



Robert L. Carlton

# A Concise Dictionary of Paleontology

*Technical Editor:*  
Brittney A. Oleniacz

 Springer

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Salem, Oregon, USA

ISBN 978-3-319-73054-7      ISBN 978-3-319-73055-4 (eBook)  
<https://doi.org/10.1007/978-3-319-73055-4>

Library of Congress Control Number: 2017963120

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Printed on acid-free paper

This Springer imprint is published by Springer Nature  
The registered company is Springer International Publishing AG  
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

*For Patricia, Morgan, Melissa, Brendan,  
and Cayden*

# Acknowledgments

This book owes its existence chiefly to my patient and forbearing Patricia. But I must also express my gratitude to my excellent editor, Brittney Oleniacz, and to the many other paleontologists whose advice and encouragement helped the project along. I am especially grateful to Paul Selden, whose detailed advice greatly improved an earlier draft. Thanks also to Frankie Jackson, David Varrichio, Ben Creisler, William Schopf, Kathleen Ritterbush, Tony Ekdale, Frank DeCourten, Phil Debarros, Tom Deméré, Ellen Thomas, Jonathan Payne, Demir Altiner, and Walter Obermiller. Special thanks to the librarians who helped me rifle the collections at the Berkeley, San Diego, and Merced campuses of the University of California; the Salem Public Library; Chemeketa College Library; Willamette University Library; and the Valley Library at Oregon State University. And finally, for actually bringing this book to life, thanks to Sherestha Saini and the very capable Springer staff.

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# Introduction

This little book is a moderately comprehensive reference handbook covering the most important paleontological taxa, terms, concepts, and localities. It is written primarily for beginning students in the field and general readers. My professional experience lies in technical writing and in teaching literature and history, with a lifelong interest in paleontology inspired by Professor Charles Higgins at U.C. Davis and by studying the geology collection in U.C. Berkeley's beautiful Bacon Hall before it was demolished in 1961. Using the essays of Loren Eiseley, Stephen Gould, and E.O. Wilson in my composition classes in the 1980s, I made critical thinking and the evolution of life on earth the center of my teaching. An interesting technical writing project in the early 1990s showed me the lack of a dictionary like this, and I began the groundwork for a good reference work as I directed student research in the history of life in my writing courses. Retiring from teaching in 2014, I have widened my understanding of paleontology with intensive study and have worked systematically to complete the dictionary in the last three years.

There are many science dictionaries and several purporting to cover natural science or earth science, but I have found them all very inadequate for paleontology. Even the larger works like the *McGraw-Hill Dictionary of Scientific and Technical Terms*, now in its seventh edition, have minimal and often outdated coverage of the field, with very little detail on relationships and significance. So I believe there is a need for a more comprehensive dictionary in print.

Online reference sites like the Paleobiology Database, the World Register of Marine Species, and Palaeos are excellent for some basic information needed by specialists, but they are of little use to the general reader. Wikipedia is good for its detailed articles and up-to-date coverage, and I found some information in it for about three-fourths of my entries. But it has surprising gaps and mistakes, and it often reflects individual opinions that are not completely trustworthy.

The lexicon of paleontology is of course too large to allow really comprehensive coverage of taxa, concepts, or terminology in a small dictionary. Here I try to include the most significant taxonomic groups down to the family level, as well as the most commonly mentioned genera in the literature. But in addition to covering these traditionally important taxa, I have included up-to-date information on several other

categories. First, I focus on taxa associated with historical turning points such as mass extinctions and first appearances of derived characters. Second, in addition to these transitional groups, I have included many entries that present phylogenetic problems because they do not fit neatly into established categories, thus inviting further research. Third, I pay detailed attention to Konservat-Lagerstätten that provide comprehensive information on the fossil communities and ecosystems of particular time frames, bringing together information from many sources on the most significant Lagerstätten and other collecting localities. Fourth, I have also tried to present the most current ideas about early hominin evolution.

With the aid of my excellent editor, Brittney Oleniacz, I have tried to maintain a mid-level tone, keeping the language accessible but including enough technical specificity to be useful for the serious student. To narrow the scope, I have kept the references to theoretical concepts to a minimum. Now let me explain my procedures.

In the entries for taxa, I state the classification and other relationships first, then a physical description of notable traits, and sometimes an indication of significance. I supply translations of names only when the etymology aids in identifying the taxon. Length measurements are nose-to-tail unless otherwise specified. The entries end with information on collecting localities and chronostratigraphic position. The references to geographic distribution indicate only the collecting localities of specimens, not necessarily the actual distribution unless so noted. The term “global distribution” excludes Antarctica, and I use the term “cosmopolitan” for taxa with widely scattered and relatively sparse occurrences in appropriate environments.

All taxa listed as entries are extinct unless noted as extant. Most dates assigned to organisms and geological periods are approximate, but I indicate greater precision and certainty when possible. For dates and capitalization of the divisions of the time scale, I follow the Geologic Time Scale and the International Chronostratigraphic Chart (2017), as published by the International Commission on Stratigraphy. The latter provides the current names and dates of the most broadly accepted subdivisions of geological periods and epochs.

The entries for descriptive terms generally include only terms used in this dictionary, and they refer only to the paleontological application of the term. Geological and biological references are made only where necessary for their paleontological significance.

I have attempted to provide the most generally accepted taxonomic relationships, generally following the classifications given by the Paleobiology Database, and also its distribution information where it is given and not contradicted by other sources. But since paleontological description and taxonomy is by its nature a work in progress, with frequent changes in classifications as a result of ongoing work by specialists, there is no question of full coverage or even of up-to-the-minute accuracy. Newly described taxa increase every day both the range of first and last appearances and the range of geographic occurrences. So the names, classifications, and dates given here are not to be taken as set-in-stone determinations but rather as handles to provide access to further information about the taxa being discussed. With this in mind, I have tried to give at least two references to related taxa for

each taxon entry. Of course, mistakes and omissions are inevitable in such an ambitious undertaking as this dictionary, and I will welcome all suggestions for improvement.

I have tried to steer a middle course between strict neo-Linnaean taxonomy and the extremes of modern cladistic systematics. As Colin Tudge so eloquently demonstrates in *The Variety of Life*, cladistic analysis is crucial in improving the accuracy of our picture of the tree of life. However, systematic taxonomy may blur the important distinctions between large groups such as dinosaurs and birds, or eurypterids and arachnids. At least for my purposes, when referring to reptiles in general, the paraphyletic classification Reptilia is far preferable to “non-avian, non-mammalian amniotes.” Also, the idea that each node in the branching of the tree deserves a new rank is a leap too far, even for most professionals, and I have chosen to ignore subgroups like microclass, parvorder, and sub-tribe.

The final section of the book, “Further Reading,” includes all of the important monographs that I have consulted, as well as many of the more important journal articles. But because writing a dictionary requires checking many print and online sources for each entry, each entry contains information from several sources, and I have not attempted to include references to all that I have consulted.

# A

***Aachenosaurus***: name given to a piece of petrified wood found in the Aachenian deposits near Moresnet, Belgium, and mis-identified in 1888 as part of a duckbill dinosaur's jaw.

***Aaptoryctes***: “unapproachable digger,” a monospecific genus of insectivorous sori-comorph mammals in the family Palaeoryctidae; 4–5 inches long and known only from three specimens found in Wyoming, the shrew-like *A. ivyi* had a stronger crushing dentition than its cousin *Palaeoryctes*; United States, late Paleocene, 57–56 Ma.

***Aardonyx celestae***: a species of anchisaurian sauropod dinosaurs described in 2010. Known from disarticulated fragments of two individuals dated at 195 Ma, it is estimated to have been about 40 feet long. *Aardonyx* seems to be intermediate between the earlier prosauropods, which were generally smaller and often ran on their hind legs, and the later, more ponderous sauropods. Spion Kop, South Africa; Early Jurassic.

**abathochroal**: an unusual type of compound eye found only in the early trilobite families of the suborder Eodiscina, comprised of a small number of lenses (about 70) with individual corneas.

***Abavornis***: a proposed genus of primitive birds of the Late Cretaceous, about 85 Ma; known only from a single bone in the shoulder process, it is tentatively classified as enantiornithine; it was found in Uzbekistan in 1998 and given the species name *A. bonaparti*.

**Abelisauridae**: a long-lived family of ceratosaurian theropod dinosaurs with two subfamilies, Majungasaurinae and Carnotaurinae; known almost exclusively from Gondwana, they were perhaps the most successful large predators there in the Cretaceous; they are characterized by strong hindlimbs, almost vestigial forelimbs, and a variety of knobs and horns on a short skull; see also ***Arcovenator***,

*Eoabelisaurus*, and *Rugops*; India, Africa, Madagascar, South America, and France; Middle Jurassic to Late Cretaceous.

***Abelisaurus***: a genus of theropod dinosaurs discovered in Patagonia, the type species of the family Abelisauridae; known from a 35-inch incomplete skull but probably bipedal, *A. comahuensis* is estimated at 25–30 feet long and 16 tons; Argentina, Late Cretaceous, about 80 Ma.

***Abrictosaurus***: a genus of basal ornithomimid dinosaurs in the family Heterodontosauridae; the size of a large dog, about 5 feet long and nearly 100 pounds, it had a long tail and was bipedal and herbivorous; it had high-crowned teeth but lacked the canine-like teeth on the lower jaw that were typical of heterodontosaurids; known from fragments of two individuals; Lesotho, South Africa, Early Jurassic.

**Abrocomidae**: a still-extant family of caviomorph South American rodents in the suborder Hystricomorpha; commonly known as rat chinchillas, the Abrocomidae diverged from the ctenomyids in the late Miocene; two extant species can be found in the central Andes.

***Abydosaurus***: a genus of herbivorous saurischian dinosaurs in the suborder Sauropodomorpha, discovered in 2010 at Dinosaur National Monument; remarkable because four skulls have been found, two of them entire, very unusual for the relatively delicate head of a sauropod; related to *Brachiosaurus*, *Abydosaurus* lived about 100 Ma; the size is unclear because all four specimens are from juveniles, which were about 25 feet long when they died; Utah, Early Cretaceous.

***Acanthochaetetes wellsi***: see **chaetetids**.

**Acanthodidae**: one of the three largest families of acanthodian fish; characterized by only one dorsal fin, they were generally edentulous, adapted to filter-feeding; North America, Europe, and Africa; Devonian to Permian.

**Acanthodii**: a paraphyletic class of primitive bony fishes in the infraphylum Gnathostomata. The first organisms to develop an efficient, moveable lower jaw, the acanthodians possessed characteristics of both chondrichthyans and osteichthyans. They are characterized by stout spines supporting numerous fins, usually two dorsal fins and a strongly heterocercal tail fin. The Acanthodii are generally considered to include the families Acanthodidae, Cladodontidae, Diplacanthidae, Gyrogoniidae, and Ischnacanthidae. Early Silurian to late Permian.

***Acanthostega***: a genus of stem-tetrapods intermediate between the lobe-finned fish of the Middle Devonian and the amphibians which began to colonize the land later in the period. The salamander-shaped *Acanthostega*, dated at 365 Ma, was 6 feet long and famously had 8 digits on its forelimbs and 7 on its hindlimbs. See **Tetrapoda**. Greenland, Late Devonian.

***Acanthothiris***: an obscure genus of articulate brachiopods in the still-extant order Rhynchonellida and extinct family Acanthothirididae; characterized by numerous hollow spines; Europe, Asia, and Africa; Early to Late Jurassic.

***Acanthothoraci***: “spine chest,” an order of primitive placoderms, closely related to the rhenanids and also similar to the ptyctodonts except for having somewhat heavier armor; characterized especially by a pair of large spines projecting from the chest; North America, Europe, Asia, and Australia; Early to Middle Devonian.

***Acari***: a still-extant subclass of arthropods in the class Arachnida that includes the mites (Actinotrichida and Anactinotrichida) and the ticks (Ixodida); by far the most numerous group of arachnids, more than 30,000 species of mites are known, with a far greater number still undescribed; global distribution, Early Devonian to Recent.

***Acervularia***: a genus of cerioid corals in the order Rugosa; characterized by dome-shaped colonies with tightly packed polygonal corallites; Europe and North America, middle Silurian to Middle Devonian.

***Achaenodon***: a genus of pig-like artiodactyl mammals in the family Dichobunidae; formerly called *Protelotherium*; North America and Africa, Eocene.

***Achelousaurus***: a monospecific genus of medium-sized centrosaurine ceratopsian dinosaurs, *A. horneri* is known from three skulls found in the Two Medicine Formation of Montana and Alberta; about 20 feet long and weighing about 3 tons, it is notable for a large skull and frill, with two small horns at the back of the frill; North America, Late Cretaceous, 74 Ma.

***Achillobator***: a genus of large maniraptoran theropod dinosaurs in the family Dromaeosauridae; similar to *Deinonychus* but at least a third larger — the type species *A. giganticus* was very large for a dromaeosaur, up to 19 feet long; Mongolia, Middle to Late Cretaceous.

***Acipenseridae***: the sturgeons, a family of “living fossils,” bony fish in the order Actinopterygii. Their ancestry reaches back to the Triassic, with true sturgeons appearing in the Late Cretaceous. They are notable for their size (the largest are more than 20 feet long and weigh more than a ton) and individual longevity (a century). Also notable for their longevity as a taxonomic family, being very little changed since the Cretaceous. Some species, such as the pallid sturgeon, *Scaphirhynchus albus*, are endangered because they are anadromous and often cannot reach their spawning grounds. North America, Europe, and Asia; Triassic to Recent.

***acritarchs***: “uncertain origin,” not a taxonomic group but a large and varied group of non-carbonate and non-siliceous organisms whose remains cannot be easily classified. Nevertheless, they are so abundant and diverse through the Precambrian and up to the Devonian that they are extremely important as biostratigraphic markers, especially for times when other fossils are not abundant. At least some of the acritarchs are thought to be the resting cysts of phytoplanktonic algae, and they may be ancestral to the dinoflagellates. Dating back to 1400 Ma (even possibly more than

3000 Ma), the collection was grouped informally in form taxa in the 1990s on morphological criteria and wall structure, but it awaits classification on a more natural basis. The acritarchs seem to have declined markedly at the time of the Cryogenian Glaciation, about 650 Ma, and also during other periods of widespread glaciation. The Doushantuo Formation in Southern China contains an important collection of acritarchs from 590 to 565 Ma, during the Cryogenian Period.

**Acrodelphidae:** an extinct family of long-snouted cetaceans in the suborder Odontoceti; North America and Europe, early Miocene to early Pliocene.

**Acrosalenia:** a genus of Mesozoic sea urchins in the still-extant family Acrosaleniidae; characterized by keeled teeth and solid spines; Europe and Africa, Early Jurassic to Early Cretaceous.

**Acrotretoidea:** a superfamily of inarticulate brachiopods in the class Lingulata and order Acrotretida; characterized by conical pedicle valves; cosmopolitan, early Cambrian to Devonian.

**Actinistia:** a subclass of sarcopterygian fish that includes the living coelacanths and several extinct families of lobe-finned fish.

**Actinocerida:** a subclass of middle Paleozoic nautiloid cephalopods; generally straight, most were about 3 feet long, with a few somewhat larger; found in shallow-water strata, they probably alternated between swimming and resting on the bottom; Early Ordovician to Devonian.

**Actinopterygii:** a large subclass of ray-finned fishes in the class Osteichthyes that includes most of the living bony fishes; the earliest actinopterygians arose in the Devonian.

**Actinostromariidae:** a family of reef-building Mesozoic demosponges; formerly considered stromatoporoids; Europe, Asia, and Mexico; Late Jurassic to Late Cretaceous.

**Actinotrichida:** see **Acari**.

**Adapidae:** a family of early primates in the suborder Strepsirrhini, probably diverging from the Plesiadapiformes in the late Paleocene, about the same time as the Omomyidae; the type genus is *Adapis*; they are generally considered to be related to the North American notharctids, including *Notharctus* and *Smilodectes*, and are possibly ancestral to the lemuroids of Madagascar; Europe, North America, and Asia; late Paleocene to late Miocene.

**adaptive radiation:** a sudden increase in diversity within a group of organisms, resulting from environmental changes that open new ecological niches in a geographically isolated area. The marsupials of Australia and the birds of the Galápagos Islands are the most widely known examples, and one of the most scrupulously described is E.O. Wilson's ground-breaking study in the 1950s of ant speciation on the island of New Caledonia.

**advanced:** of organisms: a state derived from a more primitive form, more modified and specialized than primitive ancestral species.

**Aechminidae:** a Paleozoic family of ostracods in the suborder Beyrichicopina; characterized by lobate shells with a single dorsal spine; Ordovician to early Permian.

**Aeduellidae:** a family of chondrosteian actinopterygian fish; North America and Europe, Pennsylvanian to early Permian.

**Aegyptocetus:** a genus of semi-aquatic archaeocete whales in the family Protocetidae; notable for cranial features that gave it the ability to hear underwater, but also for spinal features similar to those of other terrestrial weight-bearing protocetids such as *Rodhocetus*; Egypt, middle Eocene.

**Aegyptopithecus:** a genus of early anthropoid primates in the suborder Catarrhini, closely related to the smaller *Propliopithecus*; 2 to 3 feet long, it was probably herbivorous and arboreal; Fayum, Egypt, late Eocene to early Oligocene.

**Aegyptosaurus:** a genus of titanosaurian sauropod dinosaurs, about 50 feet long and weighing 12 tons; it had a long neck and tail, and had relatively long legs for a sauropod; the only known specimens were discovered by Ernst Strömer but were lost during World War II; North Africa, Cretaceous, 106–94 Ma.

**Aelurognathus:** “cat jaw,” a genus of small therapsids in the family Gorgonopsidae, related to *Rubidgea*; about 2 feet long, it is characterized by very long canine teeth; known from several specimens from the Karoo Basin; South Africa, late Permian.

**Aepycamelus:** a genus of giraffe-like artiodactyl mammals in the family Camelidae; about 10 feet tall, with long legs and a long neck, they browsed in open grassland; North America, early to late Miocene.

**Aepyornis:** a genus of giant ratite flightless birds in the still-extant infraclass Palaeognathae and extinct order Aepyornithiformes; commonly called “elephant bird,” *Aepyornis* was about 10 feet tall and weighed almost 900 pounds; it is known only from Madagascar and *became* extinct after humans arrived on the island; restricted to Pleistocene.

**Aerosteon riocoloradensis:** a species of carnivorous dinosaurs from 85 Ma, notable for breathing the same way as modern birds do, with a bellows-like pulmonary system; Argentina, Late Cretaceous.

**Aethophyllum:** an unranked monospecific genus of herbaceous conifers; low-growing and spreading, *A. stipulare* differs from most fossil conifers, which were trees; Europe and China, Middle Triassic.

**Aetiocetidae:** a family of basal toothed mysticete whales, notable for representing one of the transitional steps between toothed and baleen whales. From 10 to 26 feet long, aetiocetes were toothed but also possessed nutrient foramina and therefore probably some form of baleen, a synapomorphy of baleen whales. See also



**Mammalodontidae.** British Columbia, Washington, Oregon, Mexico, and Japan; early to late Oligocene.

***Aetodactylus halli*:** a species of ornithocheirid pterodactyloid pterosaur from the Early Cretaceous; it had a wingspan of 9 feet and a long, narrow snout lined with sharp, fish-catching teeth; see also ***Cimoliopterus***; Texas, 97 Ma.

**Aetosauria:** “eagle lizard,” a monofamilial order of crocodylian archosaurs, consisting of the family Stagonolepididae; generally heavily armored, they ranged from 3 to 10 feet long, and several genera bore backward-projecting spines to protect the back; some are important Triassic index fossils; although known only from the Late Triassic, they probably originated in the Middle or even Early Triassic; global distribution, Late Triassic.

**Afrosoricida:** a proposed order of mammals to include the tenrecs and golden moles (Chrysochloridae); Africa and Madagascar, Oligocene to Recent.

***Afrotarsius*:** a genus of haplorrhine primates in the family Tarsiidae; known from several fragments found in North Africa and Burma; Africa and Asia, Eocene to Oligocene.

**Afrotheria:** a large clade that includes the clade Tethytheria (proboscideans, sirenians, and desmostylians) as well as other genera that evolved in Africa, such as the aardvarks, tenrecs and hyraxes; see also **Eutheria**; Paleocene to Recent.

***Afrovenator*:** a monospecific genus of theropod dinosaurs in the family Megalosauridae, known from a single, relatively complete skeleton; 27 feet long and similar to *Allosaurus*, *A. abakensis* was smaller than *Tyrannosaurus rex* but an efficient predator with strong forelimbs and sickle claws; Niger, Middle Jurassic, 193 Ma.

**Agate Fossil Beds National Monument:** a site of lower Miocene volcanoclastic deposits in northwestern Nebraska, notable for specimens of several mammal species that are slightly different from similar species of the Oligocene White River Group fauna of the same area; one of the most striking is the helical burrow of ***Palaeocastor***, *q.v.*, and others are *Amphicyon*, *Miohippus*, and the chalicothere *Moropus*; United States, early Miocene.

***Agathoxylon*:** a genus of large gymnosperm trees in the family Araucariaceae; Europe, South and North America, Africa, and Antarctica; Middle Jurassic to late Miocene.

***Agilisaurus*:** a monospecific genus of ornithischian dinosaurs, probably related to *Heterodontosaurus*; about 4 feet long and lightly built, *A. louderbacki* was optionally quadrupedal but agile and a fast runner bipedally; known from a single complete skeleton dated between 168 and 161 Ma, it has the typical ornithischian beak-like prementary structure; China, Middle Jurassic.

***Agilodocodon*:** a monospecific genus of Jurassic therapsids in the suborder Docodonta, found in the Tiaojishan Formation and dated at about 160 Ma. Described

in 2015 as only 5–6 inches long, the shrew-like *A. scansorius* is the earliest-known tree-climbing mammaliaform animal. It had spade-shaped teeth, long claws, and flexible elbows and ankles, and probably fed on sap by gnawing through tree bark. China, Late Jurassic.

**Aglaspidida:** an order of arthropods, generally considered to be related to the chelicerates but now placed in the class Artiopoda; they are superficially similar to a trilobite with the elongate tail spine of a horseshoe crab; North America, Europe, Asia, and Australia; early to late Cambrian.

**Agnata:** a proposed phylum; erected in 1977 to include the enigmatic fossils *Salterella* and *Volborthella* of the early Cambrian; reaffirmed in 2003 but still controversial.

**Agnatha:** a class of jawless fish, a still-extant paraphyletic superclass of vertebrates; dating back as early as 530 Ma, the agnathans include the extinct ostracoderms and conodonts, as well as the modern lampreys and hagfish; see also **Gnathostomata**; early Cambrian to Recent.

**Agnosphyts:** a monospecific genus of early dinosaurs, placed variously in the families Guaibasauridae and Silesauridae; dated about 206 Ma, *A. cromhallensis* is known only from partial remains but seems to be a stem-dinosaur; England, Late Triassic.

**Agnostida:** a primitive order of small early trilobites; isopygous and generally eyeless, they had only two or three thoracic segments; some genera are thought to be planktic, but most are benthic like most other trilobites; global distribution, early Cambrian to Late Ordovician.

**Agnostus:** a genus of small trilobites in the order Agnostida and family Agnostidae; one of the earliest trilobites, especially prominent in Cambrian deposits; North America, Europe, and Asia; early Cambrian to Early Ordovician.

**Agoniatitida:** an early order of primitive ammonoids, ancestral to all later ammonoids; also known as Anarcestida; global distribution, Early to Middle Devonian.

**Agorophius:** a genus of early odontocete whales in the family Agorophiidae; first named by E.D. Cope in the 1870s, the family was long in question because the holotype of the genus was lost, but a 2016 description of a skull of *Agorophius pygmaeus* substantiates its position as a basal odontocete; North America, known only from the late Oligocene, 28–24 Ma.

**Agriochoeridae:** “wild pig,” a family of oreodont artiodactyl mammals in the sub-order Tylopoda. Superficially pig-like or sheep-like and as large as a small horse, they are now generally thought to be related to camels. Less advanced than their cousins the Merycoidodontidae, they had a selenodont dentition and claws instead of hooves, rare for artiodactyls. Widespread in North America but especially well-known from specimens in the Turtle Cove fauna of the John Day Fossil Beds. North America, late Eocene to early Miocene.

**Agriotherium:** “hunting beast,” a genus of early bears in the subfamily Agriotheriinae; formerly called *Hyaenarctos*; mainly carnivorous and about 9 feet long, it was among the larger bears of the Pliocene; North America, Europe, Asia, and Africa; late Miocene to early Pleistocene.

**Aigialosauridae:** a family of semi-aquatic varanoid lizards in the order Squamata and extinct superfamily Mosasauroidae. The type genus is *Aigialosaurus* (formerly called *Opetiosaurus*). About 3 feet long, the aigialosaurs show some aquatic specializations — a slightly flattened tail and reduced limbs — but were not structurally different from terrestrial ancestors. Considered basal mosasaurs, they are important as the earliest-known ancestors of larger and more specialized mosasaurs, which appeared about 92 Ma. Known from a small number of fragments from Europe, Late Jurassic to Late Cretaceous (Cenomanian).

**Aïstopoda:** an order of snake-like amphibians in the subclass Lepospondyli; ranging from 2 inches to 3 feet in length, some had reduced limbs but most were limbless; they appeared 20 million years after the first tetrapods; North America and Europe, Early Carboniferous to middle Permian.

**Ajacyathus:** a genus of early colonial or solitary archaeocyathan sponges; global distribution, early Cambrian.

**Alamosaurus:** “cottonwood lizard,” a monospecific genus of titanosaurian sauropod dinosaurs in the family Saltasauridae. Known from many fragmentary specimens and a nearly complete juvenile skeleton found in 2002, *A. sanjuanensis* was among the last surviving dinosaurs and possibly the largest North American dinosaur. It was first found in the Kirtland Formation of the San Juan Basin, New Mexico, and other specimens have been found in Utah and Texas. Some estimates claim that it may have weighed 80 tons and been 100 feet long. North America, Late Cretaceous, 70–66 Ma.

**Albanerpetontidae:** a long-lived family of salamander-like lissamphibians in the extinct order Allocaudata; fossorial, with a robust head and neck; North America and Europe, Middle Jurassic to Pliocene.

**Albertosaurus:** a genus of large tyrannosaurid theropod dinosaurs, 27 feet long and 2–3 tons in weight. *Albertosaurus* is characterized by two digits on the very small manus and a skull more than 3 feet long with about 60 teeth. The most significant find of *Albertosaurus* was made by Barnum Brown in 1910, in a bone bed on the Red Deer River; excavations there over the next century have uncovered more than 1100 bones from two dozen individuals. North America, Late Cretaceous, 70–66 Ma.

**Aletopelta:** a monospecific genus of armored dinosaurs in the family Ankylosauridae; known only from a partial skeleton found in Southern California, *A. coombsi* was about 20 feet long; named “wandering shield” because the formation in which it was found is a part of a tectonic plate that was several hundred miles to the south in the Late Cretaceous; United States, Late Cretaceous, 85–71 Ma.

**allochthonous:** referring to a fossil assemblage consisting of organisms removed from their place of origin before burial, as opposed to an autochthonous assemblage buried *in situ*; see also **taphocoenosis**.

**Allodesmus:** a genus of pinnipeds in the extinct family Desmatophocidae; 8 feet long and about 800 pounds but sexually dimorphic (females were smaller); *Allodesmus* had large eyes and was adapted to hearing underwater sounds; North America and Asia, Miocene.

**Allosaurus:** a genus of dinosaurs that were very similar to the later *Tyrannosaurus rex*; ranging from 20 to 32 feet long, the allosaurs were generally slightly smaller than *T. rex*, but one of the later species (known only from a skull recently discovered in Wyoming) was at least as large; mostly known from Western North America, but also found in Portugal and possibly in Tanzania; Late Jurassic, 155–150 Ma.

