M, Tennant MR (1988) Molecular systematics of higher primates: Genealogical relations and classification. Proc Natl Acad Sc 85: 7627–7631

Monod J (1970) Le hasard et la nécessité. Seuil, Paris

Morgan TH (1926) The Theory of the Gene. Yale Univ Press, New Haven

Moy-Thomas JA, Bradley-Dyne M (1938) Actinopterygian fishes from the lower Carboniferous of Glencartholn, Eskdale, Dumfriesshire. Trans R Soc Edinb 59: 437–480

Moy-Thomas JA, Miles RS (1971) Paleozoic fishes. Chapman & Hall, London

Nelson GJ, Platnick NI (1981) Systematics and Biogeography: Cladistics and vicariance. Columbia Univ Press, New York

Nilsson T (1946) A new find of *Gerrothorax rhaeticus* Nilsson. Meddelanden from Lunds Geol Miner Inst: 109

Norris DO, Gern WA (1976) Thyroxine-induced activation of hypothalamo-hypophysial axis in neotenic salamander larvae. Science 194: 525–527

Novacek MJ, Wyss AR (1986) Higher-level relationships of the recent eutherian orders: morphological evidence. Cladistics 2(3): 257–287

Obrutschev DV (1967) On the evolution of the Heterostraci. In: Lehmann JP (ed.) Colloque Int CNRS, Paris, p 37

O'Hara RJ (1988) Homage to Clio, or toward an historical philosophy for evolutionary biology. Syst Zool 37 (2): 142–155

Olson EC (1941) The family Trematopsidae. Journal Geol: 49

Olson EC, Barghausen H (1962) Permian vertebrates from Oklahoma and Texas. Part 1: Vertebrates from the Flower Pot formation, Permian of Oklahoma. Part 2: The osteology of *Captorhinikos chozaensis*. Okla Geol Survey

Orlov YA (1958) The carnivorous dinocephalians of the Isheevo faune (titanosuchians). Trudi Paleon Inst Acad Sc USSR 72: 3–113 (In Russian)

Osborn HF (1898) Additional characters of the great herbivorous dinosaur *Camarasaurus*. Bull Amer Mus Nat Hist: 10

Osborn HF (1929) The Titanotheres of ancient Wyoming, Dakota, and Nebraska. MS Geol Survey Monogr: 55

Ostrom JH (1973) The ancestry of birds. Nature 242: 136

Ostrom JH (1979) Bird flight: how did it begin? Amer Scientist 67(1): 46–56

Owen R (1871) Monograph of the fossil Mammalia of the Mesozoic formations. Palaeontogr Soc Monog: 24

Padian K (1986) Introduction. In: Padian K (ed) The beginning of the age of dinosaurs. Cambridge Univ Press, London, p 1

Panchen AL (1980) The origin and relationships of the Anthracosaur Amphibia from the late Paleozoic. In: Panched AL (ed) The terrestrial environment and the origin of land Vertebrates. Acad Press, London, p 319

Panchen AL (1985) On the amphibian *Crassigyrinus scotinus* Waston from the Carboniferous of Scotlant. Phil Trans R soc London, 309B: 505–568

Panchen AL, Smithson TR (1988) The relationships of earliest Tetrapods. In: Benton MJ (ed) The phylogeny and classification of Tetrapods. Syst Assoc Special vol 35A (1): 1–32

Parrington FR (1976) On the cranial anatomy of cynodonts. Proc zool Soc London 116: 181–197

Parrington FR (1971) On the upper Triassic mammals. Phil Trans R Soc 261B: 231–272

Patterson B (1956) Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana, Geology 13: 1–105

Patterson C, Rosen DE (1977) Review of Ichthyodectiform and other Mesozoic teleost fishes and the theory of practice of classifying fossils. Bull Amer Mus Nat Hist 158: 91–172

Pearson HS (1924) A dicynodont reptile reconstructed. Proc Zool Soc London: 827–855

Peignoux-Deville J, Janvier P (1984) L'os du requin ou la biologie au rendez-vous de la Paléontologie. La Recherche 15 (158): 1140–1142

Pilbeam D (1982) New hominoid skull material from the Miocene of Pakistan. Nature 295: 232–234

Raff RA, Kaufman TC (1983) Embryos, genes and evolution. MacMillan, New York

Rage JC (1982) La phylogénie des Lépidosauriens (Reptilia): une approche cladistique. C R Ac Sc Paris 294 (III): 399–402

Rage JC (1982) L'histoire des serpents. Pour la Science 54: 16–27

Rage JC (1986) Le radeau indien: une hypothèse qui prend l'eau? La Recherche 17 (175): 409–410

Rage JC, Rocek Z (to be published) Description of *Triadobatrachus massinoti* (Piveteau, 1936), an anuran Amphibian from the early Triassic. Paleontographica