**Altirhinus:** a monospecific genus of iguanodont ornithischian dinosaurs; characterized by a tall beak on a rounded snout, *A. kurzanovi* was 21–26 feet long; it was optionally quadrupedal and had five digits on the manus, including a thumb spike; its arched snout is similar to that of *Muttaborrasaurus*, and the two share several other similarities; Mongolia, Early Cretaceous, 125–100 Ma.

**altriciality:** of animals' young: born relatively undeveloped and needing parental care.

**Alum Shale Formation:** an upper Cambrian formation in Scandinavia; see **Orsten Lagerstätten**.

**Alveolites:** a genus of colonial favositid corals in the order Tabulata; characterized by compressed, thin-walled corallites in massive or branching bodies; Silurian to Devonian.

**Alveugena:** a genus of non-placental mammals in the family Cimolestidae, possibly ancestral to the taeniodonts; known only from two partial specimens; North America, Early Paleocene, 66–63 Ma.

**Amaltheus:** a genus of ammonoids in the order Ammonitida and family Amaltheidae; involute and up to 9 inches in diameter, it has strong ribbing and a prominently braided keel; occurring boreally and only between the strata of its relatives *Prodactylioceras* and *Dactylioceras*, it is an important index fossil in the Pliensbachian; global distribution, Early Jurassic, 186–184 Ma.

**Amargasaurus cazau:** a species of large sauropod dinosaurs from about 130 Ma, about 30 feet long and 9 feet tall; known only from an almost complete skeleton discovered in 1984, it is notable for a double row of long spines extending from the vertebrae at the base of the skull along the entire long neck; Argentina, Early Cretaceous.

**amber:** fossilized tree resin, resulting in an unusual sedimentary deposit. Although they have the drawback of not being able to be handled, amber fossils of insects, arachnids, and plants preserve exceptional detail. Amber deposits are the principal

source of spider fossils, and even though very few vertebrate fossils occur in amber, bird feathers and even a nestling enantiornithine in amber are known from about 100 Ma. Since amber occurs near trees, sometimes far from the more common aquatic depositional environments, it provides a unique sampling of the biota. The earliest amber fossils are known from the Triassic, occurring in small amounts globally; but the Baltic amber of the Eocene has produced the greatest concentration of fossils, with important discoveries also in Cenozoic Dominican and Burmese amber deposits.

**Ambiortus:** a controversial genus of primitive birds; generally classified in the Ornithomorpha, it is poorly known and phylogenetic relationships are unclear; Early Cretaceous, about 130 Ma.

**Amblypoda:** a discarded term for a polyphyletic grouping of extinct ungulates including the uinatheres and pantodonts.

**Amblypygi:** “blunt rump,” an order of chelicerate arthropods in the class Arachnida; up to an inch long, they are known as whip spiders or tailless whip scorpions; with a flattened body and posture, they have long, slender legs and no silk spinnerets; they have no tail or venomous fangs, but their spiny pedipalps can puncture their prey; dating back to the Late Carboniferous (*Graeophonus*), about 160 species are presently known in tropical and subtropical areas; cosmopolitan, Late Carboniferous to Recent.

**Ambondro:** a monospecific genus of early mammals in the family Henosferidae, *A. mahabo* is probably close to the lineage of monotremes; Madagascar, Middle Jurassic, 167 Ma.

**Amborella:** a still-extant genus of Early Cretaceous plants in the family Amborellaceae, considered possible ancestors of angiosperms; global distribution, 130 Ma to Recent.

**Ambulocetus:** “walking whale,” a genus of archaeocete whales in the family Ambulocetidae. About 10 feet long and more than 600 pounds, it was an important transitional form between ancestral land-dwelling mammals and fully marine mammals, one or more of which evolved into modern whales. *Ambulocetus* is characterized by such aquatic adaptations as a long tail and strong, paddle-like feet, but it still has land-mammal characters such as hooves on its toes and powerful jaws with shark-like teeth. It is related to *Indocetus* and *Dorudon*, and is probably ancestral to *Rodhocetus* and *Basilosaurus*. Asia, Eocene.

**Amebelodon:** a genus of large shovel-tusked proboscideans in the family Gomphotheriidae; about 10 feet high, *Amebelodon* was similar to *Platybelodon*, another shovel-tusker; see also **Gnathobelodon**; Africa, Asia, and North America; late Miocene.

**Amia calva:** a carnivorous freshwater fish, commonly called bowfin, once distributed globally but now known only in the Great Lakes and Mississippi Valley; characterized by primitive ganoid scales; Paleocene to Recent.

**ammonite:** a general term for ammonoid but sometimes also used to refer to the later ammonoids of the order Ammonitida.

**Ammonitida** and **Ammonitina:** see **Ammonoidea**.

**Ammonoidea:** a subclass of externally shelled cephalopod mollusks, notable for their chambered and coiled shells, generally with a ventral siphuncle. The ammonoids appeared in the Early Devonian and became important predators in the Paleozoic and Mesozoic seas, the last becoming extinct toward the end of the Cretaceous. The shells of almost all ammonoids follow a planispirally coiled pattern, but in the course of their 350 million years of existence they developed an unparalleled diversity of patterns and ornamentation, especially in the late Mesozoic. Spreading into all parts of the oceans, they were generally good swimmers, nekctic or nektobenthic and preying on smaller marine organisms. The ammonoids are the most important Mesozoic index fossils because of their wide geographic occurrence, their rapid diversification, and the persistence of a few genera through the Permian and Triassic extinctions.

Ammonoids' classification in orders and suborders is highly disputatious; the version given here attempts to avoid controversy. They may be divided into eight orders, in order of appearance: (1) the Agoniatitida, Middle to Late Devonian, ancestral to all later ammonoids; (2) the Clymeniida, Middle to Late Devonian; (3) the Goniatitida, Middle Devonian to Late Permian; (4) the Prolecanitida, Late Devonian to Late Triassic; (5) the Ceratitida, Permian to Triassic; (6) the Phylloceratida, Early Triassic to Late Cretaceous; (7) the Lytoceratida, Late Triassic to Late Cretaceous; and (8) the Ammonitida, Early Triassic to Late Cretaceous. These eight groups may also be placed in three large orders, based mainly on their increasingly complex suture patterns: the Goniatitida, Ceratitida, and Ammonitida.

Two large suborders of the Ammonitida, the Ammonitina and Ancyloceratina, are especially important biostratigraphically because of their generally short lifespans and wide geographic range. The Ammonitina appeared very early in the Jurassic and include 1000 known genera, organized in about 15 superfamilies. They typically follow the regular planispiral coiling pattern, with just a few heteromorph genera. The Ancyloceratina appeared in the Late Jurassic and persisted to the end of the Cretaceous, as the Ammonitina declined. They include many heteromorph genera of the Cretaceous, such as *Bostrychoceras*, *Hamites*, *Nipponites*, *Scaphites*, and *Turrilites*. Most were relatively short-lived, and they were probably weak swimmers because of their shape.

The earliest ammonoids evolved from unknown nautiloids near the beginning of the Devonian, but collection failure (scarcity of specimens of nautiloids at the end of the Silurian and in the Early Devonian, and of the early ammonoids in the Devonian) leaves the connections unclear. The Phylloceratida (sometimes considered a suborder of the Ammonitida) probably gave rise to all post-Triassic ammonoids, such as the Lytoceratida. The Cretaceous ammonoids declined toward the end of the period, and the last disappeared in the end-Cretaceous extinction. See also **Nautiloidea** and **aptychus**.

**amniotes:** animals (reptiles, birds, and mammals) which evolved ways of protecting eggs inside the mother or at least inside a protective case; the basal amniotes were tetrapods that appeared in the Carboniferous about 312 Ma, descended from some group of reptiliomorphs such as the diadectomorphs or seymouriamorphs; since they made reproduction independent of water, the appearance of amniotes was important in the development of terrestrial animal life.

***Ampechinus:*** a genus of hedgehogs, small placental mammals in the still-extant family Erinaceidae; it appeared in Europe and Asia in the Oligocene and spread worldwide in the Miocene, becoming extinct at the end of the period.

***Amphibamus:*** a genus of temnospondyl tetrapods in the superfamily Dissorophoidea and family Amphibamidae; considered by some to be close to the ancestry of modern amphibians, but the connection is in dispute; North America and Europe, Middle Pennsylvanian.

**Amphibia:** a diverse class of vertebrates, including two extinct groups, the Temnospondyli and the Lepospondyli, and one still-extant group, the Lissamphibia, including the frogs, toads, salamanders, and other smaller groups.

**Amphichelydia:** an obsolete term for a suborder of cryptodire turtles.

**Amphicyonidae:** a family of dog-like carnivorous mammals in the superfamily Arctoidea. Possibly related to the Ursidae, they generally ranged from 10 to 200 pounds, but the largest species, *Amphicyon ingens*, is estimated to have weighed more than 1000 pounds. The amphicyonids achieved a holarctic distribution in the Oligocene. North America, Europe, Asia, and Africa; Eocene to early Pliocene.

**Amphilestidae:** an enigmatic family of mammals in the order Eutriconodonta, related to the Morganucodontidae and Gobiconodontidae; Africa, Asia, Europe, and North America; Jurassic to Late Cretaceous.

**Amphimerycidae:** a family of artiodactyl ruminants in the suborder Tylopoda; Europe, late Eocene to middle Oligocene.

**Amphioxiformes:** see **Cephalochordata**.

**Amphipithecidae:** a family of early primates in the suborder Haplorrhini; includes *Pondaungia* and the more recently discovered *Myanmarpithecus* and *Siamopithecus*; middle to late Eocene.

***Amphipithecus:*** see *Pondaungia*.

**Amphisbaenia:** a group of limbless reptiles in the order Squamata, commonly called worm lizards; global distribution except Australia, Cretaceous to Recent.

***Amphissites:*** a large genus of straight-backed palaeocopan ostracods in the family Amphissitidae; global distribution, Carboniferous to Permian.



***Amphistium***: a genus of flatfish showing the movement, over millions of years, of an eye first toward the top of the skull and then over to the upper side of the body; Europe, early to middle Eocene; see also **flatfish**.

**Amphitheriida**: a poorly known order of early pantothere mammals in the super-order Dryolestoidea; scansorial insectivores, they were probably in the line of evolution toward placentals and marsupials; England, Middle Jurassic.

***Amphiura plana***: an extinct species of burrowing brittle stars in the still-extant order Ophiurida and family Amphiuridae, known from the late Cenomanian to the end of the Cretaceous; Europe, Late Cretaceous.

***Amphoracrinus***: a genus of crinoids in the family Amphoracrinidae, characterized by a flat, truncate base; North America and Europe, Carboniferous.

**Amynodontidae**: a family of hornless perissodactyl mammals in the superfamily Rhinoceroidea; some genera resemble hippopotamuses in habit and appearance, while others have a tapir-like appearance; North America, Europe, and Asia; late Eocene to Pleistocene.

**Anactinotrichida**: see **Acari**.

***Anagale***: a genus of early eutherian mammals in the order Anagaloidea; rabbit-like in appearance, it was probably insectivorous, burrowing for beetle and worms; Mongolia, known only from the early Oligocene.

**anagenesis**: a concept briefly described as evolution within a lineage, while cladogenesis is evolution leading to a splitting of the lineage; anagenesis is said to result in change in a species through a gradual accumulation of genetic and physical differences, without a branching-off of a new species (cladogenesis); anagenesis is considered the basic process involved in phyletic gradualism, while cladogenesis is basic to punctuated equilibrium.

**analogous structures**: body parts of different organisms that perform similar functions but are not necessarily built on the same anatomical plan. For example, wings of both insects and birds perform the same function and are analogous, but they are not homologous because they have no basic structural parts (such as bones) in common. See also **homologous structures** and **vestigial structures**.

***Anancus***: a genus of large proboscideans in the family Gomphotheriidae and subfamily Anancinae; a forest browser 10 feet tall and weighing about 5 tons, with strikingly long tusks in the upper jaw, as long as 13 feet; Africa, Europe, and Asia; late Miocene to early Pleistocene.

**anapsid**: a term used to refer to reptiles that lack fenestrae behind the eye sockets in the skull; traditionally, anapsids have been considered one of five main subclasses of reptiles and as ancestral to diapsids and synapsids; the group is now recognized as paraphyletic or even polyphyletic, and the term is used only informally.



**Anarcestes:** a genus of small ammonoids in the order Agoniatitida and family Anarcestidae; an important index fossil in the Eifelian Stage of the Middle Devonian; Africa, Europe, Asia, and North America.

**Anarcestida:** see **Agoniatitida**.

**Anasca:** a still-extant polyphyletic group formerly considered a suborder of bryozoans in the order Cheilostomata; characterized by the absence of an ascus (a water-filled sac with a hydrostatic function) in each zooid, but being reclassified into separate orders on the basis of other characters; Late Jurassic to Recent.

**Anaspida:** an order of small, jawless, fish-like vertebrates usually considered agnathid ostracoderms; although they have no more than a cartilaginous skeleton and only a weak headshield, some have an armor of bony scales; also characterized by a reversed heterocercal tail fin; early Silurian to Early Devonian.

**Anatolepis:** a possible early jawless fish, proposed as a heterostracan vertebrate, but known only from tooth and carapace fragments and *incertae sedis*; late Cambrian to Early Ordovician.

**Anatosuchus minor:** a small species of Cretaceous crocodiles, about 3 feet long and with a pointed, duckbill-like snout; Niger, 110 Ma.

**Anchiornis huxleyi:** a species of small, bird-like theropod dinosaurs. Probably flightless, it was less than 2 feet long, with long legs, 4 toes, and proportionally large forelimbs. It was almost covered in feathers, some colored, according to researchers using melanosomes, cells that contain the pigment melanin. The color itself is not visible in the fossil, but electron-microscope analysis of follicle structure gives indirect evidence of color. Extrapolating from colors associated with the shape of the melanosomes in modern birds, researchers believe *Anchiornis* was covered with black and white plumage but also had a reddish crest of feathers. China, Late Jurassic, 161 Ma.

**Anchisaurus:** a genus of small basal sauropodomorph dinosaurs in the family Anchisauridae; formerly called *Megadactylus* and *Amphisaurus*; from 7 to 8 feet long and 60 to 80 pounds, it browsed on small palm trees and large shrubs; known definitively only from North America, Early Jurassic, 190–174 Ma.

**Anchitherium:** a genus of horses in the extinct subfamily Anchitheriinae, related to *Meshippus* and *Sinohippus*; about 2 feet high at the shoulder, it originated in North America in the Miocene and migrated to Asia, where it became extinct in the Pliocene.

**Ancodonta:** a discarded term for a polyphyletic grouping of some primitive artiodactyl mammals.

**Ancyloceratina:** “bent horn,” a suborder of mostly heteromorph ammonoids in the order Ammonitida; see **Ammonoidea**.

**Ancylopoda:** a suborder of perissodactyl ungulate mammals characterized by long, curving, cleft claws; it includes the eomoropids and the chalicotheres in the superfamily Chalicotherioidea; holarctic distribution, Eocene to early Pleistocene.

**Ancylotherium:** a genus of very large chalicotheres in the subfamily Schizotheriinae; it was about 7 feet tall and weighed as much as 1000 pounds; Europe, Asia, and Africa; late Miocene to early Pleistocene.

**Ancyrodella rotundiloba:** a species of conodonts whose first appearance marks the beginning of the Late Devonian at 382.7 Ma; its extinction, along with that of the conodont genus *Ozarkodina*, marks the end of the Frasnian Age of the Late Devonian at 372.2 Ma.

**Andalgalornis:** a monospecific genus of large, flightless predatory birds in the family Phorusrhacidae; *A. steulleti* was about 90 pounds and 4–5 feet tall, and had a large, heavy skull; related to the larger *Kelenken*; northwestern Argentina, Miocene to Pliocene.

**Andrewsarchus:** a monospecific genus of very large carnivorous or scavenging artiodactyl mammals; known only from a single skull almost 3 feet long, *A. mongoliensis* was found by Roy Chapman Andrews, who estimated the body to have been about 12 feet long; it was formerly classed as a mesonychid but is now considered an artiodactyl, most closely related to hippopotamuses and whales; Mongolia, middle Eocene.

**Anfesta stankovskii:** an obscure species of trilobozaans; similar in shape to *Tribrachidium*, it is circular and less than an inch in diameter, with three straight radiating ridges; Russia, Ediacaran.

**angiosperms:** “vessel seed,” the flowering plants, characterized principally by seeds enclosed in an ovary. Their ancestors have obscure roots in the Triassic (see *Sanmiguelia*), and among the groups of early plants considered possible ancestors are the Nymphaeales, Amborellaceae, and the disputed order Illiciales. The first definitive angiosperms appeared in the Early Cretaceous and quickly spread worldwide. By the beginning of the Late Cretaceous, they were developing showy petals and layers of fruit to attract the insects and herbivores that were diversifying alongside the flowering plants that they fed on. As a result of this symbiotic lifestyle, the angiosperms have been the dominant plants globally since 100 Ma. See also **Amborellaceae**, **coevolution**, **Gnetales**, and **Archaeofructus**.

**Anhanguera:** a genus of pterodactyloid pterosaurs that flourished in Northern Brazil about 112 Ma; with a wingspan of up to 15 feet, *Anhanguera* is a close relative of *Ornithocheirus*, and like some other ornithocheirids it had a pair of rounded crests at the top and bottom of a long beak; known only from the Araripe Basin of Brazil, Early Cretaceous.

**Animantarx:** “animated citadel,” a monospecific mid-Cretaceous genus of ankylosaurian dinosaurs in the family Nodosauridae; about 10 feet long, *A. ramaljonesi*

was heavily armored with bony scutes and horns but no tail club; known from only a single set of remains; Utah, Early to Late Cretaceous, 104–98 Ma.

**anisograptid fauna:** see **Graptolithina**.

**Ankarapithecus metei:** a species of fruit-eating apes that inhabited Asia Minor about 10 Ma; about 60 pounds, *Ankarapithecus* is known from a fragmentary male specimen found in 1950 and an almost complete face discovered in the 1990s; with some similarities to *Sivapithecus*, the finds are important because they are among the few primate fossils of the period between 18 Ma and 5 Ma; Turkey, late Miocene.

**Ankylosauria:** a suborder of squat, heavily armored ornithischian dinosaurs that contains the families Nodosauridae and Ankylosauridae; see also ***Polacanthus***; global distribution, Late Jurassic to Late Cretaceous.

**Ankylosauridae:** a family of medium-sized ornithischian dinosaurs in the suborder Ankylosauria. Mainly herbivorous, squat, and quadrupedal, some grew to 20 feet long. Ankylosaurs are characterized by encasing armor plates, a fringe of pointed spines around the midriff of the body, and a tail club; some species had plates even over the eyelids. North America, Europe, Asia, and Australia; Cretaceous, 125–66 Ma.

**Annelida:** the phylum of segmented worms, including the subclasses Oligochaeta (earthworms) and Hirudinea (leeches), and the paraphyletic class Polychaeta. The latter are marine invertebrates with a segmented body and many bristles; their chitinous jaws, called scolecodonts, are a widespread fossil from the Cambrian to the present.

**Anodontosaurus:** “toothless lizard,” a monospecific genus of ankylosaurid dinosaurs in the subfamily Ankylosaurinae; dated between 73 and 67 Ma, *A. lambei* is known from partial specimens found in the Horseshoe Canyon Formation of Alberta; medium-sized, armored, and herbivorous, it has a wide, pointed tail club; Canada, Late Cretaceous.

**Anomalocarididae:** a family of soft-bodied animals of the Cambrian and Ordovician in the order Radiodonta. *Anomalocaris*, at 3–4 feet the largest predator in the Burgess Shale assemblage, has been a contentious stem-arthropod for decades, but is now well-known from widespread specimens, including some larger specimens in China and some from Kangaroo Bay in Australia. Both its mouth and its body were at first incorrectly identified as separate animals, “*Peytoia*” and “*Laggania*” respectively, but *Peytoia* is now accepted as the name of another anomalocaridid, related to *Hurdia*. North America, Europe, Asia, and Australia; middle Cambrian to Early Devonian.

**Anomphalus:** a genus of marine aspidobranch snails in the superfamily Trochoidea and family Anomphalidae; type species *A. rotalus*; global distribution, Early Devonian to Jurassic.

**Anoplotheriidae:** a family of artiodactyl ungulate mammals in the suborder Tylopoda and extinct superfamily Anoplotheroidea; related to camels, they were medium-sized forest browsers; Europe, Eocene to Oligocene.

**anoxia:** a chemical state characterized by a low level of oxygen, sometimes a complete lack of oxygen; anoxia favors the preservation of fossils.

**Anseriformes:** an order of waterfowl in the superorder Galloanserae; it includes many modern species as well as extinct groups such as the Gastornithidae and the earliest-known genus, *Vegavis*; Cretaceous to Recent.

**Antarctodolops:** a genus of primitive marsupials tentatively placed in the family Polydolopidae; the only marsupial yet known from Antarctica, it is represented by the single species *A. dailyi*; Eocene to possibly Oligocene.

**Antetonitrus:** a monospecific genus of sauropodomorph dinosaurs that lived between 221 and 210 Ma, found in 1981 but only in 2003 recognized as one of the oldest sauropods known; about 30 feet long and almost 2 tons, *A. ingenipes* was the largest land animal of its time, although later sauropods came to weigh as much as 100 tons; found in the Elliot Formation along with the prosauropod *Melanorosaurus*; South Africa, Late Triassic.

**Anthocyatha:** a class of solitary, occasionally colonial, organisms placed in the Archaeocyatha; characterized by a roughly cylindrical cup and numerous bars, rods, and tabulae; early to late Cambrian.

**Anthozoa:** “flower animals,” one of the three classes of cnidarians, including principally the corals and sea anemones; the class contains the subclasses Hexacorallia, Octocorallia, and Ceriantharia.

**Anthracosauria:** an obscure group of early amphibian tetrapods, probably paraphyletic, including the Embolomeri, Seymouriamorpha, and Diadectomorphs; their classification is widely debated, but they are generally considered a stem group in the lineage leading to the amniotes; Late Devonian or Middle Mississippian to Early Triassic.

**Anthracosia:** see *Carbonicola*.

**Anthracotheriidae:** an extinct family of artiodactyl ungulates, pig-like but related to hippopotamuses and possibly whales; North America, Europe, Asia, and Africa; middle Eocene to late Pliocene.

**anthropoid:** an informal term referring to the monkeys, apes, and humans; generally replaced by more specific terms; see **Haplorrhini**, **Strepsirrhini**, **Catarrhini**, and **Platyrrhini**.

**Anthropornis:** a genus of giant penguins almost 6 feet long; New Zealand and Antarctica, late Eocene to early Oligocene.

**Antiarchi:** an order of small, heavily armored freshwater placoderm fish; the anterior body is armored while the posterior is fish-like, characterized by a pair of small,

moveable pectoral appendages; the order is well-known from the genera *Bothriolepis* and *Yunnanolepis*; global distribution, early Silurian to Late Devonian.

**Antilocapridae:** “goat antelope,” a still-extant family of ruminant artiodactyl mammals. Similar in size and shape to antelopes, they are distinguished from other artiodactyls by their branching horns; there is a permanent bony core like that of bovid horns, and the horny sheath of the horn is shed annually. Four genera are known from the early Miocene to the end of the Pleistocene, but the only living species is *Antilocapra americana*, ubiquitous in Western North America since the Pleistocene. The Miocene genus *Ramoceros* had long, cervid-like forked horns with 3 or 4 tines, and other genera had a variety of horn configurations. Restricted to North America, early Miocene to Recent.

**Anura:** “tailless,” the frogs, an enigmatic order of amphibians whose evolutionary history is unclear because of the paucity of the fossil record; the order includes the family Bufonidae, the toads; see **Proanura**; global distribution, Jurassic to Recent.

**Anzu wyliei:** a species of Late Cretaceous saurischian dinosaurs in the family Caenagnathidae; the largest oviraptorosaur of North America, it weighed about 650 pounds and was about 11 feet long and 10 feet high; it had a toothless beak and prominent crest, and was probably feathered; see also *Gigantoraptor*; Hell Creek Formation, North and South Dakota; late Maastrichtian, 66 Ma.

**Apatemyidae:** a family of small Paleocene mammals in the extinct order Cimolesta and suborder Apatotheria; characterized by long, hooked teeth, they were probably insectivorous and arboreal; North America and Europe, Paleocene to Eocene.

**Apatornis:** “deceptive bird,” a genus of flying birds in the family Apatornithidae; generally considered neornithine and possibly close to the Anseriformes, but known from only one fragment found in Kansas; North America, Late Cretaceous, 84 Ma.

**Apatornithidae:** a contentious family of very early flying birds, generally placed in the order Ichthyornithiformes, the Cretaceous toothed birds; its exact affinities, however, are still in question because of a paucity of specimens; it seems to have had a well-developed keel and other flight features; North America, Late Cretaceous.

**Apatosaurus:** a genus of very large saurischian dinosaurs in the infraorder Sauropoda and family Diplodocidae; with a long neck and a long, whip-like tail, they are estimated to have been up to 75 feet long and to weigh as much as 30 tons; see also *Brontosaurus*; North America, Late Jurassic, 152–151 Ma.

**Aphrosalpingoidea:** an enigmatic superfamily of sponge-like sessile animals generally classified as archaeocyathans; they had conical or cylindrical cups 1–2 inches wide; Europe, late Silurian.

**Apidium:** see **Parapitheciidae**.

**Apinae:** the bees, a still-extant subfamily of hymenopteran insects in the superfamily Apoidea. The taxonomic classification of bees is widely debated, but they are generally accepted as monophyletic, with Apinae including all genera of bees as

well as several lesser-known insects. The earliest specimens are known from Early Cretaceous amber fossils (see *Melittosphex*), with possible bee nests found in paleosols as far back as the Late Triassic. Along with other pollinating insects, bees spread globally alongside angiosperms in the early Late Cretaceous.

***Apiocrinites*:** a genus of crinoids in the still-extant order Millericrinida, characterized by a long stem and a rigid, pear-shaped calyx; *Apiocrinites* is found now only in an abyssal form, although it was common in the Jurassic in a shallow-water environment; Middle Jurassic to Late Cretaceous.

**Aplacophora:** “bearing no shell,” a still-extant class of benthic, deep-ocean mollusks; mostly small, microscopic to 2 inches, but a few grow up to several inches; cylindrical and generally without shells (but see *Kulindroplax*), and their body is covered with small aragonitic spicules; they are carnivorous, burrowing in the substrate or feeding on cnidarians; global distribution, early Cambrian to Recent.

**apomorphy:** a derived trait, a novel specialized feature of an organism; see also **synapomorphy**.

***Apsaravis ukhaana*:** a species of primitive birds in the suborder Theropoda, a link in the chain of descent from dinosaurs to birds; Mongolia, Late Cretaceous, 80–75 Ma.

**apterygote:** referring to wingless insects.

***Apthoroblattina*:** a genus of cockroaches in the extinct family Archimylacridae, about 2 inches long and 1.5 inches wide; North America, Europe, and Russia; restricted to Pennsylvanian.

**aptychus:** a curved calcitic or horny plate, usually one of a pair of aptychi; often found with ammonoids, sometimes attached to the body at the aperture, perhaps combining the functions of an operculum and a jaw; often found singly and referred to as an aptychus.

***Arabidopsis thaliana*:** thale cress, a living member of the mustard family, the Brassica, which includes cabbages and radishes. A model plant for genetic research, it is significant for having a small genome and for its genetic similarity to many other flowering plants, including corn, wheat, and rice. *Arabidopsis* offers further proof that the genes that control cell division are similar in plants and animals, supporting the inference that plants and animals originate from a common ancestor, probably a one-celled organism from about 1.5 billion years ago. It was originally named *Pilosella siliquosa*, and its name has changed several times since.

**Arachnida:** a large class of arthropods in the subphylum Chelicerata; the most familiar order is the Araneae, the spiders, and others are scorpions, ticks, mites, and the extinct trigonotarbid; all arachnids have 8 legs, although in some families one pair has been converted to other functions; early Silurian to Recent.

***Araeoscelis*:** a genus of small, lizard-like diapsid reptiles in the order Araeoscelidia; 2 feet long, it was one of the earliest diapsids but was exceptional in that both parts

of one pair of temporal fenestrae were closed with bone; similar to *Petrolacosaurus* of the Late Pennsylvanian; North America, early Permian.

**aragonite:** a polymorph mineral of calcium carbonate, chemically identical to calcite but with an orthorhombic crystal structure, different from calcite's rhombohedral structure; aragonitic mollusk shells fossilize less readily than calcite shells because of their unstable structure, resulting in gaps in the fossil record.

**Arandaspis:** a genus of jawless heterostracan fish in the order Pteraspidoformes; dated at 465 Ma, it was perhaps the oldest known vertebrate; it was 6–8 inches long and finless, and was armored with large bony plates and straps rather than with the tiles seen in its cousin *Astraspis*; Australia and South America, Middle Ordovician.

**Araneae:** the true spiders, an extant order of arachnids with eight legs, spinnerets for web-weaving, and cheliceral venom glands; several early genera date back to the Carboniferous, and the order diversified greatly in the Jurassic, but 90 percent of the known spider fossils are in amber from the Paleogene; the oldest known spider web fragments (140 Ma) are encased in a piece of amber from Sussex, England; global distribution, Devonian to Recent.

**Araneoidea:** the larger of the two still-extant superfamilies of orb-weaving spiders in the order Araneae; araneoids weave webs of adhesive threads and share several morphological characters for spinning; see also **Deinopoidea**; middle Paleozoic to Recent.

**Araripemys:** a genus of early turtles in the order Testudines and extinct family Araripemydidae or Pelomedusidae; type species *A. barretoii*, about 2 feet long but not well-known; Brazil, Early Cretaceous.

**Araripe Plateau and Basin:** a region in Northeast Brazil that has produced a large and diverse fossil assemblage of plants and animals from the Early Cretaceous, before South America split off from Africa. See **Crato** and **Santana Formations**.

**Araripesuchus gomesii:** the type species of *Araripesuchus*, a notosuchian crocodyliform of Gondwana; a short-snouted crocodylian about 2 feet long, found in the Santana Formation of the Araripe Basin in Brazil; Early Cretaceous.

**Araripesuchus rattoides:** the second African species of *Araripesuchus* to be found; 3 feet long, characterized by buckteeth which it used to root in soil for grubs and plants; probably spent most of its time on land; Morocco, Early Cretaceous.

**Araripesuchus tsangatsangana:** the geologically most recent *Araripesuchus*, dated at 66 Ma; Madagascar, Late Cretaceous.

**Araripesuchus wegneri:** the first African species of the genus; it ran on long legs like a dog and swam well with a long crocodylian tail; about 3 feet long and omnivorous; Niger, Early Cretaceous.

**Araucaria:** a genus of plants in the still-extant family Araucariaceae, distantly related to pines. Several genera have existed almost unchanged for hundreds of



millions of years and are considered “living fossils,” such as the Norfolk Island pine (*A. heterophylla*) and the monkey puzzle tree (*A. araucana*), which is known from as far back as 250 Ma. *Araucaria* appeared in the Early Triassic and diversified rapidly worldwide, creating forests of trees as tall as 250 feet. Triassic to Recent.

**Araucariaceae:** a still-extant family of coniferous trees in the class Pinopsida and order Pinales; appearing in the Early Carboniferous, they spread worldwide in the Mesozoic but disappeared in Laurasia at the end of the Cretaceous; a notable site for them is Petrified Forest National Park in the Southwestern United States; global distribution, Carboniferous to Recent.

**Archaea:** one of the three basic domains of life forms, a group of prokaryotes, single-celled organisms without a defined nucleus; distinguished from bacteria, the other prokaryotic domain, by some eukaryotic genes and metabolic characteristics; notable for tolerance of extreme environments, many of them living near hydrothermal vents in the ocean floor; the earliest-known fossilized Archaea date back to 3.5 billion years ago, but genetic research indicates that they probably originated closer to 4 billion years ago; see also **Bacteria** and **Eukaryota**.

**Archaeofructus liaoningensis:** the best-known of three species of a genus of early (125 Ma) flowering plants in the Jehol biota, proposed as stem-group angiosperms but still poorly known; China, Early Cretaceous.

**Archaeocalamites:** a genus of the earliest-known horsetails in the order **Calamitales** (*q.v.*); Pennsylvanian to Permian.

**Archaeoceratops:** a genus of basal neoceratopsian dinosaurs in the family Archaeoceratopsidae; only 3 feet long, it had no horns or neck frills but a large skull and a small bony frill near its tail; the type species *A. oshimai*, the oldest known neoceratopsian, is dated at about 125 Ma; China, Early Cretaceous.

**Archaeoceti:** a paraphyletic suborder of ancestral cetaceans; fish-eating and dolphin-like, they grew up to 33 feet long; characterized by vestigial hindlimbs and an elongated snout; the earliest are known from the island continent of India in the early Eocene (see *Pakicetus* and *Ambulocetus*), and they diversified rapidly worldwide; early Eocene to late Oligocene.

**Archaeocidaris:** a genus of early euechinoids in the extinct order Cidaroida; global distribution, Late Devonian to late Permian.

**Archaeocopida:** a problematic early Paleozoic order of ostracods, characterized by a thin carapace and a shell with high-chitin content, only slightly calcified; Cambrian to Ordovician.

**Archaeocyatha:** “ancient cups.” The archaeocyathans were sessile and sponge-like marine organisms, mostly solitary but some colonial. Their classification has shifted considerably over time, with the current consensus placing them with the hypercalcified sponges. Among the earliest reef-builders, they were solitary or colonial, generally cup-shaped or conical, with two layers of perforated calcareous



walls, mostly between 1 and 6 inches tall. Prominent in the Tommotian biota, they were worldwide and highly diverse index fossils for the early Cambrian but began to decline by the middle Cambrian. Most genera had disappeared by the end of the Cambrian, and the last-known species, *Antarcticocyathus webberi*, became extinct just before the end of the period. After the disappearance of Archaeocyatha, there were almost no reef-building animals until the rise of the Late Ordovician reef-builders such as the stromatoporoids and stenolaemates 50 million years later.

***Archaeocyon***: a genus of small early dogs in the extinct subfamily Borophaginae; up to 2 feet long and weighing 3–4 pounds; Western North America, early to late Oligocene.

***Archaeodontosaurus descouensi***: a species of sauropod dinosaurs with prosauropod-like teeth, found in 1999 and dated at 168 Ma; it is known only from bone fragments and teeth and estimated to have been 40 feet long; Madagascar, Middle Jurassic.

**Archaeogastropoda**: a large and still-extant paraphyletic group of sea snails and limpets, prosobranch gastropods that first appeared in the Cambrian and have been very widespread and diverse since a mid-Paleozoic radiation; most are extinct, but limpets and many sea snails remain; there are several competing classification systems of the group.

**Archaeognatha**: a still-extant order of apterygote insects; also called Microcoryphia and previously considered part of the now obsolete order Thysanura; among the most primitive insects, they appeared about 390 Ma; characterized by a long, slender body, arched back, and two cerci and a medial extension on the tail; cosmopolitan, Middle Devonian.

***Archaeolythus***: a genus of primitive archaeocyathans in the order Monocyathida; solitary or colonial and branching, the small, single-walled *Archaeolythus* was one of the simplest archaeocyathans; Cambrian.

***Archaeopteris***: “ancient feather,” a genus of progymnosperm trees in the order Archaeopteridales; growing up to 25 feet high, *Archaeopteris* created the first large forests in the Devonian and was an important ancestor of later plants; *Archaeopteris* had fern-like true leaves and was similar to modern trees in its branching growth pattern; its significant characteristics include heterospory and dense gymnospermic secondary wood; global distribution, Late Devonian to Early Carboniferous.

***Archaeopteryx***: a famous genus of feathered theropods, generally considered transitional between dinosaurs and modern birds; known principally from a dozen specimens from the Solnhofen limestone quarry in Central Bavaria and dated at 150 Ma; modern bird physiology seems to have first appeared in later feathered dinosaurs found in China, about 130 Ma; about the size of a raven, *Archaeopteryx* was a weak flyer; Europe, Late Jurassic.

**“*Archaeoraptor liaoningensis*”**: one of several fake fossil specimens produced in China in recent decades, supposedly a turkey-sized feathered dinosaur capable of

flight. Publicized in 1999 by *National Geographic*, it was soon discovered to be a composite of bones from different animals; the magazine published a full retraction later, but the hoax has joined Piltdown Man as one of the most famous frauds in the history of science. Many genuine feathered dinosaurs have been found since then, mostly in China, now undergoing a much more thorough investigation than in the 1990s.

***Archaeornithomimus***: a genus of coelurosaurian theropod dinosaurs in the family Ornithomimidae; about 11 feet long and probably omnivorous, *Archaeornithomimus* is known from disarticulated skeletal specimens of several individuals; Asia, Late Cretaceous, 75–66 Ma.

***Archaeotherium***: a genus of artiodactyl mammals in the family Entelodontidae; known only from North America, *Archaeotherium* was carnivorous but mainly a scavenger; the size of a bison but looking more like a giant warthog, *Archaeotherium* closely resembled its later relative *Daeodon*; North America, late Eocene to late Oligocene.

***Archaeothyris***: a genus of small, lizard-like synapsids in the family Ophiacodontidae; less than 2 feet long, *Archaeothyris* resembled a small iguana; the three known specimens are dated between 311 and 307 Ma, and it is the earliest accepted synapsid, but see also ***Echinerpeton***; Canada, United States, and Czech Republic; Late Pennsylvanian.

***Archanodon***: a genus of large bivalves in the order Unionoida; the earliest-known freshwater bivalves; North America, Middle Devonian.

***Archelon***: a monospecific genus of marine turtles in the still-extant suborder Cryptodira and extinct family Protostegidae; the largest known turtle, about 13 feet long and 16 feet wide flipper to flipper; instead of the solid shell of most modern turtles, *A. ischyros* had a skeletal framework that supported a leather carapace; North America, Late Cretaceous, 80 Ma.

***Archeria***: a genus of primitive anthracosaurians in the family Archeriidae; about 7 feet long, it was an aquatic eel-like predator; notable for being one of the few almost complete skeletons of its type; Texas and Oklahoma, early Permian.

***Archicebus achilles***: the earliest-known haplorrhine primate, an almost complete specimen discovered in China around 2005 and dated on the cusp of the Paleocene to the Eocene; about 9 inches long, including a 5-inch tail, it weighed only an ounce but is characterized by a distinctive heel bone and by marmoset-like teeth; 55 Ma.

***Archimedes***: a genus of stenolaemate bryozoans in the order Fenestrata and family Fenestellidae; very different in appearance from other fenestellids, *Archimedes* is named for its shape, which closely resembles an Archimedes Screw; growing in upright colonies up to 3 feet high, with a fenestrate network at the edges of the screw; global distribution, Middle Mississippian to middle Permian.

**Archipolypoda:** a superorder of millipedes in the subclass Chilognatha, possibly the earliest terrestrial animals; Europe and North America, Silurian to Late Carboniferous.

**Archonta:** a proposed superorder that would include primates, Plesiadapiformes, tree shrews, and dermopterans.

**Archosauria:** a clade of advanced diapsid reptiles including modern crocodiles and birds as well as the extinct thecodonts, pterosaurs, and dinosaurs. The earliest archosaurs were the Proterosuchidae, which appeared near the end of the Permian and diversified rapidly in the Early Triassic. The archosaurs were widespread and dominant throughout the Mesozoic, but only a few families survived the mass extinction at the end of the Cretaceous. Global distribution, Permian to Recent.

**Arcovenator:** a monospecific genus of ceratosaurian theropod dinosaurs in the family Abelisauridae; *A. escotae* is known only from a partial skull but seems to have most of the abelisaurid characters; dated at 74 Ma, it was probably part of a northward migration of the Gondwanic abelisaurids toward the end of the Cretaceous; France, Late Cretaceous.

**Arctocyonidae:** a possibly polyphyletic family of primitive, unspecialized mammals; ranging in size from raccoon-like (*Chriacus*) to bear-like (*Mentoclaenodon* and *Arctocyon*), the group presents a combination of carnivore and ungulate characteristics; North America and Europe, Late Cretaceous to early Eocene.

**Arctodus:** a genus of large and very long-limbed bears in the subfamily Tremarctinae, which became extinct near the end of the Pleistocene; *A. simus*, the Great North American short-faced bear, was larger than the modern grizzly, 4 to 5 feet high at the shoulder and weighing almost a ton; North America, Pleistocene.

**Arctolepis:** a genus of early arthrodire placoderm fish in the family Phlyctaeniidae; less than a foot long, it is characterized especially by its long and stout pectoral fins and by its heavy anterior armor; also called *Acanthaspis*; North America and Europe, Early to Middle Devonian.

**Arctotypus:** a genus of griffinflies in the order Meganisoptera, with a compact and relatively heavy body, and a wingspan of about 12 inches; Europe and Asia, Carboniferous to Permian.

**Arcyzonidae:** a family of paleocopan ostracods in the superfamily Kirkbyoidea; characterized by valves with a central pit; known only from China, Early Devonian.

**Ardipithecus:** *Ar. ramidus* is a species of hominin known principally from a partial female skeleton found in 1992 in the Middle Awash region of Ethiopia, dated about 4.4 Ma. It is closely related to the last ancestor shared by chimpanzees and humans, and may be a direct ancestor of the australopithecines. It was omnivorous, not just a frugivore, and had a flexible palm and possibly bipedal feet, although it may have nested in trees. The discovery in a more heavily forested area than most hominid skeletons has led Tim White and others to question the open-savannah theory of

early hominids' development of bipedalism. Other paleontologists, however, question whether *Ardipithecus* lived in a closed forest setting; others question its classification as a hominid, and still others question whether it was bipedal. A partial skeleton whose skull was in coin-sized pieces is kept in the National Museum of Ethiopia. A second possible specimen, dated between 5.8 and 5.2 Ma and named *Arkadabba*, is known from teeth and several skeletal bones. Miocene to Pliocene.

***Argentavis***: a monospecific genus of very large predatory and scavenging birds in the family Teratornithidae; weighing up to 170 pounds, *A. magnificens* had a wingspan of about 23 feet, similar to the smaller seabird *Pelagornis sandersi*; Argentina, late Miocene.

***Argentinosaurus huinculensis***: one of the largest land animals known, a species of sauropod dinosaurs in the clade Titanosauria; although only a few vertebra and other bones have been found, *A. huinculensis* may have weighed more than 80 tons and reached more than 130 feet in length, with a long neck and tail; Patagonia, Late Cretaceous, 97–94 Ma.

***Arkanites***: a genus of goniatitic ammonoids in the family Reticuloceratidae, related to *Retites* and *Quinnites*; subglobose, with prominent ribbing and sometimes nodular bases; known only from the Midwestern United States, Early Pennsylvanian.

***Arkarua***: an Ediacaran genus tentatively placed in Echinodermata but still of uncertain relationships; somewhat similar to the trilobozoans; known only from a cast half an inch in diameter, it has a raised center with pentameral symmetry; Australia, Ediacaran.

**“*Arpylorus antiquus*”**: a supposed species of protists long considered a possible early dinoflagellate but rejected in 2012, being designated as part of a more complex organism.

***Arsinoitherium***: a genus of large paenungulate mammals in the extinct order Embrithopoda and family Arsinoitheriidae, known mainly from a complete skeleton found in the Fayum Depression; growing up to 10 feet long, they are related to elephants despite having a very different skull, which bears two very large bony horns extending forward from its nose; possibly related specimens have also been found in Europe and Mongolia but are still being investigated; Egypt and Arabian Peninsula, Eocene to Oligocene.

***Arthrodira***: “joint-necked,” a large order of placoderm fish; characterized especially by a ball-and-socket joint behind the head that allowed it to raise its head, enlarging its gape; generally armored and at first only a few inches long, many became very large during the Devonian, reaching a length of 30 feet in *Dunkleosteus*; the arthrodirans were among the dominant predators of the Devonian until their extinction at the end of the period; Silurian to Late Devonian.

***Arthropleura***: a genus of Paleozoic millipedes in the extant subphylum Myriapoda and the extinct subclass Arthropleuridea; arthropleurids were 1–7 feet long and up

to a foot wide, the larger species being the largest terrestrial invertebrates known; North America and Europe, Carboniferous to early Permian.

**Arthropoda:** “jointed foot,” the largest phylum of animals, including about 80 percent of all described extant species; characterized by a segmented body, jointed appendages, and an exoskeleton (a chitinous cuticle); among its subphyla are trilobites, crustaceans, myriapods, chelicerates, and hexapods (which includes insects); early Cambrian to Recent.

**articulate:** of brachiopods and bivalves, using teeth or sockets to hold valves together, as opposed to using muscles to secure the joint in the manner of inarticulate species.

**Artiodactyla:** an order of herbivorous hoofed mammals with an even number of toes, the most successful group of large mammals. Evolved from condylarths, the group includes most large land mammals, such as the pig, sheep, hippopotamus, pronghorn, deer, cow, giraffe, camel, llama, and bison, and dozens of species of antelope. Since the cetaceans (whales, dolphins, and porpoises) evolved from early even-toed ungulates, they are also considered to belong with artiodactyls in the clade Cetartiodactyla. Early Eocene to Recent.

**Asaphida:** a large order of trilobites in the subclass *Librostoma*, containing about 20 percent of the known trilobite species; although the order includes a great number of disparate shapes and sizes, its members are generally isopygous and have a prominent ventral suture; the superfamily *Asaphoidea* is also characterized by prominent eye-stalks; the asaphids declined at the end of the Ordovician, with only one of the six superfamilies, the *Trinucleoidea*, surviving into the Silurian; global distribution, middle Cambrian to late Silurian.

**Asaphus:** a genus of large trilobites in the order *Asaphida* and family *Asaphidae*; isopygous and rounded, they grew up to 2 feet long; Northern Europe, Early to Middle Ordovician.

**Ascidiacea:** a paraphyletic class of soft-bodied animals in the subphylum *Tunicata*; because of their scanty fossil record, there are only a few reliably identified fossils; the oldest reported is from the early Cambrian Chengjiang biota of China; among the later definitive fossil specimens are some specimens from the Jurassic and the still-extant genus *Cystodytes*, known from the Eocene; early Cambrian to Recent.

**Ascomycota:** “sac fungus,” the largest division of the Kingdom *Fungi*, generally characterized by a spore-producing ascus; known from Devonian fossils but believed to be much older.

**Asilisaurus:** a genus of very early archosaurian dinosauromorphs in the clade *Dinosauriformes* and family *Silesauridae*; quadrupedal, 3–10 feet long, and weighing as much as 70 pounds, *Asilisaurus* displays many dinosaurian traits; Tanzania, Middle Triassic, 245 Ma.

**Asioryctitheria:** a proposed order of basal eutherian mammals; insectivorous and probably the earliest modern mammals; includes the genera *Asioryctes* and *Kennalestes* and the proposed genera *Sasayamamylos* and *Ukhaatherium*; China and Japan, Early to Late Cretaceous.

**Aspidella:** an enigmatic genus of discoidal fossils of the late Precambrian, well-known from the Ediacaran fauna of Canada and Europe. Generally 3–4 but up to 7 inches wide, it has a concentric ring structure and seems to be the imprint of an anchoring disk of an organism with fronds. *Aspidella terranovica* is the name of the first Ediacaran organism to be described, in Newfoundland in 1872. See also *Charnia*.

**Aspidorhynchiformes:** a Mesozoic order of actinopterygian fish in the subclass Neopterygii; about 2 feet long with an elongated and tooth-lined jaw, they superficially resemble the modern gars but are not related; North America, Europe, and Asia; Middle Jurassic to Late Cretaceous.

**Asteraceae:** the largest family of angiosperm plants; also called Compositae, they are characterized by composite flowers with flowering heads surrounded by bracts; Late Cretaceous to Recent.

**Asteroidea:** the sea stars or starfish, a class of asterozoan echinoderms; characterized by radial symmetry, the central body extending into five or more arms, not sharply marked off from the body; since sea stars disintegrate quickly after death, the fossil record is weak; global distribution, Ordovician to Recent.

**Asterozoa:** a subphylum of echinoderms; see **Asteroidea and Ophiuroidea**.

**astogeny:** the growth and development of colonial organisms such as corals; see also **ontogeny**.

**Astrapotheria:** an order of hoofed mammals in the superorder Meridiungulata; up to 10 feet long, the larger species resembled a small, tapir-like mastodon, with long, tusk-like canines; *Trigonostylops* is a smaller Eocene version, and the Miocene *Astrapotherium* is the type genus; South America and Antarctica, Paleocene to Miocene.

**Astraspis:** a genus of jawless fish in the subclass Astraspida; 8 inches long, armored with bony tiles, which were somewhat star-shaped on its head; related to *Arandaspis*; North and South America, Middle Ordovician.

**astrophic:** of brachiopods, without a well-defined hinge line, having the two valves hinged at a point.

**Atacamitan chilensis:** name given in 2011 to a species of titanosaurian sauropod dinosaurs, possibly related to the Nemegtosauridae; originally called *Domeykosaurus*, it is known from several skeletal fragments first described in 2003 and dated near the end of the Cretaceous; Northern Chile, Late Cretaceous.

**Atelostomata:** a superorder of irregular echinoids characterized by the absence of a lantern; they are microphagous feeders, finding particles of food on the substrate.

**Athyridida:** a long-lived order of articulate brachiopods in the class Rhynchonellata; characterized by biconvex, smooth, and impunctate shells with laterally directed spires; global distribution, Late Ordovician to Jurassic.

***Atlanthropus mauritanicus:*** see **Ternifine Man.**

***Atlasaurus imelakei:*** a species of sauropod dinosaurs; known only from an almost complete skeleton found in Morocco, it is estimated at about 50 feet long and 26 tons; *Atlasaurus* is related to the larger *Brachiosaurus* but has a shorter neck and comparatively larger skull; its spoon-shaped teeth have denticles; Morocco, Middle Jurassic.

***Atrypa:*** a genus of articulate brachiopods in the order Atrypida and family Atrypidae; characterized by a round, impunctate shell with many fine ridges; the pedicle valve is convex except that it may transition to concave toward the anterior edge; the brachial valve is convex; cosmopolitan, early Silurian to Late Devonian.

***Attercopus:*** a monospecific genus of arachnids in the order Uraraneida; *A. fimbriunguis*, the oldest known proto-spider, produced silk but probably used it only to line its burrows; see also ***Perrmarachne***; North America, Middle Devonian.

***Aturia:*** a genus of nautiloids in the order Nautilida, the only genus in the family Aturiidae; it is discoidal, involute, and smooth-shelled, and has a very complex suture pattern; cosmopolitan, early Paleocene to late Miocene.

***Augustynolophus:*** a monospecific genus of hadrosaurid dinosaurs in the subfamily Saurolophinae; known from a skull, vertebrae, and limb bones, *A. morrisoni* was the first dinosaur found in California, near Fresno; it was first identified as *Saurolophus morrisoni*; late Maastrichtian.

***Aulacothyris:*** a genus of punctate articulate brachiopods in the superfamily Zeilleroioidea; characterized by a long loop and a convex pedicle valve with a strikingly large fold along the posterior to anterior plane; Triassic to Jurassic.

***Aulacocerida:*** the oldest coleoids, an order of cephalopods in the subclass Belemnoidea; global distribution, Devonian to Late Jurassic.

***Aulolepis:*** a genus of teleost neopterygian fish in the small extinct order Ctenothrissiformes; characterized by a short, deep body and a large dorsal fin; Europe, Late Cretaceous, late Cenomanian, about 95 Ma.

***Aulophyllum:*** a genus of solitary rugose corals in the extinct superfamily Zaphrenticae; closely related to *Dibunophyllum*; Great Britain, Early Carboniferous.

***Aulopora:*** an order of colonial tabulate corals in the extinct family Auloporidae; characterized by cylindrical corallites in a branching tubular structure, encrusting a hard substrate; Ordovician to Permian.



***Australopithecus***: a genus of primates in the family Hominidae. With specimens spanning the period from 4.4 to 1.5 Ma, the australopithecines are among several possible ancestors of the genus *Homo*. They exhibit both human and ape characteristics, with a cranial capacity of around 600 cc. Some authorities have classified them in two types, “robust” and “gracile,” but the continuing variety exhibited by newly found specimens indicates that there was a wide range of types of australopithecines and other early hominins living in East Africa at the time. In addition to the five species mentioned here, other proposed species named so far include, *Au. boisei*, *Au. garhi*, *Au. paranthropus*, *Au. prometheus*, and *Au. robustus*.

***Australopithecus afarensis***: the best-known species of australopithecines, known from remains of several individuals, including the famous specimen named Lucy. Found in East Africa, particularly near the border of Ethiopia and Tanzania, the remains have generally been dated as being between 3 and 4 million years old. Research indicates that *Au. afarensis* could walk upright because the foot bone exhibits an arch similar to that of modern humans. See also **Middle Awash**.

***Australopithecus africanus***: a well-known species of australopithecines, known from several sites in Southern Africa. Although anatomically similar to *Au. afarensis*, it had a larger brain and smaller teeth. *Au. africanus* is probably not a direct ancestor of *H. sapiens*. Since most of the specimens were found in caves, its dating is problematic, but it probably lived between 3.3 and 2.1 Ma.

***Australopithecus anamensis***: an early australopithecine, known from specimens found in the Middle Awash and in Kenya; about 4.1 Ma.

***Australopithecus bahrelghazali***: a species of australopithecine hominins, known from several skull and dental fragments dated between 3.5 and 3.0 Ma, about the same age as *Au. deyiremeda* and *Kenyanthropus platyops*; Chad.

***Australopithecus deyiremeda***: a proposed new hominin species, based on a 2015 description of a jaw found in Ethiopia, dated between 3.5 and Ma.

***Australopithecus sediba***: a possible human relative from around 2 Ma, known from two almost complete skeletons found in 2008 near the Malapa Cave, north of Johannesburg, South Africa. A significant find for being possibly the only hominin specimen known between the *Au. afarensis* known as Lucy (about 3.2 Ma) and the *Homo erectus* known as Turkana Boy (about 1.5 Ma). The disputed dates proposed for the more recent discovery *H. naledi* vary between 2.5 and 0.9 Ma.

***Austroptyctodus gardineri***: See **Gogo Formation**.

**autapomorphy**: a distinctive derived character possessed uniquely by a particular lineage and not possessed by others in comparison; see also **synapomorphy**.

**autochthonous**: referring to an assemblage of fossils preserved undisturbed in their life position and location; see also **taphocoenosis**.



***Avalofractus***: an Ediacaran genus of rangeomorphs; 2 inches long, its alternating fern-like fronds branched off from a central stalk; known only from the Avalon Peninsula, Newfoundland, Canada.

**Aves**: a group of winged vertebrates, almost all capable of flight to some degree. Although their origins and line of descent are still debated, the current consensus is that birds evolved from feathered dinosaurs. The Enantiornithiformes are the earliest large group of primitive birds, but others are ***Confuciusornis*** (130–125 Ma), ***Enaliornis*** (100–94 Ma), ***Ichthyornis*** (95–85 Ma), ***Hesperornis*** (84–78 Ma). See also ***Protoavis***.