Reisz RR (1980) The Pelycosauria: A review of phylogenetic relationships. In: Panchen AL (ed) The terrestrial environment and the origin of land Vertebrates. Acad Press, London, p 553

Riggs (1934) A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. Trans Amer Phil Soc 24: 1–32

Ritchie A (1964) New light on the morphology of the Norvegian Anaspida. Skr norske Vidensk Akad Oslo Nat Naturv: 1–22

Ritchie A (1968a) *Phlebolepis elegans* Pander, an Upper Silurian thelodont from Oesel, with remarks on the morphology of thelodonts. Nobel Symposium 4: 81–88

Ritchie A (1968b) New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian fo Lanarkshire. Scotland. Palaeontology 11: 21–39

Romer AS (1947) Review of the Labyrinthodontia. Bull Mus Comp Zool Hartvarof College: 99

Romer AS (1956) The osteology of the reptiles. Univ Chicago Press, Chicago

Romer AS (1969) The chanares (Argentina) Triassic reptile faune V. A new chiniquodont cynodont *Probelesodon lewsi*-cynodont ancestry. Breviora 333: 1–24

Romer AS (1970) The Chanares (Argentina) Triassic reptile fauna VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. Breviora 344: 1–18

Romer AS, Lewis AD (1973) The Chanares (Argentina) Triassic reptile fauna. 19. Postcranial material of the cynodonts *Probelesodon* and *Probainognathus*. Breviora 407: 1–26

Romer A, Price LT (1940) Review of the Pelycosauria. Geol Soc Am Spec Pap 28: 538 p

Rosen D, Forey PL, Gardiner BG, Patterson C (1981) Lungfishes, tetrapods, paleontology and plesiomorphy. Bull Amer Mus Nat Hist 167 (4): 163–275

Russel DE, Gingerich PD (1987) Nouveaux Primates de l'Eocène du Pakistan. C R Ac Sc 304 (II): 209–214

Saint-Seine P de (1947) Les Poissons de Cérin. Nouv Arch Mus Hist Nat Lyon, 2

Sanz JL, Bonaparte JF, Lacasa A (1988) Unusual early Cretaceous birds from Spain. Nature 331: 433–435

Save-Söderberg G (1937) On *Rhynchoditerus elginensis* n g, n sp, representing a new group of dipnoan-like Choanata from the Upper Devonian of East Greenland and Scotland. Ark Zool 29B: 1–8

Schaeffer B (1967) Comments on elasmobranch evolution. In: Gilbert PW, Mathewson RF, Rall DP (eds) Sharks, skates and rays. H. Hopkins Press, Baltimore, p 3

Schaeffer B, Williams M (1977) Relationships of fossil and living elasmobranchs. Amer Zool 17: 193–302

Schindewolf I (1950) Grundfragen der Paläontologie. Schweizerbart, Stuttgart, 506 p

Schoch RM (1984) Vertebrate paleontology. Van Nostrand Reinhold Comp New York

Schulze HP, Arsenault M (1985) The panderichthyid fish *Elpistosege:* a close relative of tetrapods? Palaeontology 28 (2): 293–309

Schultz CB, Schultz MR, Martin LD (1970) A new tribe of saber-toothed cats from the Pliocene of North America. Bull Univ Nebraska State Mus 9(1): 1–31

Schultz CB, Tanner LG, Martin LD (1972) Phyletic trends in certain lineages of Quaternary mammals. Bull. Univ. Nebraska State Mus 9(6): 183–195

Severtzov AN (1916) Etudes sur l'évolution des Vertébrés inférieurs. Russk Arkh Anat Gistol Embiol 1(1): 1–104

Shea BT (1984) An allometric perspective on the morphological and evolutionary relationships between pygmy (*Pan paniscus*) and common (*Pan troglodytes*) chimpanzees. In: Susman RL (ed) The pygmy chimpanzee. Evolutionary biology and behavior, New York, Plenum Press, p 89

Sibley C, Ahlquist J (1986) La classification des oiseaux d'après leur ADN. Pour la Science 102: 79–90

Sigogneau D (1970) Contribution à la connaissance des ictidorhinidés (Gorgonopsia). Palaeont afr 13: 25–38

Simons E (1961) The phyletic position of *Ramapithecus*. Postilla 57: 1–9

Simons E (1979) L'origine des hominidés. La Recherche 10 (98): 260–267

Simpson GG (1945) Principles of classification and a classification of Mammals. Bull Amer Mus Nat Hist 85 (5): 350 p

Simpson GG (1951) Horses. The story of the Horse family in the modern World and through sixty million years of history. Oxford Univ Press, New York

Simpson GG (1953) The major features of evolution. Columbia Univ Press, New York

Simpson GG (1961) Principles of animal taxonomy. Columbia Univ Press

Slaughter BH (1971) Mid-Cretaceous (Albian) therians of the Butler farm local fauna, Texas. In: Kermack DM, Kermack KA (eds) Early mammals. Linn Soc Zool Journ 50 (1): 131–143