***Aysheia***: a genus of Cambrian soft-bodied animals superficially resembling a caterpillar; one of the enigmatic animals of the Burgess Shale assemblage, possibly related to the modern Onychophora; its body consisted of 10 segments, each with a pair of appendages; North America and possibly China, early to middle Cambrian.

**Azhdarchidae**: a family of pterosaurs in the suborder Pterodactyloidea. Although several partial specimens may date back to the Early Cretaceous, it is known well only toward the end of the period. The family is known for very large species, including the leading candidates for largest pterosaur, *Quetzalcoatlus* and *Hatzegopteryx*, both of which had wingspans of about 40 feet. But a 2009 discovery of a cat-sized azhdarchoid in British Columbia (between 80 and 70 Ma) shows that some small pterosaurs were still competing with birds at the end of the Cretaceous. Global distribution, Early to Late Cretaceous.

# B

**background extinction** see **extinction**.

**Bacteria:** the major domain of prokaryotes, single-celled organisms without a defined nucleus. They are abundant in every environment from the Mariana Trench to the Himalayas, and there is even some evidence of bacteria on the surface of Mars. On Earth these microbes constitute a greater biomass than all other animals and plants combined. The earliest evidence of bacteria is cyanobacteria-like fossils 3.5 billion years old. See also **Archaea** and **Eukaryota**.

**Bactrites:** a genus of nautiloid cephalopods in the order Bactritida; generally straight-shelled, it may have been ancestral to the ammonoids and coleoids, and was also one of the few nautiloids that survived the end-Permian extinction; global distribution, Early Devonian to Early Triassic.

**Baculites:** “walking stick,” an unusual genus of large orthocone ammonoids in the order Ammonitida and superfamily Turrilitoidea. Widespread in the Late Cretaceous, *Baculites* evidently lived in large shoals, although not so numerous as the earlier orthocerid nautiloids that form key Ordovician beds worldwide. It is very similar in appearance to the orthocerids but is differentiated by a relatively simple suture pattern. From 6 inches to 6 feet long and sexually dimorphic, the male baculitids average less than half the size of the females. In cross-section it is oval and often found so because the fossil shell fractures easily. The genus contains many index fossils for the Western Interior of North America, such as *B. clinolobatus* of the Pierre Shale (69 Ma). Cosmopolitan, Cretaceous.

**Bahariasaurus:** a genus of large but swift ceratosaur dinosaurs about the same size as *Tyrannosaurus rex* and *Carcharodontosaurus*; discovered in 1924 by Ernst Strömer but lost with his other specimens in 1944; see also *Spinosaurus* and *Deltadromeus*; North Africa, Late Cretaceous, about 95 Ma.

**Balaenidae:** a still-extant family of whales in the suborder Mysticeti, including the right and bowhead whales; reaching lengths over 50 feet and weighing up to 100 tons, the balaenids are widespread in temperate and polar waters; Miocene to Recent.

**Balaenoptera:** a still-extant genus of mysticete whales in the family Balaenopteridae; its eight living species include the blue, fin, and minke whales; several fossil species are known, including *B. cephalus*, which was formerly thought to be in the gray whale's genus (*Eschrichtius*); Miocene to Recent.

**Balcoracania:** an unusual genus of redlichiid trilobites in the family Emuellidae; it is less than an inch long, with a semicircular cephalon; its most striking feature is a high number of thoracic segments (almost 100 in *B. dailyi*), some with pleural spines as long as the two genal spines; Australia and Antarctica, early Cambrian.

**Balizoma variolaris:** the type species of the genus, phacopid trilobites in the family Encrinuridae; with strikingly coarse tubercles on the cephalon, it is one of several "strawberry-headed" genera; Europe and North America, restricted to Silurian.

**Baltica:** the name given to the land mass that is now Northern Europe when it was a separate continent from the Cambrian to the Middle Ordovician.

**Baltoniodus triangularis:** a species of conodonts in the family Balognathidae; its first appearance marks the beginning of the Middle Ordovician at 470 Ma; China.

**Baluchitherium:** see *Paraceratherium*.

**Bambiraptor feinbergi:** a species of Late Cretaceous dromaeosaurs, related to velociraptors; 3 feet long and delicately boned, it was bipedal and is notable for its long, wing-like arms; known only from a single complete skeleton found in 1994 at Choteau, Montana, possibly a juvenile; United States 75 Ma.

**Banffia:** a genus of primitive animals placed tentatively in the phylum Vetulicolia; although it is known from hundreds of specimens from the Burgess Shale, its classification is unsettled; about 4 inches long, its oval body and flat tail are twisted; Canada, middle Cambrian, 508 Ma.

**Bangiomorpha pubescens:** a species of red algae in the order Bangiales; the earliest-known complex multicellular organism; also the earliest known example of sexual reproduction, as evidenced by its differential spore and gamete formation; Canada, Mesoproterozoic, 1200 Ma.

**Bankia:** a genus of shipworms, marine bivalve mollusks in the family Teredinidae; global distribution, Early Jurassic to Recent.

**Baragwanathia:** a genus of primitive plants in the order Drepanophycales; the oldest known lycopod club moss and one of the first vascular plants; known best from Australia but global distribution, late Silurian to Early Devonian.

**Barbourofelis:** a genus of nimravid carnivorous mammals in the family Barbourofelidae; muscular, leopard-sized predators, the Barbourofelidae were one

of the groups known as false sabertooth cats; they were generally smaller and more primitive than the true felids; Miocene to Pliocene, Western North America.

**barnacles:** see **Cirripedia**.

**Barychilina:** a genus of ostracods in the order Metacopida; Silurian to Carboniferous.

**Barylambdidae:** a small family of pantodont mammals in the extinct order Cimolesta; they were herbivorous and tapir-like, the largest the size of a small horse; Paleocene to early Eocene.

**Baryonyx:** “heavy claw,” a genus of theropod dinosaurs in the family Spinosauridae, very similar to *Suchomimus*. About 25 feet long and weighing more than a ton, it was characterized by a large claw on its first finger and a triangular nasal crest. The baryonychines differed from most spinosaurids in having no dorsal fin or sail, and their long, narrow gharial-like snout indicates that they were at least partly fish-eaters. England and Iberian Peninsula, Early Cretaceous, 130–125 Ma.

**Basilosaurus:** a genus of archaeocete whales in the family Basilosauridae, closely related to the slightly earlier protocetids. Fully aquatic, *Basilosaurus* is characterized by a completely flexible backbone for efficient propulsion and by vestigial external hindlimbs too small to be used for swimming. It reached lengths of up to 40 to 65 feet and was the largest marine animal of the late Eocene. Africa and North America, Eocene.

**Batesian mimicry:** the name given to camouflaging structural mimicry used for protection from predation. The mimicking organism (usually uncommon but good-tasting) closely resembles another that predators have learned to avoid because, although abundant, it is foul-tasting, venomous, or stinging. First analyzed and explained by Henry W. Bates in the 1860s, it is observed throughout the plant and animal domain but is most common in invertebrates. A related kind of deception called Müllerian mimicry involves two distasteful or poisonous species that have evolved to resemble each other. A famous example of Müllerian mimicry is the case of *Danaus plexippus* (monarch butterfly) and *Limenitis archippus* (viceroy), which were long thought to be in a Batesian relationship until the viceroy was found to be also unpalatable to predators; research continues, however, with conflicting reports. Mimicry is difficult to identify in the fossil record because it usually involves surface coloration, scent, or sound.

**Bathornithidae:** a family of birds in the order Cariamiformes; generally flightless, the family also includes at least one genus capable of flight, *Neocathartes*; closely related to the Phorusrhacidae and to the still-extant seriemas; North America, middle Eocene to early Miocene.

**Batoidea:** a superorder of chondrichthyan fish in the subclass Elasmobranchii, including the skates, rays, and sawfish; generally benthic, except for the pelagic manta rays; characterized by expanded pectoral fins which, especially in the skates

and rays, resemble wings; an example of convergent evolution compared to the unrelated rhenanid placoderms (e.g., *Gemündina*), which also had expanded pectoral fins; global distribution, Early Triassic to Recent.

**Batrachia:** the clade that includes the salamanders and the modern frogs, the Anura.

**Beecher's Trilobite Bed:** a Konservat-Lagerstätte near Rome, New York. It is in a stratum of the deep-ocean Frankfort Shale, dated at about 445 Ma, that contains a remarkable assemblage of about thirty Ordovician animals, many pyritized (replaced by iron sulfide). It is notable for preserving many soft-tissue features of trilobites (especially *Cryptolithus*, *Triarthrus*, and larval *Cornuproetus*) and other marine animals. Extensively explored by Charles Beecher in 1893, the site was thoroughly excavated by a large team in 1989. North America, Late Ordovician.

**Beelzebufo:** a genus of large toads in the still-extant family Leptodactylidae, related to the Ceratophryidae of South America. Many specimens have been found on Madagascar in strata dated around 70 Ma, after Africa and India had begun to separate from South America, isolating *Beelzebufo* from its ceratophryid cousins. Up to 16 inches long and among the largest of all frogs, it probably bore bony scutes on its head. Madagascar, Late Cretaceous.

**Beipiaosaurus inexpectus:** a genus of feathered theropod dinosaurs in the superfamily Therizinosauroidea, known from two individuals of about 120 Ma. From 6 to 7 feet long with 4-inch claws and stiff, narrow proto-feathers, it probably did not fly. Although a theropod, it seems to have adapted to a herbivorous diet. It is one of several feathered dinosaurs in the Jehol biota; China, Early Cretaceous, 120 Ma.

**Beishanlong grandis:** a species of ostrich-shaped dinosaurs in the family Deinocheiridae; one of the largest ornithomimosaur known, more than 25 feet long and weighing 1.5 tons, it had digging claws and powerful forelimbs; southern Gobi Desert, Early Cretaceous, 110 Ma.

**Belantsea:** a genus of chondrichthyan fish in the family Petalodontidae. It was 2–3 feet long, deep-bodied with large pectoral and ventral fins but a small tail fin. *Belantsea*'s body plan suggests it was a slow swimmer. It is characterized by a bulbous shape and an unusual petalodont dentition which enabled it to eat crinoids and encrusting organisms like sponges. Montana, Early Carboniferous, about 350 Ma.

**Belemnitida:** “dart-shape,” a large order of Mesozoic squid-like cephalopods in the still-extant subclass Coleoidea and extinct superorder Belemnioidea. Belemnites were from 4 to 8 inches long and had ten arms; like other cephalopods, they had an ink sac, beak, tentacles, and large eyes. Unlike other cephalopods, they had a bullet-shaped calcitic internal structure called a rostrum, which was often fossilized. The belemnites appeared in the Triassic and were widespread in the Jurassic and Early Cretaceous. All belemnoids became extinct at the end of the Cretaceous, but they are closely related to modern cuttlefish.

***Bellinurus***: an extinct genus of freshwater arthropods in the order Xiphosurida; though less than 2 inches long, it is related to modern horseshoe crabs (see *Limulus*); Europe, Devonian to Carboniferous.

**bellerophontids**: a large group of sea snails, gastropods in the order Archaeogastropoda (or possibly monoplacophorans); they were generally coiled symmetrically; up to 2 inches long, the type genus is *Bellerophon*; Ordovician to Triassic.

**Bennettitales**: a group of small cycadeoid or anthophyte trees, growing to about 7 feet high; their leaves resemble cycads, but they are probably not related; widespread Triassic to Cretaceous and surviving sparsely to the Oligocene.

**benthic**: living at the lowest level of a body of water, from eulittoral to abyssal, as opposed to living in the water column; generally referring to oceans but also to lakes and rivers; see also **nektic** and **nektobenthic**.

***Bernissartia***: a genus of small, semi-aquatic crocodylomorphs in the family Bernissartiidae; similar to modern crocodiles, it is considered a neosuchian; it was less than 3 feet long, and its dentition was adapted to crushing shellfish and crustaceans but also to catching fish; named for specimens found at the Bernissart mine in Belgium; North America and Europe, Early Cretaceous, 135–125 Ma.

**Bernissart site**: a Belgian coal mine where many significant fossils of the Early Cretaceous have been found, especially important for the specimens of iguanodonts found there in the 1870s.

***Berriasella jacobi***: a species of ammonoids whose first appearance marks the beginning of the Early Cretaceous at 145.0 Ma; Europe.

**Bertie Waterline**: name given to several upper Silurian deposits in New York that contain well-preserved arthropod and plant fossils, known especially for *Eurypterus remipes*; United States, late Silurian.

***Bethia serraticulma***: a species of brachiopods placed variously in the orders Orthida and Strophomenida, known only from one specimen found in a carbonate nodule (see **Herefordshire Nodules**); the digital reconstruction of *Bethia* shows excellent soft-part morphology; England, Silurian.

**Beyrichicopina**: a suborder of dimorphic ostracods in the extinct order Palaeocopida; North America and Europe, Ordovician to Early Mississippian.

**Biarmosuchia**: a suborder of basal therapsids, including *Biarmosuchus* and *Eotitanosuchus*; generally similar to sphenacodonts, with long canine teeth; Russia, early Permian.

**Bighorn Basin**: an arid area in northern Wyoming that is an important study site for the transition from Paleocene to Eocene; about 10,000 square kilometers in area, notable for the plant life and the large numbers of mammal species recorded in its varied strata.

**bilateralism:** having a definite and symmetrical left and right side, as opposed to amorphous animals like sponges and jellyfish.

**bilaterians:** the bilaterally symmetrical animals, excluding sponges, cnidarians, placozoans, and ctenophores; characterized by bilateral symmetry and an anterior-posterior body orientation; the oldest known specimen may be microfossil embryos from an Ediacaran deposit in China (see *Vernanimalcula guizhouena*), thought to be 580 million years old; these are also the earliest-known embryos of complex animals; Ediacaran to Recent.

**Billingsellida:** an order of articulate brachiopods in the class Strophomenata; one of the first and most primitive articulate brachiopods, it is characterized by a wide hinge-line; middle Cambrian to Middle Ordovician.

**biocoenosis:** an assemblage of organisms living together at one time, an ecological community.

**biochron:** a period of time represented by a relatively small biostratigraphic zone, one characterized by a particular fauna or flora.

**biosphere:** 1. the area favorable for the occupation of living organisms, including the lithosphere, hydrosphere, and atmosphere. 2. All the living organisms of the Earth and its atmosphere.

**biostratigraphy:** the science of correlating geographically separated rock strata by identifying the biotic content and time relations of the strata; it is based on faunal succession, the process in which species change over time.

**biostratinomy:** a subsection of taphonomy, dealing with the orientation of the remains of an organism and what it says of the processes the organism experienced between its death and its burial, such as transportation and chemical change.

**biota:** the total fauna and flora living or preserved as fossils within a certain area or period of time.

**biozone:** a stratigraphic unit of specific geological strata defined by various combinations of taxa present in the strata.

**bird-hipped dinosaur:** general term referring to the ornithischian dinosaurs.

**birds:** see *Aves*.

***Birgeria americana*:** a species of large predatory fish in the family Birgeriidae, known from a partial skull described in 2017; a bony fish about 7 feet long, it lived in water warmer than previously thought possible for the development of eggs; Nevada, United States, Early Triassic, 251 Ma.

***Bison priscus*:** a species of large-horned bison of North America; its extinction in the late Pleistocene was probably related to human activity.

***Biston betularia*:** the peppered moth, a still-extant species of lepidopterans in the family Geometridae. Two forms (*B. b. f. typica* and *B. b. f. carbonaria*) have evolved

in the Holocene and have been studied in detail since the 1850s. Their variation in color over two centuries, caused by industrial melanism, results in differential predation by birds and is now generally accepted as a clear example of Darwinian natural selection in action. Global distribution, Recent.

**bitheca:** a smaller theca that appears in many graptolites, alternately on both sides of the autothecae.

***Bithecocamara:*** an enigmatic genus of pterobranch encrusting graptolites in the order Camaroidea; the only camaroid with bithecae; Baltic, Ordovician.

**bivalves:** mollusks that typically have shells with two hinged valves, not related to the two-valved brachiopods, which are different organisms that have developed a similar shell because of a similar lifestyle, an example of convergent evolution. The two valves of a bivalve are usually symmetrical, but there are several exceptions. The rudists, for example, are horn- or tube-shaped bivalves whose external morphology seems to bear no similarity to other bivalves. And shipworms (see ***Bankia*** and ***Teredo***) have only a pair of very small shells, at the anterior end of a tube-like body, with which they bore through wood. Global distribution, early Cambrian to Recent.

***Bjuvia:*** a genus of short trees with a crown of broad lanceolate leaves atop a squat, branchless trunk; Europe, Early Triassic.

**Blackberry Hill:** a Lagerstätte in Wisconsin consisting of several quarries; it is best-known for its extensive trace fossils, mostly trackways left in a shallow-water sandstone formation; notable also for body fossils of a phyllocarid and a euthycarcinoid (for the latter, see ***Mosineia***), considered by some to be the earliest body fossils of a land animal; United States, middle or late Cambrian.

**Blastoidea:** a class of sessile pelmatozoan echinoderms in the subphylum Blastozoa; they are sometimes called sea buds because of their nut shape; commonly stacked, they were attached to the sea floor on a stem; global distribution, Ordovician to late Permian.

**Blastozoa:** an extinct subphylum of echinoderms; characterized by hydrospires, small folds beneath the lancet plates; Cambrian to Permian.

**Blattodea:** the order of insects that includes cockroaches and termites; the ancestors of cockroaches are known from the Carboniferous, and modern roaches appeared in the Triassic; termites probably evolved in the Permian, but specimens are known only as far back as the Early Cretaceous; also called Blattoptera.

***Blikanasaurus:*** a proposed genus of sauropodomorph dinosaurs, known only from one limb bone; South Africa, Late Triassic, 210–202 Ma.

**Bobasatraniidae:** a small family of deep-bodied chondrosteian fish, in the crown group of the Actinopterygii; characterized by a diamond-shaped body, a forked tail fin, and long, thin pectoral fins; North America, Europe, and Africa; late Permian to Early Triassic.



**body plan:** see **Cambrian** and **Ediacaran biota**.

**bone bed:** a fossil site that contains a large number of animal macrofossils. Of special importance are bone beds where many animals died abruptly, leaving whole-body fossils. Those where whole-body fossils of many different species are found together raise questions about the cause of the deaths, from flash floods to accumulations of poisonous substances. The Messel Shale Pit, for instance, contains many different types of animals, including birds and bats, and also turtles that died in the act of copulating; poisonous gases have been the most common cause suggested. Toxic algae have been proposed as a possible cause of the deaths of several layers of fossils in the Maevarano site in Madagascar. No conclusive evidence has been found in either case.

**bony fish:** see **Osteichthyes**.

***Bootherium nivalens*:** a species of musk ox in North America whose extinction in the late Pleistocene may have been caused by humans.

***Borealopelta*:** a monospecific genus of nodosaurid dinosaurs, known from a whole-body specimen described in 2017. Recovered from an oil sands mine in Alberta, *B. markmitchelli* is the best-preserved specimen known of an ankylosaur, with soft tissue as well as its armor (many sharp-pointed osteoderms and two long shoulder spines) in life-position. Like other nodosaurids, it has no club at the end of the tail. The keratin in skin and scales indicates countershading, with a dark reddish-brown coloration above and a lighter underside. Canada, Early Cretaceous, 110 Ma.

***Borealosuchus*:** a genus of crocodylians widespread in North America from the Late Cretaceous up to the middle Eocene; about 9 feet long, it is one of several genera of crocodylians that survived the end-Cretaceous extinction.

**Boskovice Furrow:** a large site in Moravia that contains a series of deposits in upper Carboniferous and lower Permian strata; important for tetrapods from the Permian strata, especially in the family **Discosauriscidae**, *q.v.*; Czech Republic.

***Bostrychoceras*:** a genus of heteromorph ammonoids in the order Ammonitida and family Nostoceratidae; loosely coiled but slightly tighter than its cousin *Nostoceras*, its shell is covered with fine, dense ribs and forms a long, slightly open helical spire; Europe, Africa, and North America; known only from the Campanian Stage near the end of the Cretaceous.

***Bothriocidaris*:** an unresolved genus of echinoderms, generally considered an echinoid; it was globular and was covered with spines and tube feet; known only from Upper Ordovician deposits in Estonia, Scotland, and North America.

***Bothriolepis*:** a genus of heavily-armored placoderm fish in the order Antiarchi, bottom-dwelling and mainly freshwater rather than marine. Generally 1 foot long, with some almost 3 feet, *Bothriolepis* had a slender and somewhat flattened body, and was notable for a pair of long, spine-like pectoral fins with small spines on them. Its eyes were located on the top of the headshield, along with a light-receptive

pineal eye. It had heavy anterior armor but no posterior armor, not even scales. Widespread, abundant, and diverse in the Middle to Late Devonian, it became extinct with all other placoderms at the end of the Devonian.

**Botryococcus:** a still-extant genus of one-celled freshwater algae that can also grow in brackish water environments; notable for a high hydrocarbon content in and outside its thick, waxy cell walls, held together by a lipid biofilm; useful in interpreting paleoenvironments; Triassic to Recent.

**Bovidae:** a family of horned, cloven-hoofed, ruminant mammals in the order Artiodactyla, including cattle, sheep, bison, goats, buffaloes, and antelopes; distinguished from the Cervidae by their hollow, non-deciduous, unbranched horns, all male bovids and two-thirds of the females have two or more horns; the earliest-known genus is *Eotragus*, which appeared in Eurasia around 20 Ma; global distribution, early Miocene to Recent.

**bowfin:** see *Amia calva*.

**Brachiopoda:** “arm foot,” a phylum of solitary marine invertebrates characterized by a dorsal (brachial) and a ventral (pedicle) valve; a pedicle, a muscular extension of the body wall used by most genera to attach to the substrate; and an internal lophophore, which is bilobate and typically horseshoe-shaped but often in long loops. In some articulate brachiopods, the two lobes of the lophophore are supported by calcareous support structures called brachidia, which are attached to the brachial valve (see **Spiriferida**).

Called lampshells, brachiopods are superficially similar to bivalves but are not mollusks; the two halves of their shells are not mirror-images of each other, as in bivalves, but symmetrical, just in a different plane. The internal body parts are relatively sparse compared to the those of the bivalves. Most fossil brachiopods are 1–3 inches wide, and the largest known is about 8 inches wide. See also **punctate**.

Several genera were epi-planktic and a few were nekctic, swimming in the style of scallops. They were widespread in the Paleozoic, but only one-third of the genera survived the end-Permian extinction. Although the bivalve mollusks have become dominant, brachiopods have continued to increase slightly in number in the Cenozoic, with about 250 species of brachiopods still extant, the most famous being *Lingula*, which has remained essentially unchanged in shape since the Cambrian. Extinct brachiopods are significant index fossils in the Paleozoic because of their broad distribution and their abundance and diversity at several taxonomic levels, especially for the Devonian and Carboniferous. Cambrian to Recent.

**Brachiosaurus:** a genus of titanosaurian sauropodomorph dinosaurs in the family Brachiosauridae; estimated at 85 feet long and 32 tons, it is one of the largest sauropods; its forelimbs are relatively elongated, and its neck is very long; United States, Europe, and Africa; Jurassic.

**Brachyaspidion:** a genus of small trilobites in the order Ptychopariida; *B. microps* (1 cm) and *B. sulcatum* (4 cm) are among the dozens of trilobites in the Wheeler Shale Lagerstätte; North America, middle Cambrian.

***Brachyceratops***: an obscure genus of ceratopsian dinosaurs, known only from partial juvenile specimens found in Campanian strata in Montana and Alberta; North America, Late Cretaceous.

**brachydont dentition**: low-crowned teeth with long, narrow roots; they do not grow throughout life in all animals, but do in some, such as rodents.

***Brachylophosaurus***: a genus of hadrosaurid ornithischian dinosaurs in the subfamily Saurolophinae; the type species is *B. canadensis*, but the genus is known from many skeletons and casts showing soft-tissue detail, including tendons and hundreds of thin tracks that have been interpreted as evidence of stomach parasites; Montana and Alberta, Late Cretaceous, 80–75 Ma.

***Brachysaurus***: synonym: *Prognathodon*.

**Brachythoraci**: the largest suborder of armored arthrodires; the early Brachythoraci were relatively small, like the agnathans, but the best-known was the gigantic *Dunkleosteus*, which grew to 30 feet long; like all other placoderms, they became extinct at the end of the Devonian.

***Bradgatia***: a monospecific genus of Ediacaran fossils, possibly a rangeomorph; dated at about 570 Ma, *B. linfordensis* is a small, bush-like petalage, a cluster of 6–8 petals a few inches high; found especially in the Ediacaran assemblages at Mistaken Point and Charnwood Forest; Canada and England, Ediacaran.

**Bradoriida**: an order of basal crustaceans widespread in the early Paleozoic; they were small, with a bivalved carapace over the head and body; global distribution, Cambrian to Ordovician.

**bradyodont**: having paired hard, enameled toothplates in the upper and lower jaw, used to crush prey; characterizes several groups of fish that flourished in the Carboniferous and are sometimes referred to as Bradyodonti; Late Devonian to Permian.

**Branchiopoda**: “gill foot,” a still-extant class of small, generally freshwater, crustaceans. The class includes several living groups like the fairy shrimp (Anostraca), which are as long as 7 inches. Branchiopods have a long (see *Lepidocaris rhyniensis*) but incomplete fossil record, and they may be more closely related to insects than to other crustaceans. They are thought to have originated in a marine environment but to have adapted to freshwater environments because of competition. Late Cambrian to Recent.

**branchial**: referring to gills.

**branchiostegal**: having covered gills.

**Branchiostomiformes**: see **Cephalochordata**.

***Brontosaurus***: a contentious genus of sauropod dinosaurs; long considered a junior synonym of *Apatosaurus*, *Brontosaurus* is now considered by some to be a separate genus; for description, see *Apatosaurus*.

**Brontotheriidae:** “thunder animal,” a large family of herbivorous perissodactyl mammals, a sister group to the Equidae in the suborder Hippomorpha. Also called titanotheres, they were almost elephant-sized, ranging in height from 2 to 9 feet. They are marked especially by a variety of bony frontal horns, even with a pair of blunt nasal horns in *Megacerops*. Although similar in appearance to rhinoceroses, they are more closely related to horses. The earliest brontothere, the dog-sized *Eotitanops*, appeared in the early Eocene. North America, Europe, and Asia; early to late Eocene.

**bryophytes:** “moss plant,” a common name for the group of primitive land plants that includes the mosses (clade Bryophyta), hornworts (clade Anthocerotophyta), and liverworts (clade Marchantiophyta). Not vascular and lacking true roots and leaves, the bryophytes reproduce by spores. Molecular phylogenetic research indicates that the bryophytes were the earliest land plants, probably appearing in the Ediacaran. The earliest definitive bryophytic fossils (such as *Sporogonites*) are dated Early Devonian. See also *Protosalvinia*.

**Bryozoa:** “moss animals,” a still-extant phylum of small colonial animals that secrete calcified skeletons around the individual organisms’ bodies, a process seen also in reef-building corals. Bryozoa is the only phylum of animals that are wholly colonial. The bryozoans are the only phylum with an extensive fossil record to have arisen later than the Cambrian — the earliest-known bryozoan fossils date from the Early Ordovician. Bryozoans are one of the dominant groups of Paleozoic fossils, with tens of thousands of named species. Only a few families survived the end-Permian extinction, but there are still about 6,000 living species.

***Bubalus cebuensis*:** an extinct species of dwarf water buffalo, less than 3 feet high and weighing about 350 pounds; descended from much larger buffalo, they experienced island dwarfism when stranded on the small Philippine island of Cebu by a rising sea level between 100,000 and 20,000 years ago; see also *B. mindoroensis*.

***Bubalus mindoroensis*:** the tamaraw, a still-extant species of dwarf water buffalo found on the Philippine island of Mindoro; an example of island dwarfism, being descended from larger buffalo stranded on the island by rising sea levels about 20,000 years ago.

***Buchia*:** a genus of edentulous bivalves in the superfamily Buchioidea; they have a slender shape, with the left valve larger than the right valve; known around the Pacific Rim, Jurassic to Cretaceous.

***Bumastus*:** a genus of large (up to 6 inches) bottom-dwelling trilobites in the order Corynexochida and family Styginidae; notable for a smooth, rounded, isopygous body and well-developed compound eyes; global distribution, Early Ordovician to late Silurian.

**bunodont dentition:** low-crowned, conical or rounded teeth with ridged cusps; separate, often quadrate in shape; typical especially of early artiodactyl and suiform mammals.

**Burgess Shale:** name given to one of the most important Konservat-Lagerstätten, a calcareous black shale formation dated at 508 Ma. Located near Kicking Horse Pass in the Rocky Mountains of eastern British Columbia, the formation is unique in containing a surprisingly well-preserved assemblage of soft-bodied animals from the middle Cambrian. The fossils are allochthonous, probably having been removed from their living location by a series of mudslides. The assemblage evidently represents a complete marine community that includes both nektic and benthic animals. The great diversity and excellent preservation of these very unusual fossils — discovered in 1909 by Charles Walcott — provides a rare view of this period of rapid diversification of animal species. Several specimens are the only known representatives of phyla that are unlike any modern phyla. See also **Chengjiang biota**. Canada, middle Cambrian.

**byssus:** a bundle of tough, hairlike filaments commonly used by bivalve mollusks to attach themselves to objects, usually rocks or other hard substrate but sometimes, as with *Modiolus*, to detritus in sediment.

# C

**Caelifera:** the grasshoppers and locusts, a suborder of chewing herbivorous insects in the order Orthoptera; mostly ground-dwelling and stridulatory, with strong hind-legs and wings; global distribution, Early Triassic to Recent.

**Caenolestidae:** a family of small South American marsupials in the order Paucituberculata; commonly called shrew opossums and rat opossums, they were once abundant but are now confined to small regions in the Andes Mountains; late Oligocene to Recent.

**Cainotheriidae:** a family of small, herbivorous artiodactyl mammals in the suborder Tylopoda and extinct superfamily Anoplotheroidea; characterized by a rabbit-like, strongly curved back, they resemble modern hares and rabbits but are unrelated; they diversified rapidly in the Eocene, with only a few persisting into the Oligocene, but then diversified again before disappearing by the end of the period; Europe, Eocene to Oligocene.

**Calamitales:** an order of arborescent sphenopsid plants; resembling giant horse-tails, they were reed-like plants with horizontal rhizomes and segmented and grooved stems; up to 100 feet high and 12 inches in diameter; global distribution, Late Devonian to Permian.

**Calcarea:** a class of small marine sponges; the only sponges with spicules of calcium carbonate, they are found mainly in shallow tropical waters but have been found as deep as 4,000 feet; global distribution, early Cambrian to Recent.

**Calcaronea:** a still-extant subclass of sponges in the class Calcarea, with three- or four-rayed spicules; they may have appeared as early as the Cambrian, were especially prominent in the Cretaceous, and still exist worldwide.

**Calceola:** a genus of solitary rugose corals in the family Goniophyllidae; known as slipper coral because of its shape, *Calceola* was semicircular and rested on the sea floor, convex side down; Northern Europe, Early to Middle Devonian.

**Calcinea:** a still-extant, probably paraphyletic subclass of sponges in the class Calcarea; a generally spreading habit, usually yellow or red, with regular three- or four-rayed spicules; global distribution, Permian to Recent.

**Calclamna:** a genus of sea cucumbers, echinozoans in the class Holothuroidea and extinct family Calclamnidae; Europe and Asia, Early Triassic to Cretaceous.

**Callavia:** a monospecific genus of early Cambrian olenellid trilobites; *C. broegeri* is known from several sites in northeastern North America.

**Callistophytales:** an order of vinelike pteridosperms widespread in the late Paleozoic; North America, Europe, and Asia; Carboniferous to Permian.

**Callograptus salteri:** a species of irregularly branching graptolites in the order Dendroidea; characterized by a fine net of branches with many small thecae; Europe, Asia, and North America; late Cambrian to Early Carboniferous.

**Calsoyasuchus:** see *Goniopholis*.

**Calymene:** a genus of phacopid trilobites; some well-preserved specimens of *Calymene* and its relative *Flexicalymene* show appendages and soft body parts; specimens are frequently found enroled, rolled into a ball in the manner of the modern terrestrial isopods; global distribution, Ordovician to Devonian.

**calyx:** primarily, the central cup-shaped body of crinoids, resting on a stem, with arms extending outward and upward; also, the cup formed by the sepals of a flower.

**Camarasaurus:** “chambered lizard,” a genus of very large herbivorous dinosaurs, the most common sauropod of North America in the Late Jurassic. The largest species was about 75 feet long and weighed about 52 tons, with a relatively short neck. *Camarasaurus* is named for air sacs in the vertebrae that were connected to the lungs. Many specimens have been found in the Morrison Formation, some well-preserved. North America, Europe, and Africa; Late Jurassic to Early Cretaceous.

**Camaroidea:** an order of sessile encrusting graptolites known mainly from the Ordovician of the Baltic Sea area; characterized by thecae with a balloon-shaped base and vertical chimney; the best-known genus is *Bithecocamara*; Baltic and Siberia, late Cambrian to Early Ordovician.

**Cambaytherium:** a genus of early placental mammals in the family Cambaytheriidae, formerly placed in the Anthracobunidae; now considered a basal perissodactyl. It is known from several fragmentary specimens found in strata dated 54.5 Ma, when the Indian island continent was nearing Asia after splitting off from Gondwana. The size of a small pig, it has five digits and seems close to the ancestry of horses, rhinoceroses, and tapirs. Its discovery has led to the conclusion that perissodactyls evolved in Asia and spread to North America during the Eocene. Gujarat, India, early Eocene.

**Cambrian:** the first period of the Paleozoic Era, 541 to 485 Ma. Its macrofossil record is primarily marine, with just a few traces of early terrestrial invertebrates.

The marine environment was dominated at first by reef-building Archaeocyatha and other small animals, and then increasingly by primitive deuterostomes. Some of the basic animal body plans had appeared in the Ediacaran, but most are known first from the early Cambrian, probably between 535 and 530 Ma. These early species diverged morphologically in a short period of time in what is known as the Cambrian Explosion. The first primitive marine vertebrates (see *Mylokunmingia*, *Haikouichthys*, and *Zhongjianichthys*) appeared near the end of this brief time.

**Camelidae:** an extant family of even-toed ungulates in the suborder Tylopoda. The first camelids (see *Protylopus*) appeared in North America about 45 Ma and evolved into several distinct genera, especially in the late Eocene and early Miocene. They were known only in North America until the early Pliocene, 4 to 5 Ma, when some families crossed the new land bridge to South America, developing there into the modern guanacos, llamas, vicuñas, and alpacas. Then in the early Pleistocene, North American camelids crossed the newly dry Bering Strait into Asia, where they developed into the modern camels. Camelids disappeared from North America soon afterward.

**Camelops:** a late genus of camels, one of a dozen North American camelids that became extinct at the end of the Pleistocene.

**Camerata:** a large extinct subclass of stalked crinoids. Its two main orders appeared in the Middle Ordovician; the Diplobathrida disappeared in the Carboniferous, while the Monobathrida continued up to the end-Permian extinction; the small order Cladida is restricted to the Devonian. All are characterized by a long, flexible stem, rigidly sutured calyx, and more than ten free arms. Middle Ordovician to late Permian.

**Cameroceras:** see **Endoceratidae**.

**Camptosaurus:** a genus of mid-sized herbivorous dinosaurs in the order Ornithomimiformes, formerly called *Camptonotus*. About 26 feet long, it had a very small head and small, flat teeth, and is estimated to have weighed up to 1 ton. Clawless and basically bipedal, it had four toes on each pes and was a good runner. North America and Europe, Early Jurassic.

**Caninae:** a subfamily of carnivorous mammals in the order Carnivora and family Canidae; it includes the dogs, wolves, foxes, coyotes, dingoes, and jackals, as well as their most recent ancestors, such as *Leptocyon*; Oligocene to Recent.

**canine:** conical mammal teeth between the incisors and premolars, adapted for grasping and piercing prey; generally two pairs, upper and lower, but vestigial in many herbivores.

**Caninia:** a genus of large, solitary rugose corals in the family Cyathopsidae; living mainly in shallow lagoons, it was often affected by storms; global distribution, Devonian to Permian.

**Canobius:** a genus of small palaeoniscid actinopterygian fish. Three inches long, it is notable for its vertical jaw suspension, as opposed to the diagonal arrangement of



other palaeoniscids. Its larger gape allowed it to swallow great volumes of plankton, catching them on its very small teeth, which grew even on its gills. Scotland, Early Carboniferous.

***Cantius***: a genus of early strepsirrhine adapiform primates in the family Notharctinae; lemur-like, it is known from numerous teeth and jaw fossils; North America and Europe, early Eocene.

***Capinatator***: “seizing swimmer,” a genus of large arrow worms in the phylum Chaetognatha; *C. praetermissus* is known from specimens found at the Burgess Shale site and described in 2017; it was 4 inches long and is characterized by two dozen mobile grasping spines on each side of its mouth, with which it captured prey; Canada, middle Cambrian, 508 Ma.

**Capitosauridae**: a family of temnospondyl tetrapods, generally considered primitive amphibians; cosmopolitan, Early to Late Triassic.

**Captorhinida**: a paraphyletic order of stem reptiles of the late Paleozoic; formerly called cotylosaurs; see **Pareiasauridae** and **Procolophonia**.

***Captorhinus***: a genus of small, lizard-like reptiles in the family Captorhinidae; it was specialized, characterized by a hooked snout with procumbent front teeth; its skull was 5 inches long and its limbs were slender; global distribution, early Permian.

**carapace**: the hard, protective dorsal body covering of many arthropods and some reptiles, such as turtles; it is composed of chitin or bony substances.

***Carbonicola***: a genus of vagrant freshwater clams in the family Anthracosiidae; formerly called *Anthracosia*; several short-lived species are index fossils in the British Coal Measures; Europe, Carboniferous.

**Carboniferous**: the fifth period of the Paleozoic Era, from 359 to 299 Ma. For North American strata, the Carboniferous is divided into two sub-periods: the Mississippian, from 359 to 323 Ma, and the Pennsylvanian, from 323 to 299 Ma; both the Mississippian and the Pennsylvanian are divided into Early, Middle, and Late epochs. The period saw the culmination of a long period of increasing levels of oxygen in the atmosphere, reaching as high as 35 percent. The Carboniferous is characterized globally by coal-bearing beds resulting from large forests. It was also marked by several periods of widespread glaciation, especially in the last half of the period and extending into the Permian. The seed ferns continued to be an important part of the flora, the first gymnosperms appeared and spread rapidly, and the conifers and ancestors of the cycads appeared near the end of the period. An important development for vertebrates was the evolution of the amniotes. Late in the Carboniferous, these later tetrapods diversified rapidly, one branch producing the first reptiles. Terrestrial arthropods and flora also increased greatly in diversity.

***Carcharodon***: a still-extant genus of large white sharks in the family Lamnidae; synonym: *Carcharocles*; the largest shark known to have lived was *C. megalodon*,

which may have grown to a length of more than 60 feet and became extinct only around 50,000 years ago; cosmopolitan, Miocene to Recent.

***Carcharodontosaurus saharicus***: a species of theropod dinosaurs in the family Carcharodontosauridae. Named for the resemblance of its serrated teeth to those of *Carcharodon*, it reached a length of almost 40 feet and was a top predator. It was as large as *Tyrannosaurus rex* but slightly smaller than *Spinosaurus*. Tunisia and Egypt, Late Cretaceous, 90 Ma.

***Cardiocephalus***: a genus of microsaurian lepospondyl amphibians in the family Gymnarthridae; it was lizard-like, with four short legs and a long tail, and is named for its heart-shaped head; North America, early to middle Permian.

***Cardioceras***: a genus of nektic ammonoids in the order Ammonitida and superfamily Stephanocerataceae; up to 10 inches across, it is notable for its strong ribs, evolute circular shell, and prominent crest on the margin; the first appearance of *C. redcliffense* defines the beginning of the Late Jurassic at 163.5; global distribution, Jurassic.

**carnassial teeth**: upper and lower cheek teeth in most carnivorous mammals, adapted for shearing flesh, as opposed to crushing or tearing.

**Carnivora**: a diverse order of placental mammals in the superorder Laurasiatheria. The primary suborders are the Caniformes, Feliformes, and Pinnipedia. The earliest were the Miacidae, which appeared in North America in the late Paleocene, and their descendants radiated rapidly throughout the world. Classified on the basis of dentition, some members of the order are omnivorous while others are herbivorous. Paleocene to Recent.

**carnosaurs**: traditionally, a polyphyletic group of many large carnivorous saurischian dinosaurs but now restricted to the allosaurs; a large head, a short neck, and generally short forelimbs are characteristic structures of the group; global distribution, Jurassic to Cretaceous.

***Carnotaurus***: a genus of large carnivorous dinosaurs in the family Abelisauridae, characterized by a large head, two short but stout horns above the eyes, relatively small teeth, and very small vestigial forelimbs; *C. sastrei* is the type species, known from a well-preserved skeleton found by Paul Sereno in Patagonia; Argentina, Late Cretaceous, 72–70 Ma.

***Carnufex carolinensis***: an ancestral crocodile, among the earliest crocodylomorphs, known from a North Carolina specimen described in 2015, with a skull, spine, and forelimbs. It was about 9 feet long; judging from size and weight distribution, it may have stood on its hind legs. Its diet consisted of early mammals and small armored reptiles. North America, Late Triassic, 231 Ma.

**carpoids**: see **Homalozoa**.

**cast**: casts are formed when original parts of an organism are dissolved and the resulting space is filled with sediment or other mineral matter.

***Castor canadensis***: the North American beaver, a genus of rodents in the family Castoridae; 3 feet long and almost extinct after centuries of trapping for its pelt, it has recovered; it has many subspecies but is not related to *Aplodontia*, the “mountain beaver”; North America, Miocene to Recent.

***Castorocauda lutasimilis***: a fish-eating species of Jurassic semi-aquatic mammaliaforms in the order Docodonta. It was similar to beavers and otters but not related to them. Recorded as the earliest semi-aquatic mammal, dated between 170 and 165 Ma, it is the largest known mammal of the Jurassic at 1–2 pounds and almost 2 feet long. It had webbed feet; a flat, beaver-like scaly tail; otter-like vertebrae; and teeth like those of a seal. Northern China, Middle Jurassic.

**Catarrhini**: an infraorder of anthropoid primates that includes men, apes, and Old-World monkeys (see also **Platyrrhini**). The Catarrhini are characterized by nostrils that face downwards; most have tails, but they are non-prehensile. They diverged from the Platyrrhini in the late Eocene or early Oligocene yet remained primarily alike because of parallel evolution. The Catarrhini are subdivided into Cercopithecidae (Old-World monkeys), Hominidae (humans, gorillas, chimpanzees, orangutans, and australopithecines), and Hylobatidae (gibbons). Eocene to Recent.

**catastrophism**: see **uniformitarianism**.

***Catenipora***: a large genus of tabulate corals in the family Halysitidae; Baltic, Late Ordovician to early Silurian.

***Cathaymyrus***: a genus of early Cambrian cephalochordates; similar to *Pikaia*, it is long and slender (1–2 inches) and seems to have a notochord in the depression along the center of its back; Chengjiang biota, China, 530–515 Ma.

***Catopithecus***: possibly the earliest-known primate; a squirrel-sized monkey known from several finds in the Fayum Depression, including tooth and skull fragments found in 1995; characterized by shovel-shaped upper front teeth, a flattened face, forward-looking eye sockets, and a fused forehead bone; the latter is a key difference between lemurs and the higher primates; all known specimens are dated at about 36 Ma; Egypt, late Eocene.

***Caudipteryx***: “tail feather,” a genus of theropod dinosaurs with considerable plumage, including a large tail fan. Although it was bird-like and the size of a peacock, its body was covered with only short feathers and it probably lacked the aerodynamic qualities required for flight. Dated at 125 Ma, it is one of several feathered dinosaurs in the Jehol biota. China, Early Cretaceous.

**Cavellinidae**: a family of Paleozoic ostracods in the order Platycopida and suborder Cytherelliformes; characterized by sexual dimorphism and a ridged shell surface; Silurian to Permian.

**Caytoniales**: an order of Mesozoic seed ferns, important because of their possible transitional relationship to the angiosperms; their four-part palmate leaves (form

genus *Sagenopteris*) are similar to some later flowering plants, and they bear a carpel-like case containing seeds (form genus *Caytonia*); a direct relationship is still unclear, however, and they may be gymnosperms; global distribution, Late Triassic to Early Cretaceous.

***Cebochoerus*:** a genus of basal artiodactyl mammals in the extinct superfamily Dichobunoidea and family Cebochoeridae; pig-like but unspecialized, the cebochoerids may have an ancestry in the little-known Helohyidae; Europe, middle Eocene to early Oligocene.

**cell division:** see **mitosis**.

**Cenophyticum:** term sometimes used for a paleobotanic division of time roughly corresponding to the Cenozoic Era and characterized by the plant life of the Cenozoic; the abundant angiosperm floras of the Late Cretaceous are also generally considered cenophytic.

**Cenozoic Era:** the third division of Phanerozoic geologic time, following the Paleozoic and Mesozoic and extending to the present.

**Centronellidina:** a suborder of articulate brachiopods in the order Terebratulida; characterized by a primitive loop structure and an incurving ventral beak; North and South America, Early Devonian to late Permian.

**Centrosaurinae:** a subfamily of horned ornithischian dinosaurs in the family Ceratopsidae; medium-sized, averaging less than 20 feet long, these herbivores ranged across Western North America from Alaska to Arizona, with at least one species, *Sinoceratops*, found in China in 2010; important especially for several embryos found in nest sites; North America, 84–66 Ma.

***Centrosaurus*:** a genus of ceratopsian dinosaurs in the subfamily Centrosaurinae; the type species *C. apertus* was found in southeastern Alberta, where great numbers of the genus have since been found; a medium-sized ceratopsian, it had a large nasal horn and several small horns on its frill, two of them pointing forward; the frill had large fenestrae; not related to *Kentrosaurus*, a stegosaur of the Late Jurassic; Canada, Late Cretaceous, 77–76 Ma.

***Cephalaspis*:** “head shield,” a genus of freshwater ostracoderm fish in the extinct order Osteostraci; these primitive armored fish were about 1 foot long and characterized by a flattened headshield and large pectoral fins; with a mouth located under its head, *Cephalaspis* probably fed on detritus on the bottom of streams; Early Devonian.

**Cephalochordata:** the least numerous subphylum of the chordates, characterized by a stiff notochord throughout life, as well as a dorsal nerve cord and gill slits. They are generally fish-like marine animals with a notochord the length of the body, which ranges from 2 to 6 inches long. Because they have no hard parts, the fossil record is sparse. However, it extends from *Pikaia gracilens* of the Burgess Shale to

the modern lancelets, including dozens of modern genera in the Branchiostomiformes (also called Amphioxiformes). See also **Tunicata**. Middle Cambrian to Recent.

**Cephalodiscidae:** the largest family of small, worm-like animals in the class **Pterobranchia**, *q.v.*; Late Ordovician to Recent.

**Cephalogale:** “helmet head,” a genus of carnivorous mammals in the family Ursidae and subfamily Hemicyoninae; among the earliest ancestors of bears, it was dog-like and the size of a raccoon, and later species became omnivorous; *Cephalogale* appeared in Eurasia in the middle Oligocene and in North America in the early Miocene, and was replaced in the Miocene by more advanced ursids.

**cephalon:** the front section of an arthropod; in trilobites the cephalon consists of specialized parts, such as the eyes and glabella, and also the free cheeks in most genera.

**Cephalopoda:** a still-extant class of marine mollusks that includes ammonoids, nautiloids, and coleoids (squids, octopuses, the Spirulida, and cuttlefish); probably descended from a monoplacophoran such as **Knighthoconus**, *q.v.* Global distribution, late Cambrian to Recent.

**Ceramoporidae:** a family of bryozoans in the extinct order Cystoporata; the early Ceramoporinae were simple encrusting organisms, while the later Crepiporinae had branching colonies; Ordovician to Late Devonian.

**Ceratiocarididae:** a family of phyllocarid crustaceans in the order Archaeostraca; a new species, *Ceratiocaris winneshiekensis*, was reported in 2016 as the oldest known representative of the family; North America, Middle Ordovician to Silurian.

**Ceratitida:** an order of ammonoids generally characterized by smooth saddles and frilled lobes. This ceratitic suture pattern consists of strongly indented and sometimes interlocking loops; it is more complex than the earlier goniatitic pattern but less complex than the ammonitic pattern characteristic of most Jurassic and Cretaceous ammonoids. The Ceratitida include most of the Triassic ammonoids (about 400 genera). Global distribution, Permian to Triassic.

**Ceratogaulus:** a genus of fossorial horned rodents in the family Mylagaulidae, the only known horned rodent. About a foot long and generally marmot-like, it is notable for a pair of sturdy, sharp horns on the snout, between the nostrils and the eyes. The function of the horns is disputed; they may have aided in digging but were probably used mainly for defense. *Ceratogaulus* is an example of convergent evolution with the unrelated *Peltephilus* of South America, the only other known fossorial horned mammal. Originally called *Epigaulus*. Western North America, late Miocene to early Pleistocene.

**Ceratomorpha:** a suborder of perissodactyl mammals that includes the Tapiroidea and Rhinoceroidea; characterized by a strong transverse crest on the molars; global distribution, late Paleocene to Recent.

**Ceratopsia:** “horned face,” a large suborder of herbivorous ornithischian dinosaurs that originated in the Late Jurassic and thrived in the Cretaceous across the Northern Hemisphere. Only 3 to 7 feet long, the early ceratopsians (such as the basal *Yinlong* of the late Jurassic and the Psittacosauridae of the Early Cretaceous) were hornless and bipedal. The later genera developed a great variety of horns and frills on the head and neck, and became quadrupedal as they grew larger. The first-named specimens were given the names *Ceratops* and *Proceratops*, but these are now considered dubious names since the specimens have all been assigned to later genera or discarded as too fragmentary. North America, Europe, and Asia; Late Jurassic to Late Cretaceous.

**Ceratosauria:** a large clade of theropod saurischian dinosaurs that arose around 225 Ma; carnivorous, generally bipedal, and at first quite small, by the Middle Jurassic they had evolved into larger species up to 9 feet long and by the Late Jurassic others as long as 19 feet; ceratosaurs gave rise to the carnosaurs of the Late Jurassic, a group of large carnivores that included the very widespread allosaurs; Late Triassic to Late Cretaceous.

**Cercidiphyllum:** a still-extant genus of riparian trees that was common in the early Cenozoic in the northern areas of Asia, Europe, and North America; a relative of the modern *Katsura* tree, now found only as two species in Eastern Asia.

**Cercopithecoidea:** the Old-World monkeys, including macaques, mandrills, and baboons; classified with humans and great apes in the infraorder Catarrhini; early Miocene to Recent.

**Ceriantharia:** a small subclass of anthozoan cnidarians, consisting of only one order of the same name; called tube-dwelling anemones, they are classified as a sister-group of the corals; they are almost absent from the fossil record because they have no hard parts, but an early Cambrian microfossil named *Eolympia pediculata* was described in 2010 and classified as a ceriantharian.

**cerioid:** of corals, having generally polygonal individual corallites packed tightly together.

***Cervalces alaskensis:*** the stag-moose, a large ancestor of the modern moose; Alaska, late Pleistocene.

**Cervidae:** a family of cloven-hoofed ruminant ungulate mammals in the order Artiodactyla; distinguished from the Bovidae by their solid, deciduous, generally branching antlers; a probable early ancestor is *Diacodexis* (middle Eocene), and one of the earliest cervids is *Leptomeryx* (Eocene to Miocene); global distribution, Oligocene to Recent.

**Cetacea:** a still-extant order of marine artiodactyl mammals that includes the modern whales, porpoises, and dolphins. Long thought to be descended from the large group of protungulate land mammals called mesonychids, the earliest ancestral whales are now generally considered more closely related to the hippopotamuses. The direct ancestors of *Pakicetus* and other early whales are still unclear, however.

For the evolution of marine mammals, see *Aegyptocetus*, *Ambulocetus*, *Basilosaurus*, *Indocetus*, *Indohyus*, *Pakicetus*, *Pezosiren*, *Protocetus*, and *Rodhocetus*. Global distribution, early Eocene to Recent.

**Cetartiodactyla:** the clade including cetaceans and other artiodactyls.

**chaetae:** chitinous bristle-like setae found on some insects, especially characteristic of polychaete annelid worms.

**Chaetetes:** a genus of demosponges in the family Chaetitidae, widespread from Ordovician to Jurassic.

**chaetetids:** small tubular organisms formerly classified as anthozoans, specifically tabulate corals, or even as algae; now considered a polyphyletic group of demosponges. They generally formed globular colonies composed of fused tubular skeletons, in mounds sometimes as large as 10 feet. Appearing in the Ordovician and widespread through the Permian, they had been thought to be extinct at the end of the Jurassic, but some extant species (such as *Acanthochaetetes wellsi*) have been discovered off the northeastern coast of Australia.

**Chaetognatha:** a phylum of arrow worms known from the Cambrian to the present; obscure because of a paucity of whole-body fossils, but a significant zooplanktonic component in modern oceans; see also *Capinatator* and *Eognathacantha*; Cambrian to Recent.

**Chalicotherioidea:** a superfamily of clawed perissodactyl mammals in the suborder Ancylopoda, comprising two families, the widespread Chalicotheriidae and the Eomoropidae, which are known mainly from Asia. Some genera were about the size of a horse, probably browsers but their habits are not completely known. Their claws, often long, made movement awkward, but some may have been able to raise the claws enough to walk on their pads. They are related to brontotheres, horses, rhinoceroses, and tapirs. Holarctic distribution, early Eocene to Pleistocene.

**Chamitataxus:** a genus of caniform carnivores in the family Mustelidae and subfamily Taxideinae; known only from a skull found in New Mexico, *Chamitataxus* existed alongside *Taxidea*, the modern American badger, in the late Miocene.

**Champsosaurus:** a genus of diapsid reptiles in the order Choristodera and family Champsosauridae, widespread in the Late Cretaceous and Paleocene; superficially similar to the modern gharial, *Champsosaurus* was almost completely aquatic; its jaws were adapted to catching fish, with powerful muscles attached to its broad skull; it was generally about 5 feet long, although the largest species, *C. gigas*, grew to 12 feet; North America and Europe, Late Cretaceous to Eocene.

**Chañares Formation:** an important Early Carnian site in northwestern Argentina; notable for tetrapods and archosaurs, including possible ancestors of the earliest dinosaurs; the Santa Maria Formation of Southern Brazil also has outcrops of the same strata; Late Triassic, 235–233 Ma.



**Chancelloriidae:** a poorly known group of sponge-shaped Cambrian organisms, possibly related to *Halkieria*; sessile and probably filter-feeders, sometimes found attached to other organisms; they had a bag-shaped body covered with spines and sclerites, 1–8 inches long and narrow at the bottom; North America, Asia, and Australia; early to late Cambrian.

**character:** a distinctive heritable feature or property, usually morphological, that defines a taxon, differentiating it from other taxa.