Sokal RR, Sneath P (1963) Principles of numerical taxonomy. Freeman, San Francisco

Sondaar PY (1968) The osteology of the manus of fossil and recent Equidae with special reference to phylogeny and function. North Holland, Amsterdam

Sondaar PY (1969) Some remarks on horse evolution and classification. Zeitsch f Säugetierk 34(5): 307–311

Stensiö EA (1927) The Downtonian and the Devonian vertebrate from Spitzbergen. A. Family Cephalaspidae. Skr Svalbard Nordishavet 12: 1–391

Stensiö EA (1964) Les Cyclostomes fossiles ou Ostracodermes. In: Piveteau J (ed) Traité de Paléontologie, vol 4(2) Masson, Paris, p 96

Stensiö EA (1969) Anatomie des Arthrodires dans leur cadre systématique. Ann Pal 55: 151–192

Sues HD (1987) On the skull of *Placodus gigas* and the relationships of the Placodontia. J vert Pal 7(2): 138–144

Suteehorn V, Buffetaut E, Helmeke-Ingavat R, Jaeger JJ, Jongkanjanasoontorn Y (1988) Oldest known Tertiary mammals from South East Asia: middle Eocene primate and anthracotheres from Thailand. N Jb Geol Paläont Nh 9: 563–570

Tarsitano S, Hecht MK (1980) A reconsideration of the reptilian relationships of *Archaeopteryx*. Zool J Linnean Soc 69 (2): 149–182

Tassy P (1985) La place des mastodontes miocènes de l'ancien monde dans la phylogénie des Proboscidea (Mammalia): hypothèses et conjectures. Thèse Univ P et M Curie, Paris

Tillier S, Cuif JP (1986) L'animal conodonte est-il un mollusque Aplacophore? C R Ac Sc Paris II, 7: 627–632

Tintant H (1986) La loi et l'événement. Deux aspects complémentaire des Sciences de la Terre. Bull Soc Géol Fr 8 (2,1): 185–190

Traquair RH (1914) A monograph of the fishes of the Old Red Sandstone of Britain. Pt 2. The Asterolepidae. Palaeontogr Soc Monogr: 63–134

Traquair RH (1899) On *Thelodus pagei* Powrie, sp from the Old Red Sandstone of Forforshire. Trans R Soc Edinb 39: 595–602

Valverde JA (1964) Remarques sur la structure et l'évolution des communautés de vertébrés terrestres. Rev Ecol Terre et Vie 111: 121–154

Vandebroek G (1961) The comparative anatomy of the teeth of the lower and non-specialized mammals. Int Colloq on the evolution of Mammals. Kon Kl Akad Vererisch Brussels 1: 215–320

Vandebroek G (1969) Evolution des vertébrés. Masson, Paris

Walker AD (1972) New light on the origin of birds and crocodiles. Nature 237: 257–263

Walker A, Leakey RE (1978) Les hominidés du Turkana oriental. Pour la Science: 48–65

Walker CA (1981) New subclass of birds from the Cretaceous of South America. Nature 292: 51–53

Wängsjö (1952) The Downtonian and Devonian vertebrates of Spitzbergen. IX, morphologic and systematic studies of the Spitzbergen cephalaspids. Skr norske Polarinst 97: 19611

Watson DMS (1917) A sketch classification of the pre-Jurassic tetrapod vertebrates. Proc of the Zool Soc London: 167–186

Watson DMS (1937) The acanthodian fishes. Phil Trans R Soc B.228: 49–146

Watson JD, Crick FH (1953) The structure of DNA. Cold Spring Harbor Symp Quant Biol 18: 123–132

Watson JD (1968) Biologie moléculaire du gène. Paris, Ediscience

Weismann A (1892) Das Keimplasma: eine Theorie der Vererbung. Gustav Fischer, Jena

Welles SP (1952) A review of the north American Cretaceous Elasmosaurs. Univ Calif Public Geol: 29 (3)

Whetstone KN, Martin LD (1979) New look at the origin of birds and crocodiles. Nature 279: 234–236

Wild R (1978) Die Flugsaurier (Reptilia, Pterosauria) aus der oberen Trias von Gene bei Bergamo, Italien. Boll Soc Pal Italiana 17: 176–156

White EI (1935) The ostracoderm *Pteraspis* Kiaer and the relationship of the agnathous vertebrate. Phil Trans R Soc B 225: 381–457

White MJD (1978) Modes of speciation. Freeman and Co, San Francisco

Williston SW (1892–1893) Kansas pterodactyls. Kansas Univ Quaterly: 1 and 2

Woodward AS (1909–1911) The fossil fishes of the English chalk. Palaeontograph Soc

Wright S (1978) Evolution and the genetics of populations. IV Variability within and among natural populations. Univ. Chicago Press, Chicago and London

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