**Charassognathus:** a monospecific genus of small therapsids in the suborder Cynodontia; the earliest-known cynodont, *C. gracilis* is known only from a skull and one leg but is estimated to have been 1–2 feet long; South Africa, late Permian, 260 Ma.

**Charnia:** an enigmatic genus of Ediacaran animals. It was benthic, probably in a deep-water environment, and was superficially similar to sea pens. The central stalk rose from a bulbous holdfast set in sediment. The long, narrow fronds display a series of fine ridges along the entire length, up to 6 feet. It is found in association with *Aspidella* and may have been attached to it. Named for Charnwood Forest in England, where it was first found; Europe and North America, 579–555 Ma.

**Charniodiscus:** a feather-shaped Ediacaran animal, the tallest more than a foot long. Like its relative *Charnia*, it was benthic and sessile, with a central branch rising from a bulbous or disc-shaped holdfast. It was a filter-feeder with about 20 secondary branches on each side of the central shaft, with polyps on each branch. *Charniodiscus* is morphologically similar to the pennatulaceans of the Cambrian, but its affinities are uncertain. It has been found as a trace fossil in ferruginous impressions in the upper surfaces of Ediacaran paleosols in Australia. Global distribution, 565–555 Ma.

**Charophyceae:** a class of freshwater green algae in the division Charophyta; Silurian to Recent.

**Charophyta:** a division of calcareous freshwater green algae; the gyrogonites of some charophytes are stratigraphically important; early Silurian to Recent.

**Chasmatosuchus:** synonym: *Proterosuchus*.

**Chasmosaurus:** a genus of medium-sized ceratopsid dinosaurs in the subfamily Chasmosaurinae; up to 17 feet long and herbivorous, characterized by a short nasal horn and very large fenestrae in the large neck-frill; North America and Asia, Late Cretaceous, 78–75 Ma.

**Chaunograptus:** a possible genus of graptolites, the earliest known, common in the Burgess Shale, 508 Ma; *C. sphaericola* has been identified in a Devonian deposit in Estonia; North America and Europe, middle Cambrian to Devonian.

**Cheiracanthus:** a small genus of freshwater acanthodian fish in the family Acanthoessidae; deep-bodied and about a foot long, it is notable for having only one



dorsal fin; whole-body specimens are known from Europe, and its distinctive scales have been found as far away as Antarctica; global distribution, Middle Devonian.

***Cheirolepis***: a basal genus of freshwater actinopterygian fish, the only genus in the family Cheirolepididae; almost 2 feet long, it is characterized by a heterocercal tail fin, a moveable jaw that gave it a wide gape, and ganoid scales locked together in a peg-and-socket design; see also *Moythomasia*; North America and Europe, Middle to Late Devonian.

**Chelicerata**: a class of arthropods that includes the arachnids, scorpions, eurypterids, horseshoe crabs (Xiphosurida), and possibly the sea spiders (Pycnogonida), all of which have living representatives; several other animals as far back as the Burgess Shale fauna have been proposed as chelicerates, but the earliest unchallenged ones (eurypterids) appeared in the Middle Ordovician; named “claw horn” because of their principal synapomorphy, jointed appendages (cheliceræ) which are usually pincers; Ordovician to Recent.

**Chelonian**: see **Testudines**.

**Chelydridae**: a small family of cryptodiran turtles; it was once known throughout the Northern Hemisphere, but its range has shrunk so that only two genera of snapping turtles of North and South America are still extant; North America, Europe, and Asia; Late Cretaceous to Recent.

**Chengjiang biota**: an important assemblage of early Cambrian fossils found in several Konservat-Lagerstätten in the Maotianshan Shales. Dated between 530 and 515 Ma, at least 7 million years earlier than the Burgess Shale, the strata are mostly finely bedded mudstones and preserve a great variety of soft-tissue fossils. In contrast to the organisms of the Burgess Shale, those in the Chengjiang sites are generally autochthonous, preserved in their living position. One of the largest groups is the arthropods, many of them bivalved crustaceans (see *Kunmingella*). Several, such as *Waptia* and *Anomalocaris*, are congeneric with the Burgess biota, and species of other organisms, such as the lobopods *Hallucigenia* and *Aysheaia*, are also closely related. See also *Yunnanozoon*. China, early Cambrian.

***Chesaconcaus***: a genus of barnacles in the still-extant family Balanidae and subfamily Concaevinae; North America and Europe, Miocene to Pliocene.

**chevrotain**: see **Tragulidae**.

**Chileata**: one of the three extinct classes of articulate brachiopods in the subphylum Rhynchonelliformea; characterized by a large perforation in the ventral valve, they have either strophic or astroptic hinges; Cambrian to Silurian.

**Chilobolbinidae**: a family of dimorphic ostracods in the suborder Beyrichicopina and superfamily Hollinoidea, characterized by a frill and a straight hinge; Ordovician to Silurian.

**Chilopoda:** a still-extant class of myriapods that includes the centipedes; carnivorous and venomous, they have only one pair of legs on each body segment; Silurian to Recent.

***Chindesaurus:*** a genus of theropod dinosaurs in the family Herrerasauridae; one of the first true dinosaurs, it was up to 7 feet long, bipedal, and carnivorous; it is known primarily from several partial skeletons found in the Chinle Formation of the Southwestern United States, dated between 221 and 216 Ma; North America, Late Triassic.

**Chiniquodontidae:** a family of advanced carnivorous therapsids in the suborder Cynodontia; closely related to the immediate ancestors of mammals; South America and possibly Europe and Africa, Late Triassic.

***Chiosella timorensis:*** a species of conodonts whose first appearance is generally taken (but challenged in 2016) to mark the beginning of the Middle Triassic at 247.2 Ma; Romania and China.

***Chippewaella patellithea:*** a species of primitive snails, the earliest-known gastropod mollusk; known only from specimens found in Wisconsin, it has a round, cap-shaped shell about an inch in diameter; see also ***Strepsodiscus***; United States, late Cambrian, 500 Ma.

***Chirodus:*** a genus of actinopterygian fish in the extinct suborder Platysomoidei and family Chirodontidae; deep-bodied with very short dorsal and pectoral fins and a crushing dentition; Carboniferous to Triassic.

**Chirognathidae:** a family of conodonts in the suborder Prioniodinina, among the earliest of the suborder; characterized by multiple denticles on the teeth; Ordovician.

**Chiroptera:** “hand wing,” the bats; the order is divided into two suborders, Megachiroptera (large frugivorous bats that do not use echo-location) and Microchiroptera (small echo-locating bats, generally insectivorous); the classification of bats is disputed, but they are generally considered closer to primates than to rodents; early Eocene to Recent.

**chitinozoans:** an enigmatic group of middle Paleozoic microfossils. Distinctively flask-shaped, they may be eggs or a juvenile stage of unknown marine animals, possibly orthocone cephalopods. Occurring worldwide and especially abundant in Ordovician and Silurian strata, they are important index fossils because of their wide distribution and rapid evolution. Early Ordovician to early Mississippian.

**chitons:** see **Polyplacophora**.

***Choeropotamus:*** a genus of pig-like entelodont artiodactyl mammals, the only genus in the family Choeropotamidae; related to the Cebochoeridae and possibly descended from the little-known Helohyidae; late Eocene.

**Choiia:** a genus of demosponges in the order Monaxonida; about an inch wide, its conical body was surrounded by a thicket of spicules; the fossils of some species resemble stars; it was originally thought to have rested on the sea floor but is now believed to have floated, attached to the substrate by three long spines; Canada, United States, China, and Africa; Cambrian to Ordovician.

**Chondrostei:** a still-extant, paraphyletic subclass of primarily cartilaginous fishes in the class Actinopterygii. The chondrosteans flourished in the late Paleozoic and the Triassic, declining in the Cenozoic. Some Mesozoic families have essentially ossified skeletons and other similarities to the teleosts, so that the modern chondrosteans' cartilaginous condition is probably derived. Cosmopolitan, Silurian to Recent.

**Chonetes:** a long-lived genus of articulate brachiopods in the extinct order Productida and superfamily Chonetoidea; *Chonetes* was characterized by a row of short, angled spines along its margin that it used to anchor itself; Late Ordovician to Jurassic.

**Chordata:** the phylum of deuterostome organisms that includes the subphyla Vertebrata, Cephalochordata, and Tunicata; characterized by a dorsal nerve cord and pharyngeal apertures (gill slits); early Cambrian to Recent.

**Choristodera:** an order of semi-aquatic diapsid reptiles, possibly in the Archosauromorpha; similar to modern gharials, the choristoderans are represented principally by the families Champsoosauridae and Simoedosauridae, which appeared in the Cretaceous and survived the end-Cretaceous extinction into the middle Eocene; champsosaurs are significant especially for specimens found near Ellesmere Island, high in the Canadian Arctic; North America, Europe, and Asia; Middle Jurassic to Miocene.

**Chromogisaurus:** a monospecific genus of sauropodomorph dinosaurs in the family Guaibasauridae; about 7 feet long and dated at 231 Ma, it is one of the earliest dinosaurs; *C. novasi* is known from one specimen, a partial disarticulated skull and skeleton found in a middle Carnian layer of the Ischigualasto Formation; Argentina, Late Triassic.

**chronocline:** a time series of fossil specimens showing transitional morphological changes in a taxon in successive strata.

**Chronoperates paradoxus:** "puzzling time-wanderer," a problematic Paleocene fossil jaw; originally thought to be an extremely late survivor of the cynodonts, the therapsid ancestors of mammals which became extinct 100 million years earlier, midway through the Cretaceous; it is now considered a late-surviving symmetrodont mammal; Alberta, late Paleocene.

**Chrysochloridae:** a family of insectivorous burrowing mammals in the order Afrosoricida; called golden moles, they are so like the marsupial moles of Australia that some researchers have claimed they are related; Southern Africa, early Miocene to Recent.

**Cidaroida:** a still-extant order of primitive sea urchins in the subclass Perischoechinoidea, the only order of the subclass to survive into the Cenozoic Era; characterized by large and widely separated primary spines; early Permian to Recent.

**Cimolesta:** a proposed order of eutherian mammals; related to several other early groups of mammals such as the creodonts, dinoceratans, and pantodonts; North America, Europe, Asia, and Africa; Cretaceous to Eocene.

**Cimoliopterus:** a genus of pterodactyloid pterosaurs with a wingspan of about 16 feet; the two species are *C. cuvieri* (England) and *C. dunnii* (Texas), and they are closely related to a slightly older pterosaur from Texas, *Aetodactylus halli*; Early Cretaceous, 94 Ma.

**cinctans:** an enigmatic group of slow-moving early Paleozoic animals thought to be non-pentamer basal echinoderms; sometimes called Homostelea; only a few centimeters long, they are composed of interlocking, generally rectangular plates arranged in an oval shape resembling a small tennis racket, with a short extension at the narrow end; Europe and North Africa, middle Cambrian, 509–497 Ma.

**Cirripedia:** the barnacles, a subclass of marine crustacean arthropods traceable to the Cambrian but uncommon in the fossil record until the middle Cenozoic. The shell is typically constructed of six triangular plates in a conical shape. They are generally sessile and cemented to the substrate by a firm base, living in the highly erosional tidal zone. Since only a few genera live in deep water, they are sometimes used as indicators of paleodepths, estimated by the degree of disarticulation of the shells. See also *Chesaconca* and *Priscansermarinus*. Global distribution, middle Cambrian to Recent.

**Citipati:** a genus of theropod saurischian dinosaurs in the family Oviraptoridae; they are carnivores similar to *Troodon* and *Oviraptor*, notable for bird-like reproductive behavior; Mongolia, Late Cretaceous, 84–75 Ma.

**clade:** a monophyletic group of two or more species with a common ancestor, as well as all the other descendants of that ancestor.

**cladodont dentition:** broad-based teeth with a large primary cusp and several secondary cusps, common in Paleozoic sharks but little known after the Triassic.

**cladogenesis:** see **anagenesis**.

**Cladoselachidae:** an early family of sharks; about 6 feet long and almost scaleless, they were characterized by cladodont dentition, two dorsal fins, and large and paddle-like pectoral fins, but they had no anal fin; Devonian to Carboniferous.

**Cladoxylon:** a genus of early vascular plants in the large group called cladoxylpoids; it grew only about a foot high and may have been leafless, but its central stem marks it as a forerunner of sizeable trees that appeared in the Devonian; global distribution, Middle Devonian to Early Carboniferous.

**Clarkecaris:** a genus of crustaceans in the order Anaspidacea and proposed family Clarkecarididae; Brazil, early Permian.

**Clarno Nut Beds:** a botanically rich site near John Day, Oregon; although the Nut Beds of the Clarno Formation contain few vertebrate fossils, they are one of the most important paleobotanical sites in the world; they contain hundreds of well-preserved botanical fossils from a large forest of the Eocene, dated at 44 Ma; North America, middle Eocene.

**Clathropteris meniscioides:** a species of reticulate ferns, known worldwide from the Late Triassic to Middle Jurassic.

**Clavatoraceae:** a Mesozoic family of charophytic algae; several species representing gradual evolutionary changes are index fossils from the Late Jurassic to the end of the Cretaceous.

**Cleveland-Lloyd Dinosaur Quarry:** an important Late Cretaceous site, especially for dinosaurs. Located on the site of a boggy marsh dated at 147 Ma, the quarry's Morrison Formation strata have produced thousands of disarticulated dinosaur bones. There are also dinosaur tracks in the vertical cliffs and specimens from all other vertebrate classes. Of the dinosaurs, many more carnivores than herbivores are represented. Only a few whole skeletons have been found, evidently because of the slow turbidity of the clay sediments in the bog. Central Utah, Late Jurassic.

**Climacograptus:** a genus of scandent graptolites important as index fossils in the Ordovician; characterized by a single serrated stipe; Middle Ordovician to Lower Devonian.

**Climatiiformes:** an order of small, spiny acanthodian fish, only about 3–4 inches in length; they had several stout spines and a heterocercal tail fin; global distribution, Silurian to Carboniferous.

**Climatius:** a primitive genus of acanthodians in the family Climatidae; although only about 3 inches long, it had 15 spines on its body and fins; North America and Europe, late Silurian to Early Devonian.

**Cloudina:** an Ediacaran microfossil found as a tube with double-layered walls of calcium carbonate; thought to have been made by a suspension-feeding worm; named for American paleontologist Preston Cloud; Namibia, late Ediacaran.

**Clymeniida:** a large early order of ammonoids, notable for an unusual dorsal siphuncle, as opposed to the ventral siphuncle of other ammonoids; less than 2 inches across and very diverse in shell type and ornamentation; they diversified rapidly in the Famennian, the final stage of the Devonian, but then abruptly disappeared at the end of the period; Europe, North Africa, and possibly Australia; Middle to Late Devonian.

**Clypeasteroidea:** the modern sand dollars, an order of euechinoids in the superorder Gnathostomata; global distribution, late Paleocene to Recent.

***Clypeus ploti*:** “swimming shield,” a species of irregular echinoids in the family Clypeidae, called the “pound-stone” because it fossilized as a rounded, fist-sized stone of about 22 ounces; common in eighteenth-century Oxfordshire, England, it was among the first echinoids studied; Europe and Africa, Middle Jurassic.

**Cnidaria:** a phylum of diploblastic animals, mostly marine, usually with stinging tentacles around a mouth; comprising chiefly the corals, sea anemones, and jellyfish, the phylum includes more than 10,000 named species, divided into three classes: Anthozoa, Scyphozoa, and Hydrozoa; Ediacaran to Recent.

**coccolithophore:** a one-celled planktic algae that surrounds itself with a many-layered calcite skeleton (a coccosphere); the skeletons are the major component of chalk deposits around the world, and coccolithophores are considered the main calcite producer in the ocean; significant in the fossil record since the Triassic, especially as an indicator of climate change.

***Coccosteus*:** an important Devonian genus of arthrodire placoderms in the extinct suborder Brachythoraci; similar in some ways to its much larger cousin *Dunkleosteus*, *Coccosteus* was 8 to 16 inches long and is found mainly in freshwater deposits; it had large pectoral and pelvic fins and a long finned tail; the arthrodires were joint-necked fish, and *Coccosteus* had two joints, which allowed it to feed on large prey; Europe and North America, Middle to Late Devonian.

**Cochliodontidae:** a large family of elasmobranch fish similar to sharks but with a bradyodont toothplate dentition; Devonian to Permian.

**Coelacanthidae:** an extinct family of actinistian lobe-fin fish in the order Coelacanthiformes; Permian to Jurassic.

**Coelacanthiformes:** an order of lobe-fin fish, considered extinct since the Cretaceous until two species of the genus *Latimeria* were discovered in the Indian Ocean in 1938. *Latimeria* (Latimerioidei: Latimeriidae), which appeared in the Triassic, is very similar to the Cretaceous coelacanths. Even with a poor fossil record, coelacanths are significant in evolution because they are closely related to the early lobe-finned fish, which are thought to be the first fish to develop air-breathing skills that let them begin to live on land about 400 Ma. Devonian to Recent.

**Coelenterata:** an obsolete term, formerly considered a phylum that included a large group, the Cnidaria, and a smaller group, the Ctenophora; these are now considered separate phyla.

***Coelodonta*:** a genus of large perissodactyl mammals in the extant suborder Ceratomorpha and subfamily Rhinocerotinae; coelodonts were the woolly rhinoceroses of Eurasia, surviving up to about 10,000 years ago; they were similar in size to the modern rhinoceros, typically about 13 feet long and weighing 3 tons, with some almost 7 feet high; they bore two forward-pointing horns on the nose; Europe and Asia, Pliocene to late Pleistocene.

***Coelophysis*** a genus of early saurischian dinosaurs, theropods in the family Coelophysidae; bipedal, lightly built, and about 10 feet long, it is a typical coelurosaur; there is some inconclusive evidence that it was gregarious, perhaps hunting in packs; North America, Late Triassic to Early Jurassic.

**coelurosaur:** “hollow-tailed lizard,” a large group of small, lightly built, theropod dinosaurs in the order Saurischia; these bipedal predators, some of them feathered, gave rise to later saurischians such as the Ornithomimidae and Tyrannosauridae, and to birds; Triassic to Late Cretaceous.

**Coenopteridales:** a large and varied group of ancestral ferns, usually considered as belonging to the order Primofilices; Devonian to Triassic.

**coevolution:** an evolutionary process in which unrelated lineages exert selective pressure on each other, resulting in evolutionary changes in both. The best-documented cases are the interactions between insects and entomophilous and entomophagous flowers, and between birds and ornithophilous flowers, but many other cases have been described of coevolutionary relationships between predatory animals and prey and between herbivorous animals and plants.

**Coleodontidae:** a family of conodonts in the order Neurodontiformes, with teeth characterized by a lamellar structure; Ordovician to Triassic.

**Coleoidea:** a subclass of soft-bodied mollusks in the class Cephalopoda, including the extinct belemnites and the still-extant squids, octopuses, and cuttlefish; disputed specimens are known from as early as the Cambrian, but the earliest definitive coleoids are dated as Mississippian.

**Coleoptera:** the beetles, an order of pterygote insects in the clade Neoptera. They are named “sheathed wing” for the hard elytra, the front pair of wings that protect the membranous back wings and the abdomen. The oldest definitive beetle dates back to the Permian, but a possible specimen has been found at the Late Carboniferous Mazon Creek site. Following the end-Permian extinction, the Coleoptera diversified rapidly in the Triassic. Global distribution, Pennsylvanian? to Recent.

**Collembola:** a still-extant order of primitive apterygote arthropods; up to half a centimeter long, they are commonly called springtails because of the jumping ability given them by a furcula, a tail-like forked appendage at the end of the abdomen, normally folded under the body; known from the Early Devonian *Rhyniella praecursor* and other fossil specimens beginning in the Cretaceous.

**Collenia:** a widespread genus of cyanobacteria that produced stromatolites; Precambrian.

**Collignoniceras:** a small genus of ammonoids in the order Ammonitida and superfamily Acanthoceratoidea; up to 7 inches across, evolute, and very strongly ribbed, *Collignoniceras* is the type genus of the family Collignoniceratidae; global distribution, Late Cretaceous, 96–88 Ma.

**Collinsium ciliosum:** see *Hallucigenia*.



**Collyrites:** a genus of small irregular euechinoids in the family Collyritidae, possibly paraphyletic; they were oval, up to an inch long, and did not have a lantern; Europe and Asia, Middle Jurassic to Early Cretaceous.

**Columba omnisanctorum:** an extinct species of early Pliocene pigeons in the order Columbiformes; found on the Gargano Peninsula of Italy, related to a similar columbiform found nearby, *C. pisana*; see also *Deinogalerix*.

**Columbia:** see **Rodinia**.

**Colymbosathon eplecticos:** a species of ostracods notable for the well-preserved soft-tissue features in one intact specimen buried by volcanic ash about 425 Ma and found in a carbonate nodule. Although the fossil is only 0.2 inches long, organs visible in a digital three-dimensional image include eyes, gills, a circulatory system, anus, and penis. The presence of the penis makes this specimen the oldest known definitively male fossil. See **Herefordshire Nodules**. England, Silurian.

**comb jellies:** see **Ctenophora**.

**Como Bluff:** a Konzentrat-Lagerstätte on a ridge in Wyoming noted for the many dinosaurs discovered there in strata of the Morrison and Sundance Formations; United States, Middle and Late Jurassic.

**Composita:** a genus of brachiopods in the extinct order Athyridida; from 1 to 2 inches in diameter, smooth-shelled, with a distinct fold and sulcus; global distribution, Late Devonian to Early Triassic.

**compound eye:** an eye formed of a mosaic of smaller eyes, characteristic of many arthropods.

**Compsognathus:** “dainty jaw,” a genus of theropod saurischian dinosaurs; bird-like, small and light in build, its body was as long as 2 feet and it weighed up to 8 pounds; a fast runner, it had long hind legs and a longer tail; Jurassic.

**concretions:** hard, layered structures, usually rounded, formed by precipitation and cementation of minerals in the soil or rock, sometimes enclosing a fossil.

**condylarths:** an informal group of primitive placental mammals ancestral to the perissodactyl ungulates and to the cetaceans. Previously considered an order, the condylarths have all been assigned more precisely to different orders. Arising in the Cretaceous, they underwent an extensive radiation of species in the Paleocene and Eocene. They were mainly herbivorous, but some had hooves and some had claws. Global distribution except Australia, Late Cretaceous to Oligocene.

**condyle:** an articular process on the joint of a bone (or mandible of an insect).

**Confuciusornis:** a genus of primitive birds in the family Confuciusornithidae, of which *C. sanctus* is the type species. Crow-sized, it is the earliest-known toothless beaked bird and seems to be the earliest that could fly for a considerable distance. About 11 inches high and bearing true feathers, it was similar to *Archaeopteryx* except that it was toothless and probably had more feathers. Three other species



have been named, all found in the Yixian and Jiufotang Formations of northeastern China (see **Jehol biota**) and dated between 130 and 125 Ma, 10–15 million years after *Archaeopteryx*. *Confuciusornis* was probably not in the line of descent to modern birds. China, Early Cretaceous.

**Coniconchia:** a proposed class of mollusks to include the hyoliths and tentaculites; 2017 research, however, indicates the hyoliths are lophophorates and closely related to brachiopods; the tentaculites have generally been considered as an order in their own right, the Tentaculitida.

**conifers:** see **Pinopsida**.

**Coniopteris:** a genus of Mesozoic ferns in the still-extant family Dicksoniaceae; it bore lanceolate or lobate leaves 2–4 inches wide; its spores were carried marginally, in cup-shaped pouches at the end of lateral veins; especially common in the Jurassic; global distribution, Permian to Cretaceous.

**Conocardium:** a genus of rostroconch mollusks in the family Conocardiidae; up to 6 inches long, its thick shell surface is marked by fine rays; global distribution, Devonian to Permian.

**Conoclypeus:** a genus of euechinoids in the order Clypeasteroidea and family Conoclypidae, sand dollars with a high test about 1.5 inches across and petaloid ambulacra; Europe, early Eocene to Miocene.

**Conodonta:** a class of enigmatic eel-like chordates. Although considered vertebrates, they are still known mainly by their feeding apparatus, referred to as conodont elements; fossil specimens show no soft-tissue detail. Their jaw structure differs greatly from that of later animals. They are now classified as chordates and divided into protoconodonts, paraconodonts, and euconodonts. Appearing in the early Cambrian, they ranged from an inch to more than a foot long. Only a few whole-body specimens are known, the best-known of which is *Promissum pulchrum*, *q.v.* Many conodonts became extinct at the end of the Ordovician, but they recovered and continued to be important stratigraphically through the Paleozoic, becoming completely extinct at the end of the Triassic.

**conodont elements:** the earliest tooth fossils, in the form of rudimentary teeth and very rudimentary jaws; despite the inability until recently to discover whole-body specimens of the animal which bore them, conodont elements have long been important in stratigraphic research; see for example *Iapetognathus* and *Streptognathodus*.

**Conophyton:** one of many plant-like organisms that formed stromatolites in the Mesoproterozoic Era; North America and Africa, Archaean.

**Constellaria:** a genus of stenolaemate bryozoans in the extinct order Cystoporata and family Constellariidae; they formed branching colonies and are distinguished by generally star-shaped maculae on the surface of branches about half an inch across; global distribution, Middle Ordovician to early Silurian.

**continental drift:** see **paleogeography**.

**Conulariida:** a problematic clade of extinct cnidarians, generally considered scyphozoans but not well understood. Their superficially shell-like structure consists of rows of calcium phosphate rods that form a quadrilateral cone, with new rods being added at the broader end. The surface has a wavy ridged appearance, with the rows of rods intersecting at a slight angle in the middle of each side. The narrow end was attached to the substrate, and soft tentacles extended from the broad end. The larger conulariids were as long as 20 inches, but most were about 4 inches. Also called Conulata and Conularia. Late Cambrian to Early Triassic.

**Conulidea:** a superfamily of echinoids in the order Echinoneoidea; Europe, Asia, and North America; Early Cretaceous to Eocene.

**Conulus:** a small genus of conulidean euechinoids in the order Echinoneoidea and family Conulidae; dorsally high-domed, almost conical, smooth and non-petaloid; the flat oral side has a faint pentamerous pattern; Europe, Asia, North America; Early to Late Cretaceous.

**convergent evolution:** the process in which unrelated lineages living in similar ecological niches independently develop superficially similar adaptations.

**Cooksonia:** a genus of tracheophytic plants in the family Rhyniaceae; it is the oldest demonstrably vascular plant and is close to the point in time when the lycopsids branched off from other plants; cosmopolitan, middle to late Silurian.

**Cope's Rule:** the name given to the observation that groups of animals tend to evolve toward larger size over evolutionary time. The idea is associated with the nineteenth-century paleontologist Edward Drinker Cope and has been elaborated by many others. The tendency is obvious in many lineages but absent in others, and of course must be subject to limitations of sufficient food sources and of the ability to move efficiently. See also **Unspecialized Descent**.

**Copodus:** a little-known genus of primitive holocephalic fish in the extinct family Copodontidae; bradyodont, with one tooth plate in each jaw; North America and Europe, Devonian and Carboniferous.

**coprolites:** fossilized residues from the digestive tracts of animals. Their contents may provide evidence of the existence of other organisms, and they are important in investigating eating habits of animals, but it is difficult to identify the producer. The largest known specimen is about 17 inches long, found in Saskatchewan in 1995, thought to have come from a large tyrannosaur just before the end of the Mesozoic era. Usually in the form of dung, coprolites may also be regurgitalites (regurgitated) or cololites (fossilized inside the body).

**corallite:** the chamber or skeleton constructed by an individual coral animal.

**corals:** marine animals that secrete corallite skeletons composed of calcium carbonate, often in conjunction with algae; they generally thrive in warm, shallow water, but some cold-water corals that do not need algae are found as deep as

3,000 feet; see **Rugosa**, **Tabulata**, and **Scleractinia**; worldwide, Cambrian to Recent.

***Cordaicarpus***: the form genus of seeds of the family Cordaitaceae.

**Cordaitales**: an order of primitive gymnosperm plants in the class Pinopsida; they were tree-like, growing as high as 100 feet, with long, strap-like leaves; possibly ancestral to conifers, cycads, and ginkgos; global distribution, Carboniferous to Late Triassic.

***Coronacollina***: the earliest-known animal with skeletal body parts, possibly related to sponges. A genus of benthic organisms 1–2 inches high, with 3 spicules radiating from a central thimble-shaped body; the long spicules probably supported the animal on the ocean floor. Its resemblance to the Cambrian sponge *Choia* indicates a link between the two periods. Described in 2012 from hundreds of specimens found in upper Ediacaran strata in Australia, 560–550 Ma.

***Coronodon havensteini***: a species of mysticete whales known only from a large, complete skull with unusual dentition. It has strikingly ridged molar teeth that show no wear from cutting and shearing prey, leading some to consider *Coronodon* evidence of a transition from the toothed condition of the early odontocete whales to the baleen of the mysticetes. The very large molars, 3–4 inches in diameter, might have sieved food from the water as baleen does in modern mysticetes; however, this interpretation is in dispute. United States, early Oligocene.

**Corynexochida**: a diverse order of early trilobites that appeared at about the same time as the short-lived Redlichiida and the Ptychopariida; generally characterized by large eyes and large glabella extending nearly to the front of the cephalon; early Cambrian to Middle or Late Devonian.

**Coryphodontidae**: “peaked tooth,” a family of pantodont mammals in the extinct order Cimolesta; the type genus *Coryphodon* was 3 feet at the shoulder and about 8 feet long, and some genera were larger; although the canine teeth were relatively long, it was a forest browser; North America, Europe, and Asia; late Paleocene to middle Eocene.

**Corytospermaeae**: a family of seed plants in the order Peltaspermales; similar to seed ferns, but the relationship is obscure; characterized by pairs of heavily veined leaflets on a central stalk; widespread in the Triassic throughout Gondwana and present also at least in China; Early to Late Triassic.

***Corythoraptor jacobsi***: a species of feathered theropod dinosaurs in the family Oviraptoridae, known from one almost-complete skeleton. Described in 2017, *C. jacobsi* was 5–6 feet long, with small forelimbs and strong hindlimbs, probably flightless but a fast runner. In shape it resembled the modern cassowary, especially because of a tall, characteristic crest. It is one of several oviraptoroids found recently in the Nanxiong Formation; Southern China, Late Cretaceous, 84–66 Ma.

**Corythosaurus:** “Corinthian-helmet lizard,” a hadrosaurid dinosaur in the subfamily Lambeosaurinae; similar to *Lambeosaurus*, it was about 30 feet long, with a stocky body and long tail; its most notable feature was a tall crest on the top of its head that may have made a loud trumpet call possible; North America, Late Cretaceous, 80–74 Ma.

**cosmopolitan distribution:** existing in appropriate but scattered environments across all or most of the world.

**Cotylorhynchus:** a genus of synapsids in the family Caseidae; it was 10–12 feet long, with a large, barrel-shaped body and a very small head; the type species *C. romeri* was widespread in the southern part of North America in the early Permian; North America, Carboniferous to middle Permian.

**cotylosaurs:** an informal term for the paraphyletic Captorhinida.

**craniate:** having a specialized and distinctly formed head, distinguishing most chordates from tunicates and cephalochordates.

**Crassatella:** a long-lived genus of articulate marine burrowing bivalves; *Crassatella* was 1.5 inches long, with a strong shoulder on both shells and strong concentric ribs; Cretaceous to Recent.

**Crato Formation:** a Lower Cretaceous Konzentrat-Lagerstätte in the Araripe Basin of Northern Brazil, dated uncertainly but probably between 115 and 112 Ma, slightly earlier than the neighboring Santana Formation. The occurrence of the Crato fossils differs from that of the Santana fossils, which are found in limestone concretions. Those of the Crato, found in finely bedded limestone similar to that of Solnhofen, are predominantly arthropods, especially insects and arachnids, with some specimens of fish such as *Dastilbe* and crested pterosaurs such as *Anhanguera*. There are other vertebrates and a variety of plants including gymnosperms and other early seed plants, as well as a few angiosperms.

**Craugastor:** a still-extant genus of tree frogs known from amber fossils found in the Dominican Republic and Mexico, about half an inch long; late Oligocene to Recent.

**creodonts:** an informal term for a polyphyletic group of flesh-eating mammals formerly considered an order, including the Oxyaenidae and Hyaenodontidae; the diverse group included carnivores as small as squirrels and as large as bears; Late Cretaceous to Miocene.

**Crepiporinae:** see **Ceramoporidae**.

**Cretaceous:** the third and final period of the Mesozoic Era, from 146 to 66.0 Ma, divided into Early (146–100) and Late (100–66.0) Epochs. It was a period of high levels of carbon dioxide, very little polar ice, and the highest sea levels in Earth’s history, with shallow, saline seas covering much of the land. The first angiosperms appeared early in the period and by the end of the Cretaceous were the dominant

plants worldwide. Insects and spiders diversified rapidly along with the angiosperms. Dinosaurs continued their reign on land, and marine life was dominated by the greatly diversified bony fish and large predators such as sharks and mosasaurs.

**Cretaceous extinction:** the most recent and second-most severe of the five great extinctions, ending the Mesozoic Era at about 66.0 Ma. The most striking result was the disappearance of the last of the dinosaurs and pterosaurs. Other large terrestrial animals were also decimated, so that the largest that survived into the Paleocene was about the size of a turkey. In the seas, the last of the ammonoids and other groups became extinct, as well as the plesiosaurs and mosasaurs. As to possible causes, the preponderance of evidence points to a large asteroid striking the Earth off the Yucatan Peninsula and causing global environmental disruption, and the volcanic eruption creating the basalt flows called the Deccan Traps in India may have contributed; but, as with the four earlier mass extinctions, the causes are uncertain. Although the number of dinosaur species decreased during the last several million years of the Cretaceous, the evidence for a relatively abrupt extinction event is stronger than in the other mass extinctions.

**Cretaceous Inland Seaway:** see **Western Interior Seaway**.

**Cretaceous Terrestrial Revolution:** abbreviated as KTR, the period of angiosperm radiation from 125 to 90 Ma, when flowering plants, insects, and spiders radiated dramatically, leading to an accompanying radiation of many other animals.

**Cretoxyrhinidae:** an extinct family of very large Cretaceous sharks in the still-extant order Lamniformes; up to 23 feet long and characterized by very sharp 3-inch-long teeth, they preyed on mosasaurs, bony fish, and turtles; cosmopolitan, Late Cretaceous, 94–70 Ma.

**Crinoidea:** commonly called “sea lilies” but actually animals, a class of echinoderms in the subphylum Crinozoa. There are 100 extant genera and 600 extant species of crinoids. About 7000 extinct species are known, with the greatest diversity in the Paleozoic. They may have arisen from the Edrioasteroidea or from the eocrinoids and their descendants the cystoids. Crinoids were widespread and numerous throughout the Paleozoic up to the end-Permian extinction, and many Paleozoic limestones are made up almost entirely of crinoid fragments. There are stalked, unstalked, and free-swimming genera, but the classic Paleozoic genera were stalked. Crinoids declined rapidly in the Mesozoic for poorly understood reasons. Early Ordovician to Recent.

**Crocodylia:** a still-extant order of predatory, semi-aquatic reptiles; global distribution, Late Cretaceous to Recent.

**Crocodylomorpha:** a large superorder of archosaurs that includes the crocodylians and their extinct relatives, going back to the sphenosuchians of the Late Triassic; global distribution, Late Triassic to Recent.

**Cro-Magnon:** the common name for the hominins who competed with Neanderthals in Europe after 40,000 years ago; now referred to as “European early modern humans,” the Cro-Magnons are classified in the same subspecies as modern humans, *H. sapiens sapiens*, because the skeletal differences between the two are insignificant.

**Crossopterygii:** see **Sarcopterygii**.

**crown group:** a monophyletic group comprised of a set of extant species, together with their ancestors back to their latest common ancestor and all other descendants of that common ancestor; see also **stem group**.

**Crustacea:** a large subphylum of arthropods that includes crabs, lobsters, shrimp, krill, barnacles, ostracods, branchiopods, and other similar animals; middle Cambrian to Recent.

**Cryogenian Glaciation:** A period of global cooling around 650 Ma; see **acriarchs** and **icehouse conditions**.

***Cryolophosaurus*:** a genus of early theropod dinosaurs found in Antarctica in 1991, probably tetanuran but with some dilophosaurid features, distinctively a thin bony crest across the top of its forehead. Weighing half a ton and about 21 feet long, *Cryolophosaurus* had a shallow skull and a long, stiff tail. It is known only from an immature specimen, but it was one of the largest theropods of its time and was probably an efficient predator. Antarctica, Early Jurassic, 190 Ma.

***Cryptoclidus*:** a genus of slender plesiosaurs in the superorder Sauropterygia; Europe, Asia, and South America; Middle Jurassic.

**Cryptodira:** a still-extant suborder of turtles in the order Testudines, including most of the modern turtles and tortoises. They differ from the Pleurodira in several ways, notably by retracting the head inside the shell by vertical flexure, directly back instead of to the side. They evolved along with the pleurodires in the Early Jurassic, and by the end of the period had largely replaced them. Global distribution except Australia, Early Jurassic to Recent.

***Cryptograptus*:** a genus of scandent pterobranch-like graptolites in the suborder Glossograptina; cosmopolitan, Middle Ordovician to late Silurian.

***Cryptolithus*:** a genus of asaphid trilobites in the family Trinucleidae; almost circular in shape and eyeless, but with a pitted fringe around its head that may have allowed it to sense the direction of ocean currents as it fed on small animals in ocean sediments; in addition to this “lace collar,” *Cryptolithus* was remarkable for its pair of long genal spines; it became extinct in the Ashgill event, 440 Ma; cosmopolitan, Late Ordovician.

**Cryptostomata:** an order of Paleozoic colonial bryozoans in the still-extant class Stenolaemata; the zoaria are short but erect, and the colony forms bifurcating branches; Ordovician to Permian.

***Cryptovolans***: see *Microraptor*.

***Cryptozoon***: an enigmatic genus of stromatolitic reef-forming algae common in the Cambrian and Ordovician, possibly still-extant in the stromatolites of Shark Bay, Australia.

**Ctenodactylidae**: a still-extant family of rodents in the suborder Hystricomorpha, named for the stiff bristles on their hind feet. The earliest definitive specimen is from the late Eocene, but DNA evidence indicates that the first Ctenodactylidae appeared in the early Eocene in Asia. The family is still represented by several pika-like North African genera, called gundis, which are commonly called “comb-rats.” Asia, Europe, and Africa; Eocene to Recent.

***Ctenodonta***: a genus of burrowing bivalve mollusks, about 1 inch long, in the subclass Palaeotaxodonta and order Nuculida; Early Ordovician to Silurian.

***Ctenodus***: “comb-tooth,” a genus of sarcopterygian fish in the order Dipnoi; ancestral to the modern lungfishes in a well-documented evolutionary line; North America, Europe, and Australia; Early Carboniferous.

**Ctenophora**: the comb-jellies, a phylum of gelatinous marine animals that move by the beating motion of their cilia; generally bell- or ribbon-shaped, they are hermaphroditic and predatory, feeding on zooplankton and fish larvae; global distribution, early Cambrian to Recent.

**Ctenothrissiformes**: a small order of teleost fish in the subclass Neopterygii, well-known from the genera *Ctenothrissa* and *Aulolepis*; appearing only in the Cenomanian Stage of the Late Cretaceous, they seem to be close to the ancestry of most modern bony fish; deep-bodied and about a foot long, characterized by ctenoid scales and large dorsal and pectoral fins without true spines; Europe and Southwest Asia, Late Cretaceous, 95–90 Ma.

***Ctenurella***: “small tail comb,” a genus of benthic ptyctodontid placoderm fish; about 5 inches long, it was lightly armored, like the other ptyctodontids; it had a whip-like tail and two dorsal fins, the one near the tail comb-shaped, long and low; it had small toothplates and was probably viviparous; Germany and Australia, Late Devonian.

**cursorial**: of terrestrial animals, adapted to rapid running movement in open country.

***Cuvieronius***: a genus of New-World proboscideans in the extinct family Gomphotheriidae; a small gomphothere, *Cuvieronius* (also known as *Cordillerion*) was 9 feet high, weighed about 4 tons, and was notable for its two spirally twisted tusks; it lived in North America from the Pliocene up to the end of the Pleistocene, and in South America until about 9,000 years ago, the latest specimen being found in Chile; Pliocene to Holocene.

**Cyanophyta**: a phylum of bacteria, one of the earliest forms of life on Earth, found in Precambrian deposits as old as 3 billion years. Since they produce oxygen through



photosynthesis, they may have significantly changed the composition of the atmosphere when they arose. Also called cyanobacteria and “blue-green algae” (although not algae at all).

**Cyathaspidiformes:** an order of jawless heterostracan fish, the second-largest group of heterostracans; fusiform and heavily armored, they were all benthic; Middle Ordovician to Middle Devonian.

**Cycadales:** one of the two orders of the Cycadopsida, the Cycadales include the living cycads and their immediate ancestors; they are subtropical plants with large, stiff, fernlike leaves, forming a crown around the top of the stem; cycads are gymnosperms and are not related to palms, which are angiosperms; early Permian to Recent.

**Cycadeoidales:** the second order of tree-like plants in the Cycadopsida; the Cycadeoidales include the many extinct cycad-like plants that were widespread, along with the true cycads, throughout the Mesozoic; Permian to Cretaceous.

**Cycadofilicales:** see **Pteridospermatophyta**.

**Cycadopsida:** the class of early seed plants that includes principally the cycads; early Permian to Recent.

**Cyclacantharia:** a genus of productid brachiopods variously placed in the family Richthofeniidae or the family Cyclacanthariidae; with a large conical valve cemented to the substrate, it is an aberrant form, characterized by many prop-like spines; known especially from specimens found in the Glass Mountains of Texas, with the calcite shell replaced by silicification; United States, Africa, and Asia; early to late Permian.

**Cyclida:** an enigmatic order of arthropods, formerly considered crustaceans but now classified as maxillopod branchiurans, related to modern fish-lice; originally called Cycloidea, they are crab-shaped with a circular carapace 1–3 inches in diameter; a dozen genera are recognized, including *Apionicon*, *Carcinaspides*, *Halicyne*, and *Hemitrochiscus*; Europe and North America, Carboniferous to Late Cretaceous.

**Cyclocystoidea:** a small class of echinoderms in the subphylum Echinozoa, formerly placed in the class Edrioasteroidea; small and disc-shaped, characterized by a marginal ring of ossicles around a plated disc; North America and Europe, Middle Ordovician to Early Carboniferous.

**Cyclomedusa:** a very contentious fossil widespread in the Ediacaran biota, possibly related to *Aspidella*. Circular in shape and up to 10 inches in diameter, it is generally flat, with many concentric growth ridges, and some specimens display fine radial lines and possible stems. It is variously considered a holdfast, possibly from an octocoral-like organism; a colonial microbial organism; or an anemone-like benthic polyp. Global distribution, Ediacaran.

**Cyclopygidae:** a family of small to medium-sized trilobites in the order Asaphida; characterized by very large eyes and found mainly in deep-ocean sediments; along



with many other groups of trilobites, it became extinct at the end of the Ordovician; global distribution, Early to Late Ordovician.

**Cyclostomatida:** a still-extant order of bryozoans in the class Stenolaemata; dominant in the Mesozoic and declining since then, but still widespread; also called Tubuliporata; Early Ordovician to Recent.

**Cyclothyris:** an obscure extinct genus of articulate brachiopods in the still-extant order Rhynchonellida; subtriangular shape, with an erect beak; cosmopolitan, Cretaceous.

**Cynodesmus:** a genus of dog-like mammals in the still-extant family Canidae and extinct subfamily Hesperocyoninae; it was long considered the immediate ancestor of *Tomarctus*, but studies since the 1990s indicate a more distant relationship; North America, late Oligocene to early Miocene.

**Cynodictis:** a genus of carnivorous mammals in the family Amphicyonidae, possibly ancestral to many modern carnivores; Europe and Asia, late Eocene to early Oligocene.

**Cynodontia:** “dog tooth,” a large suborder of therapsids that arose in Africa in the late Permian, following the theriodonts in the line leading to mammals; the cynodonts, one of the few synapsids that survived the end-Permian extinction, diversified globally in the Middle Triassic and probably gave rise to the chiniquodontids, possible ancestors of mammals; the cynodonts were then displaced by mammals by the end of the Jurassic; see also *Charassognathus* and *Procynosuchus*; late Permian to Late Jurassic.

**Cynognathus:** a genus of large early Mesozoic cynodonts, about the size of a wolf; South Africa and South America, Early Triassic.

**Cyonosaurus:** a genus of gorgonopsian therapsids of the late Permian; there is recent but inconclusive evidence that it may have survived the end-Permian extinction; South Africa, late Permian.

**Cypridea:** a genus of freshwater podocopid ostracods, possibly related to the modern Cyprididae; Middle Jurassic to Cretaceous.

**Cystoidea:** a class of primitive echinoderms in the subphylum Blastozoa; attached to hard substrates by a stalk and generally characterized by pentameral symmetry and triangular pore openings; may have given rise to the crinoids (see also **Edrioasteroidea**); Middle Ordovician to Devonian.

**Cystoporata:** “sac-like passages,” an order of marine bryozoans in the still-extant class Stenolaemata; characterized by elongated zoecia on supporting blister-like vesicular structures called cystopores; Ordovician to Permian.

# D

***Dactyloceras***: a genus of planulate ammonoids in the order Ammonitida; only 3 inches wide at the most but very numerous; it was part of the radiation of ammonitids that followed the extinction of most ceratitid ammonoids at the end of the Triassic; occurring in the Pliensbachian, always in a stratum just above that of *Amaltheus*, it is a significant index fossil; global distribution, Early Jurassic, 200–172 Ma.

***Daedon***: a genus of artiodactyl mammals in the family Entelodontidae; mainly a scavenger, it was bison-sized and resembled a giant warthog; the type genus, *D. shoshonensis*, was the largest entelodont, 12 feet long, 6 feet high at the shoulder, and with a skull 3 feet long; widespread across North America, Oligocene to middle Miocene;

***Dakosaurus***: “biting lizard,” a genus of large marine crocodylomorphs in the clade Thalattosuchia and family Metriorhynchidae. It was up to 16 feet long and a good swimmer, with a finned tail and paddle-shaped limbs. The skull was up to 3 feet long, with a jaw containing dozens of sharp, serrated teeth. *Dakosaurus* was mainly marine, but whether it gave birth at sea or on land is unclear. North and South America, Europe, and Russia; Late Jurassic to Early Cretaceous, 160–135 Ma.

***Dalmanites***: a genus of phacopid trilobites in the suborder Phacopina and family Dalmanitidae; 2 to 3 inches long, *Dalmanites* is characterized by large and raised schizochroal compound eyes and a significant tail spine; global distribution, Silurian to Early Devonian.

***Dapedium***: a genus of actinopterygian fish in the order Semionotiformes and family Dapediidae; a durophagous fish, it had peg-like teeth useful for crushing hard-shelled invertebrates; it was up to 16 inches long, deep-bodied, protected by thick dermal head bones and a covering of rhombic ganoid scales; North America and Europe, Late Triassic to Late Cretaceous.

***Daphoenodon***: a genus of large carnivorous canids in the family Amphicyonidae; widespread in North America, late Oligocene to Miocene.

***Darwinius masillae***: a contentious species of early cat-sized primates from about 48 Ma, about 2 feet long. A nearly complete skeleton was found in 1983 in the Messel Shale Pit that has opposable thumbs and fingernails rather than claws; absent are the toothcomb and grooming claws characteristic of more primitive animals. Its authenticity and importance, however, are in dispute, partly because of collection difficulties. Like most specimens from Messel, the specimen of *Darwinius* is part and counterpart of a split bedding plane, covered with resin to preserve it, so that the bones cannot be individually handled and carefully examined. Germany, Middle Eocene.

***Darwinopterus***: a genus of pterosaurs in the family Wukongopteridae; dated at 161 Ma, it is notable for possessing characteristics of both large groupings of pterosaurs, the “rhamphorhynchoids” and their descendants the pterodactyls; China, Late Jurassic.

***Daspletosaurus torosus***: “horrible muscular lizard,” the only named representative of a genus of large tyrannosaurs in the subfamily Tyrannosaurinae; closely related to the later *T. rex*, *Daspletosaurus* grew up to 30 feet long; there is some evidence that it lived in social groups; Alberta and Montana, Late Cretaceous, 77 to 74 Ma.

***Dastilbe***: a genus of gonorhynchiform fish in the family Chanidae; from 1 to 2 inches long, it has been found in large numbers in the Crato Formation of Brazil; South America and Africa, Early Cretaceous, 125–110 Ma.

***Dasyatidae***: a family of rays in the order Myliobatiformes; commonly called whiptail stingrays, they are characterized by flattened fin discs and a generally oval outline, and also by venomous stingers at the base of the tail; they may have originated in the Late Jurassic and were widespread from the early Eocene to the late Miocene; global distribution, Early Cretaceous to Recent.

***Dasyuromorphia***: the still-extant order of marsupial mammals that includes the Dasyuridae and the extinct Thylacinidae; Australia and New Guinea, early Oligocene to Recent.

***Davidsonina septosa***: a spire-bearing species of articulate brachiopods in the class Rhynchonellata, order Spiriferinida, and family Davidsoninidae, significant as an index fossil; Europe, Early Carboniferous.

***Daxatina canadensis***: a species of ceratitid ammonoids in the family Trachyceratidae; its first appearance marks the beginning of the Late Triassic at 237 Ma; Italy.

***Dayiidae***: a family of brachiopods in the class Rhynchonellata, order Atrypida, and superfamily Dayioidea; Europe, Asia, and North Africa; early Silurian to Early Devonian.

**Deccan Traps:** an area of large volcanic flows in India, mainly basalt, resulting from an eruption near the end of the Cretaceous; it is one of the largest geological features of Earth, covering an area about 200,000 square miles.

**Decennatherium:** a genus of artiodactyl mammals in the family Giraffidae, similar to the later *Sivatherium*, *q.v.* *Decennatherium* has been known for several decades from several specimens found in Spain and is now well-known from an almost complete skeleton described in 2017. The recent specimen, named *D. rex*, was about 10 feet tall and 7 feet at the shoulder; it has two small ossicones behind its eyes and two longer ones at the back of its skull. Europe, late Miocene, 9 Ma.

**Declinognathodus nodiliferus:** a species of conodonts whose first appearance marks the beginning of the Late Carboniferous (Pennsylvanian) at 323.2 Ma; United States.

**Deinocoelurus:** a genus of primitive theropod dinosaurs in the family Deinocoeluridae; 36 feet long, it was the largest ornithomimid; known mainly from its large forearms, which were 8 feet long, and its hands tipped with three 10-inch claws; Mongolia, Late Cretaceous, 71–69 Ma.

**Deinogalerix:** “terrible shrew,” a genus of omnivorous hedgehogs in the family Erinaceidae. Some species grew to the size of a wolf, an example of island gigantism. *Deinogalerix* had a long, thin skull and hair, not the spines of modern hedgehogs. Restricted to the Gargano Peninsula of Italy, which was the location of several islands during the Miocene; Miocene to Pliocene.

**Deinonychus:** a monospecific genus of saurischian dinosaurs in the family Dromaeosauridae; about 11 feet long, with 3 claws on each manus and pes, *D. antirrhopus* was an efficient predator; like other dromaeosaurs, it had a sickle claw on the second toe of each pes; North America, Early Cretaceous, 115 to 108 Ma.

**Deinopoidea:** a still-extant superfamily of orb-weaving spiders in the order Araneae. They produce a web of cribellate silk that appears to be combed, and in which insect legs become caught in the same way that the Velcro fastening fabric works. Fossil specimens of their webs are sometimes found because of insects trapped in them; the oldest known complete orb web with prey attached (a fly, a mite, a beetle, and a wasp leg) was found in 2005 in a Lower Cretaceous deposit in Spain. Inconclusive phylogenomic research has challenged the monophyly of the Deinopoidea. See also **Araneoidea**. Global distribution, Middle Jurassic to Recent.

**Deinosuchus:** “terrible crocodile,” a genus of gigantic crocodylians that lived for less than 10 million years, from about 81 to 73 Ma; about 30 feet long and weighing up to 5 tons, *Deinosuchus* inhabited the shallow sea in the middle of North America, where its diet included dinosaurs and turtles; a five-foot long skull found in Texas in 1997 bears teeth 5 to 6 inches long; Late Cretaceous.

**Deinotheriidae:** a family of late Cenozoic elephant-like proboscideans whose most notable feature was the pair of long, down-curving tusks on the lower jaw; similar to the modern elephant but probably not ancestral to it; their extinction

coincided with the worldwide Quaternary extinctions of many large mammals; Europe, Asia, and Africa; Miocene to late Pleistocene.

***Deiphon***: a genus of phacopid trilobites in the family Cheiruridae; characterized by a set of numerous strong spines and by the warty surface of the glabella, which is similar to that of *Phacops rana*; Silurian.

***Deltadromeus***: a genus of ceratosaurian theropod dinosaurs; agile and probably a fast runner although it weighed up to 2 tons and grew to 26 feet long; its relationship to the similar *Bahariasaurus* is still unclear; Kem Kem beds, between Morocco and Algeria, Late Cretaceous.

***Deltatheridium***: a genus of basal metatherian mammals in the order Deltatheroidea and family Deltatheridiidae; 6 inches long, scansorial, and carnivorous, it has a combination of marsupial and placental characteristics; Mongolia and possibly North America, Late Cretaceous, 80 Ma.

**Deltatheroidea**: an order of basal metatherian mammals, near the beginning of the line of descent leading to the marsupials; they were scansorial omnivores and widespread in the Cretaceous; see also ***Gurbanodelta kara***; Central Asia and North America, Early Cretaceous to late Paleocene.

**Delthyridina**: see **Spiriferidina**.

***Deltoblastus***: a genus of blastoid echinoderms in the order Spiraculata; characterized by a conical shape with depressed ambulacra; attached to the substrate, from 1 to 3 inches long; similar but not directly related to the better-known *Pentremites*, it was one of the last of the Blastoidea, which disappeared at the end of the Permian.

**Demospongiae**: the largest and most diverse class of the phylum Porifera, the sponges; ranging from encrusting forms to large genera up to 3 feet in diameter, they comprise 80 percent of known modern sponges; their skeletons are composed of siliceous spicules, spongin fibers, or both; see also **Sphaeractinoidea**; Cambrian to Recent.

***Dendrerpeton acadianum***: an obscure species of temnospondyl amphibians, an early tetrapod known only from disarticulated fossils; Nova Scotia, Early Pennsylvanian.

***Dendrograptus***: a genus of irregularly branching graptolites in the order Dendroidea; Europe, Asia, and North America; late Cambrian to Middle Devonian.

**Dendroidea**: an order of sessile branching graptolites that originated in the middle or late Cambrian, the earliest order of the Graptolithina; probably ancestral to the other major graptolite order, the Graptoloidea, which appeared in the Early Ordovician; most genera of the Dendroidea were benthic, attached by holdfasts to the substrate and often bushy; the order is exemplified by *Dendrograptus*, *Callograptus*, and *Dictyonema*; early Cambrian to Early Carboniferous.

***Dendropithecus***: a genus of early primates in the superfamily Hominoidea and family Pliopithecidae; 2 feet tall, it may be ancestral to the gibbons; East Africa, early to middle Miocene.

**Denisovans**: an extinct species of humans in the genus *Homo*. The Denisovans were a relatively small group of hominins who lived in Southern Siberia between 110,000 and 50,000 years ago. They are related to Neanderthals, who are known to have lived between this area and Western Europe up to 40,000 years ago, and they may also have interbred with other hominins, such as *Homo erectus*. This culture supplies more evidence that many types of slightly differentiated hominins co-existed with *H. erectus* for long periods of time.

**denticle**: pointed, placoid scales of cartilaginous fish; also, serrations on the teeth of other animals.

**dentition**: Since teeth fossilize easily and are the most common fossil specimens of many animals, patterns of dentition are paleontologically important. The type of tooth often tells a great deal about diet and lifestyle, and the number and types of teeth are often used in classifying animals.

The manner of replacement of teeth is also sometimes a significant descriptive characteristic. Monophyodonty refers to having only one lifetime set of teeth. Diphyodonty refers to having two sets of teeth, one deciduous (“milk teeth”) and one permanent, and is one of the characters that differentiate mammals from therapsids. Polyphyodonty is the condition of having an indefinite number of tooth replacements. See also **brachyodont**, **bradyodont**, **bunodont**, **heterodont**, **hypso-dont**, **lophodont**, **petalodont**, **sectorial tooth**, and **selenodont**.

**Deperetellidae**: a family of perissodactyl mammals in the superfamily Tapiroidea, ancestral to modern tapirs; Asia, middle to late Eocene.

**derived character**: a novel character that first appears in the most recent common ancestor of a lineage and is passed on to its descendants.

**dermal ossicles**: bony plates attached to the skin or cuticle of many animals, sometimes constituting an armored covering; found in dinosaurs, reptiles, turtles, echinoderms, and several xenarthran mammals, such as the ground sloth *Paramylodon* and the glyptodonts.

***Desmatochelys***: a genus of cryptodiran marine turtles in the extinct family Protostegidae; the older of its two species, *D. padillai*, is the oldest known sea turtle, 7 feet long and dated at around 120 Ma; South America, Early Cretaceous.

***Desmatosuchus***: a genus of aetosaurs in the family Stagonolepididae; about 16 feet long, the crocodile-like *Desmatosuchus* bore a series of striking spines on its sides, the farthest forward as long as 18 inches and pointing backward; North America, Late Triassic, 230–210 Ma.

**Desmodonta**: a suborder of bivalve burrowing mollusks; characterized by the absence of lateral teeth and few if any cardinal teeth; Ordovician to Permian.

**Desmostylia:** “bundle pillar,” an order of quadrupedal aquatic perissodactyl ungulates, the only known extinct order of marine mammals. About 6 feet long and up to 450 pounds, they were very similar to proboscideans and modern manatees, but the similarities may be only a result of convergence. Desmostylians are characterized by forward-pointing incisors and tusks, and by a dentition of closely packed molars resembling a bundle of pillars. Japan and North America, late Oligocene to early Miocene.

**Deuterostomia:** a superphylum including the phyla Chordata and Echinodermata, and the subphylum Hemichordata; the earliest deuterostomes are microscopic organisms of the early to middle Cambrian, the earliest accepted being *Saccorhynchus*, dated at 540 Ma; see also **Vetulicolia**; cosmopolitan, early Cambrian to Recent.

**Devonian:** the fourth period of the Paleozoic Era, from 416 to 359 Ma, divided into Early, Middle, and Late Epochs. Known as the age of fish, the Devonian saw a great radiation of marine and freshwater fish, including the first sharks. The first ammonoids developed from the bactritid nautiloids in the Early Devonian. Evolutionarily, the period is most important for its terrestrial developments. Aquatic fish like *Eusthenopteron* in the Middle Devonian gave rise to tetrapods like *Tiktaalik* and *Ventastega* that began to move ashore toward the end of the period. The first insects appeared at the same time as a rapid radiation of terrestrial plant life. At the beginning of the period, the tallest plant was only about 3 feet high, but as the vascular plants spread, trees and even forests appeared. The progymnosperms and other ancestors of most living plant groups were present by the end of the period.

**Devonian extinction:** a series of closely spaced extinction pulses during the last 5 million years of the period (some argue for seven events over the final 25 million years). The principal extinctions occurred at the beginning and end of the Famennian Stage, respectively the Kellwasser and Hangenberg Events. Major groups that disappeared included the placoderms and most agnathans. The coral and stromatolite reef-builders were so severely affected that there was little reef-building until the rise of the scleractinian corals in the Mesozoic. The trilobites were especially affected by the Kellwasser Event, and only those of the order Proetida survived into the Carboniferous. Some have pointed to global cooling and widespread anoxia in the oceans as a cause of some of these extinctions, but the evidence is inconclusive.

**Diacodexis:** a genus of small Eocene mammals in the family Dichobunidae; *Diacodexis* is the oldest known artiodactyl mammal, although its feet still had five toes, with elongated third and fourth digits; it was less than 2 feet long, but it had a longer tail; North America, Europe, and Asia; early to middle Eocene.

**Diadectomorpha:** a group of bulky anthracosaurian amphibians closely related to the early amniotes, although their mode of reproduction is still obscure; reptile-like and among the largest early tetrapods, some herbivorous genera (such as *Diadectes*) grew up to 10 feet long; North America, Europe, and Asia; Late Mississippian to late Permian.



**Diadematoidea:** a still-extant order of euechinoid sea urchins; characterized by very long and slender spines and ten buccal plates around the mouth; Late Jurassic to Recent.

**Diademopsis:** a genus of primitive echinoids in the order Pedinoidea and family Pedinidae, a common echinoid in Europe during the Early Jurassic. Generally 1–2 inches wide, with tessellate plating; long, slender spines; and a lantern with broad, grooved teeth. Probably ancestral to euechinoids. Europe and South America, Late Triassic to Early Jurassic.

**diagenesis:** in geology, a term for the process of changes in a rock over time, such as a sedimentary rock becoming metamorphosed. In paleontology, diagenesis refers to the final taphonomic process undergone by a fossil, especially to the process of mineralization, which varies widely according to the burial site (such as in sediment, amber, tar, hydrothermal vent, or volcanic material). Successive diagenetic events may occur if the burial environment is disturbed.

**Diania cactiformis:** a wormlike animal dated at about 520 Ma, related to an extinct group of armored lobopods; characterized by robust spiny limbs, possibly jointed; it may be a forerunner of true arthropods; Chengjiang, China, early Cambrian.

**Dianulitidae:** a family of stenolaemate bryozoans in the extinct order Cystoporata; North America, Europe, and Asia; Ordovician and Silurian.

**Diapsida:** “two arches,” the stem group of early amniotes that gave rise to snakes, lizards, and crocodiles; identified by two temporal fenestrae behind each eye, except that modern snakes and lizards have lost one or both of these openings; the diapsids appeared late in the Pennsylvanian, after the first synapsids.

**diatoms:** a kind of glassy-shelled algae in the class Bacillariophyceae; generally flat and round like two pie plates stuck together, they constitute an important area of study in micropaleontology; they appeared in the fossil record in the early Jurassic and exist globally in marine and freshwater bodies of water; see also *Stephanodiscus*.

**Diatrypa:** see *Gastornis*.

**Dibunophyllum:** a genus of solitary rugose corals in the family Aulophyllidae; North America and China, Late Devonian to Late Pennsylvanian.

**Dicellograptus:** a widespread and varied genus of graptoloids in the family Dicranograptidae; part of the leptograptid fauna, an important graptolite index fossil group in the Late Ordovician; global distribution, Middle to Late Ordovician.

**Diceratherium:** “two-horned beast,” a genus of large perissodactyl mammals in the family Rhinocerotidae; it weighed about a ton and was characterized by a pair of horns side by side on the nose, the first rhinocerotoid to develop horns; widespread in North America, Europe, and Asia; Oligocene to Miocene.



**Dichobunidae:** a family of primitive artiodactyl mammals, characterized by bunodont upper teeth and typified by *Diacodexis*, *q.v.*; global distribution, Eocene and Oligocene.

**dichograptid fauna:** an important fossil group of the Ordovician, including the many-branched *Dichograptus* and other graptoloid index fossils; see **Graptolithina**.

***Dichograptus octobrachiata:*** an unusual species of graptolites, living in a circular colony 3–4 inches in diameter; its 8 equal-length stipes were slender, with very small individual animals; North America, Europe, and Australia; Early Ordovician.

***Dicksonia:*** an enigmatic genus of flat-bodied fossils in the family Dickinsoniidae. It is an iconic member of the Ediacaran biota and variously considered to belong to the fungi, the coelenterates, or an otherwise unknown class. The body is a bilaterally symmetrical ribbed oval, usually a few inches long, but the largest known was about 3 feet long and 2 feet wide. Although hundreds of specimens have been studied, little is known about its mode of life. Its trace fossils, generally ferruginous impressions on the underside of an overlying stratum, have been dated between 579 and 555 Ma. Australia and Eastern Europe, Ediacaran.

***Dicksonia:*** a still-extant genus of pteridophyte tree ferns in the order Cyatheaales and family Dicksoniaceae; Australia and New Zealand, Jurassic to Recent.

***Dicranograptus:*** “two-headed,” a genus of bilateral graptolites in the order Graptoloidea and family Dicranograptidae; a planktic member of the leptograptid fauna, it is characterized by convoluted thecae; cosmopolitan, Early to Late Ordovician.

***Dicranurus:*** “two-head-tail,” a genus of spiny trilobites in the order Odontopleurida and family Odontopleuridae; a very spinose trilobite, characterized by two thick, curling spines behind the head; similar to the spiny trilobites of the order Lichida; North America, North Africa, and Australia; middle Silurian to Lower Devonian.

***Dicroidium:*** a poorly known genus of woody seed ferns in the family Corystospermaceae; its leaves have been found attached to branches and some reports refer to it as a tree dozens of feet high, but its fossils are known mainly as leaves of a wide variety of types; widespread in Gondwana throughout the Triassic.

***Dictyoclostus:*** a genus of brachiopods in the extinct order Productida and family Productidae; its concave and convex valves are characterized by a network of fine lines, grooves, and spines; *D. americanus* is an index fossil in the Late Pennsylvanian; global distribution, Carboniferous to Permian.

**Dictyonellida:** a Paleozoic order of articulate brachiopods in the class Chileata; characterized by a fine network of rays on the surface of the shell; Ordovician to Permian.

***Dictyonema:*** “net thread,” an important genus of many-branched dendroid graptolites; sessile, characterized by its net-like structure and many small thecae; late Cambrian to Early Ordovician.

**Dictyospongia:** a genus of hexactinellid reticulate sponges in the family Dictyospongidae; characterized by a smooth reticulum and an inverted cone shape; North America, Silurian to Carboniferous.

**Dictyothyris:** a genus of articulate brachiopods in the still-extant order Terebratulida and superfamily Terebratuloidea; characterized by an erect beak and large pedicle aperture; Middle Jurassic to Early Cretaceous.

**Dicynodontia:** an infraorder of herbivorous therapsids; short and strongly built, with some genera such as *Placerias* growing two tusks, they appeared in the middle of the Permian; along with the theriodonts, they were the sole synapsid survivors of the end-Permian extinction; they then diversified globally in the Triassic, most disappearing in the end-Triassic extinctions, but some possibly surviving in Australia into the Cretaceous.

**Didelphidae:** “two wombs,” the opossums, a still-extant family of arboreal marsupials; didelphids probably originated in North America in the Early Cretaceous; they were abundant in the Late Cretaceous but became extinct there in the Miocene; after migrating in the Eocene to Europe and spreading worldwide, they again appeared in North America near the end of the Pliocene.

**Didelphodon:** a genus of marsupial mammals in the family Stagodontidae; the type species *D. vorax*, although only as large as a small badger, is estimated to have had a stronger bite than a hyena; North America, Late Cretaceous.

**Didolodontidae:** an extinct family of middle-sized condylarths in the superorder Meridiungulata; about 2 feet long, they were scansorial insectivores; South America, Paleocene to early Miocene.

**Didymograptus:** “double branch,” one of the larger graptolites, a graptoloid genus identified by its two long branches; often referred to as the “tuning fork” graptolite; Early to Middle Ordovician.

**Dielasma:** a widespread genus of articulate terebratulid brachiopods; it had a rather smooth shell surface, with the pedicle valve much larger than the brachial valve; Carboniferous and Permian.

**Diictodon:** one of the most successful synapsids of the Permian, a genus of herbivorous dicynodont therapsids in the family Pylaecephalidae; less than 2 feet long and armed with a pair of tusks extending down from the upper jaw, *Diictodon* burrowed helical tunnels as deep as 5 feet where articulated skeletons have been found; known mainly from Southern Africa but also Asia, 260 to 254 Ma.

**Dikelocephalus:** a genus of large North American asaphid trilobites in the family Dikelocephalidae; only slightly longer than wide, it was 16–20 inches long; late Cambrian.

**Dikika baby:** found in 2000 and possibly the most complete example of *Australopithecus afarensis*, a fossil of a baby of nursing age; it includes a complete

torso, a face, and some leg bones; 3.3 Ma, Dikika region of Ethiopia, across the Awash River from Hadar.

***Dilong***: a monospecific genus of small dinosaurs in the family Proceratosauridae; in the Jehol biota, it is generally considered an early tyrannosauroid (perhaps the oldest) although it seems to have had a feather-like body covering; from 5 to 6 feet long, *D. paradoxus* is known from almost complete specimens from the Lower Cretaceous Yixian Formation; China, 125 Ma.

***Dilophosaurus***: “two ridges,” a monospecific genus of theropod dinosaurs; relatively small but an efficient predator. *D. wetherilli* was about 23 feet long and weighed about 1100 pounds, with long teeth; its most distinctive feature is a pair of crests along the front of its skull; Kayenta Formation, Arizona, Early Jurassic, 193 Ma.

***Dimatherium***: a monospecific genus of early paenungulate mammals in the order Hyracoidea; *D. patnaiki*, discovered in 2010, is the earliest-known hyracoid; Fayum, Egypt, late Eocene.

***Dimetrodon***: a genus of large synapsids in the family Sphenacodontidae, characterized by its very large spinal fin, which gives it the nickname “sailbacked.” Most species of *Dimetrodon* ranged from 6 to 15 feet long, and it was an apex predator. It is named for its unusual heterodont dentition, having several sizes of teeth in a large jaw. The sail may have regulated body temperature, but recent researchers have challenged that theory; other theories also have little support. North America and Europe, early Permian.

***Dimorphodon***: a genus of rhamphorhynchoid pterosaurs. It had a wingspan of almost 5 feet, a large head, and three large claws on its wings. *Dimorphodon* is named for its heterodont dentition, having sharp, protruding anterior teeth and also shorter and flatter teeth toward the back of the jaw. The type species is *D. macronyx*, and a possible second species (*D. weintraubi*) was named in 1998. Europe and possibly Mexico, Early Jurassic.

**Dimylidae**: an extinct family of insectivorous mammals in the still-extant superfamily Erinaceoidea; 4–8 inches long, it is distantly related to the modern desman and hedgehog; known only from the Miocene in Europe.

***Dinaelurus***: a genus of feliform carnivores in the family Nimravidae; known only from a relatively broad skull and partial skeleton found in the John Day Fossil Beds; North America, Oligocene to early Miocene.

**Dinocephalia**: “terrible head,” a clade of large therapsids of the Permian. Ranging from dog-sized (*Pampaphoneus biccai*) to more than 15 feet long (*Moschops*), they were the least advanced therapsids and were similar to their ancestors the pelycosaurs. Among the largest animals of the Permian, some were herbivorous and others carnivorous. The dinocephalians are known only from the period 272 to 260 Ma, becoming extinct with no known descendants. See also *Titanophoneus potens*. South America, Europe, Asia, and South Africa; middle to late Permian.

**Dinocerata:** an order of large, herbivorous ungulate mammals; the niche of the Dinocerata as large browsing animals was gradually taken over in the late Eocene by the brontotheres; the best-known dinoceratan is *Uintatherium*; Laurasia, late Paleocene to late Eocene.

**dinoflagellates:** “whirling whips,” an enigmatic group of protists; second only to diatoms as primary producers in the oceans, dinoflagellates are also present in brackish and freshwater environments; on the basis of biomarkers, they are thought to have appeared in the late Proterozoic or early Cambrian, but suggested specimens from the middle Paleozoic have been rejected (see *Arpylorus*); known more fully from the Triassic to Recent.

**Dinornithidae:** a family of moas, giant flightless ratite birds in the infraclass Palaeognathae. The largest of the moas grew to about 12 feet high and weighed more than 500 pounds; moas displayed a wide degree of sexual dimorphism, the female being much larger than the male. Along with the other family of moas, the Emeidae, they were extant in New Zealand from the Pleistocene until about two centuries ago, when the last of the moas were killed off by the Maori inhabitants.

**Dinosaur Cove:** a location on the coast of Victoria in southeastern Australia that has produced specimens of several dinosaurs, including the only *Leaellynasaura* and the first *Allosaurus* of the Southern Hemisphere.

**Dinosauria:** a large and diverse group of animals that dominated terrestrial life in many parts of the world for almost 160 million years. Several primitive dinosauriforms in the Middle and Late Triassic have been suggested as ancestors (see for example *Saltopus*), but definitive dinosaurs appeared only in the Late Triassic. The superorder Dinosauria is generally taken as including two orders, the “lizard-hipped” Saurischia and the “bird-hipped” Ornithischia. Both probably evolved from one of the thecodonts in the Late Triassic around 220 Ma and became widespread in the Jurassic. A contentious large group of dinosaurs is the Theropoda, which includes the coelurosaur, the most likely ancestral group of birds. The theropods have traditionally been classified as belonging to the Saurischia, but 2017 research argues that they are a separate group that shares more traits with the Ornithischia; this proposal joins them with the Ornithischia in the revived clade Ornithoscelida.

Ranging from rat-sized to whale-sized, various families radiated into almost all the terrestrial ecological niches, and the larger dinosaurs are the largest terrestrial animals known. None became completely marine animals, but most were probably capable of swimming, as swim tracks in Spain and Utah have shown. It seems probable that all dinosaurs were oviparous, often burying the eggs. Some genera have left clear evidence of nest-building, and some seem to have cared for the hatchlings. On this point, see for example **Egg Mountain**, *Maiasaura*, *Oviraptor*, **Titanosauria**, and *Troodon*. The number of dinosaur species declined toward the end of the Cretaceous, and none survived the end-Cretaceous extinction. Global distribution, Triassic to Cretaceous.

**Dinosaur National Monument:** a large Konzentrat-Lagerstätte on the border of Colorado and Utah that contains several hundred important fossil sites from near the end of the Jurassic; the fossils occur in strata of the Morrison Formation and consist mainly of dinosaurs and other large vertebrates; see also *Abydosaurus*; United States, Late Jurassic.

**Dinosauromorpha:** a clade of archosaurian reptiles that includes the clade Dinosauria (including birds) and the Lagerpetidae; Middle Triassic, 245 Ma, to Recent.

**Dinosaur Provincial Park:** a World Heritage Site in southern Alberta, Canada; renowned for its fossil assemblage from the Campanian Stage of the Cretaceous, it is the richest source of Late Cretaceous dinosaurs in the world.

**Diogenornis:** a basal genus of rheas in the family Rheidae; the earliest-known ratite, they were about two-thirds the size of the modern rhea; South America, Paleocene.

**diphyodonty:** see **dentition**.

**Diplacanthus:** a genus of small, edentulous acanthodian fish in the order Climatiformes and family Diplacanthidae; named for their two prominent and deeply embedded dorsal spines; synonym: *Rhadinacanthus*; North America and Europe, Middle to Late Devonian.

**Diplichnites:** the generic name for a type of trace fossil consisting of two parallel rows of tracks; it differs from *Protichnites* only in the absence of a medial furrow and could be made by the same animal.

**Diplobathrida:** an order of crinoids in the subclass Camerata, characterized by a conical or dicyclic cup and two circlets of plates; Middle Ordovician to Late Mississippian.

**diploblastic:** a term referring to animals whose blastula is composed of two germ layers, the ectoderm and endoderm; the principal diploblastic animals are the Cnidaria and Ctenophora.

**Diplocaulus:** a genus of large, flattened, newt-like amphibians in the extinct subclass Lepospondyli and order Nectridea; 3 feet long, it had the nectridean boomerang-shaped skull; North America, early to late Permian.

**Diplodocus:** “double-beam,” a genus of large sauropod dinosaurs; the name refers to the two rows of bones on the underside of the tail vertebrae, which helped to support an extremely long tail; one of the largest dinosaurs, *Diplodocus* reached lengths of more than 90 feet; its head, however, was only 2 feet long; the largest species, *D. hallorum*, was formerly called *Seismosaurus*; North America, Late Jurassic.

**diplograptid fauna:** one of the important graptolite faunas of the middle Paleozoic; characterized by the diplograptid pattern of long, feather-like stipes; see **Graptolithina**; global distribution, Middle Ordovician to early Silurian.

**Diplograptus:** a genus of scandent biserial graptolites in the order Graptoloidea; characterized by a cap-shaped float to which featherlike stipes containing large assemblages of organisms were attached; cosmopolitan, Ordovician and Silurian.

**diploid:** double or twofold.

**Diplomystus:** “double whiskers,” a genus of primitive herring-like fish in the order Clupeiformes; generally small but some genera 2 feet long; distantly related to modern herrings and sardines; well-known from the Green River Formation in Wyoming, in association with *Knighitia*; global distribution, Early Cretaceous to early Eocene.

**Diplopoda:** a still-extant class of myriapod insects that includes the millipedes; generally detritivorous, they are named “double foot” because they typically have two pairs of legs on each body segment; see also **Archipolypoda** and **Arthropleura**; Silurian to Recent.

**Diploporita:** an extinct class of blastozoan echinoderms in the class Eocrinoidea, characterized especially by paired pores in the thecal plates; similar to the Rhombifera; Early Ordovician to Middle Devonian.

**Diplotrypa:** “double hole,” a genus of stenolaemate bryozoans in the order Trepostomata; generally a dome-shaped colony up to 4 inches across, composed of circular tubes inhabited by autozooids; named for these holes and the larger holes bored in the surface by other organisms; global distribution, Early Ordovician to middle Silurian.

**Diplura:** “twintail,” a still-extant order of eyeless arthropods superficially similar to springtails (Collembola); characterized by two pairs of appendages, two antennae and two cerci, in most genera all equally long; divided into three families: Campodeidae, Japygidae, Parajapygidae, and Testajapygidae; also commonly called telsontails; Carboniferous to Recent.

**Dipneusti:** see **Dipnoi**.

**Dipnoi:** a long-lived order of bony fish, one of the oldest still-extant groups of animals; the Dipnoi flourished from the Early Devonian to the Triassic, declining since then but still represented by the tropical freshwater lungfish.

**Dipodidae:** the jerboas, a still-extant family of primitive omnivorous rodents in the infraorder Myomorpha; from 2 to 10 inches long, some with tails three times longer than their body, they are notable for their bipedal jumping ability; North America, Europe, Asia, and Africa; Eocene to Recent.

**Diprotodon:** a genus of marsupial mammals in the family Diprotodontidae; the largest marsupial known, *Diprotodon* was 10 feet long and more than 6 feet high at the shoulder, and weighed 3 tons; its clawed forefeet turned inward like those of its descendant the wombat; it inhabited open and wooded grasslands across the entire continent of Australia from the early Pleistocene to about 45,000 years ago; the date of its extinction is contentious, however, with some reports that it may have occurred as late as 28,000 years ago.

**Diprotodontia:** a still-extant, very diverse order of marsupial mammals, generally considered restricted to Meganesia; the order includes kangaroos and wallabies (see **Macropodidae**), koalas (see **Phascolarctidae**), wombats (see **Vombatidae**), and others; the largest were the extinct Diprotodontidae (see *Diprotodon*); Australia, Tasmania, and New Guinea; Oligocene to Recent.

**Diprotodontidae:** a family of herbivorous Australian marsupials in the still-extant order Diprotodontia; the family includes genera that can be characterized as marsupial hippopotamuses and rhinoceroses; the last of the Diprotodontidae became extinct about 11,000 years ago; Australia, late Oligocene to Pleistocene.

**Diptera:** “two wings,” a large order of insects considered the true flies, estimated to contain more than a million species, about 125,000 of them named. Dipterans are distinguished from other insects by having only one pair of wings, which are attached to the first thoracic segment; the second pair evolved into balancing organs. None have stings, but they generally have sucking mouth-parts and can bite. They seem to have evolved much later than the earliest insects, appearing only in the Triassic; early dipterans are numerous in the insect fauna of the Madygen Formation of Kyrgyzstan. Global distribution, Middle Triassic to Recent.

**Dipteronotus:** a genus of ray-finned fish in the family Perleididae; 2–4 inches long, the freshwater and marginally marine *Dipteronotus* was abundant in the Grès à Voltzia and is also known from a few other occurrences in Europe; Middle to Late Triassic.

**Dipterus:** a genus of bony sarcopterygian fish in the order Dipnoi; about 14 inches long and having a lung, it also closely resembles the modern lungfish in other respects; it is known only from strata of the uppermost Devonian; Europe and Australia, Late Devonian.

**Disasteridae:** a family of euechinoids in the superorder Atelostomata; no lantern, ovoid and some heart-shaped; Europe, Jurassic and Cretaceous.

**Discinoidea:** a small but long-lived superfamily of inarticulate brachiopods in the order Acrotretida; characterized by a cap-shaped, discoidal brachial valve; Early Ordovician to Recent.

**Discoidiidae:** a family of globular or conical euechinoids in the extinct order Holecypoida; Jurassic to Cretaceous.

**Discosauriscus:** “little-disk lizard,” a genus of aquatic stegocephalian seymouriamorph stem-tetrapods in the family Discosauriscidae; about 16 inches long, flattened, with wide jaws, and similar to its larger cousin *Seymouria*; characterized by a small discoidal structure in the vertebrae; known definitively only from several hundred juvenile specimens found in the lacustrine deposits of the Boskovic Furrow site in the Czech Republic, where the genus constituted a near monoculture; restricted to early Permian, 299–290 Ma.



***Discoserra***: a genus of actinopterygian fish in the small order Guildayichthyiformes, proposed as a possible stem neopterygian; its circular body is more than 12 inches in diameter and is characterized by rhombic ganoid scales and small forward-facing hooks on the dorsal scute; North America, Early Carboniferous.

**disjunct endemism**: the ecological occurrence of a species in a unique geographic range and nowhere else in the world.

**Distacodontidae**: a family of primitive conodonts characterized by a fang-like structure resulting from separation of the lamellae of the teeth; formerly called Distacodidae; Ordovician to Silurian.

**distal**: see **proximal**.

***Ditomopyge***: a genus of small trilobites in the family Phillipsiidae; only an inch long, it had strong genal spines and a broad and distinctively furrowed glabella; one of the last of the trilobites; Late Carboniferous to the end of the Permian.

**division**: a level of classification used in botanical taxonomy, the equivalent of an animalian phylum.

**Docodonta**: the shortest-lived and least diverse order of mammals in the Mesozoic. Slightly larger than mice, in the Middle and Late Jurassic they radiated mainly in Laurasia but almost globally. Their rectangular, multi-cusped teeth were well-adapted for crushing and grinding; some genera may have been aquatic. Middle Jurassic to Early Cretaceous.

***Docofossor brachydactylus***: a species of early mammaliaforms in the order Docodonta; found in the Tiaojishan Formation and dated at about 160 Ma, the 6-inch-long *Docofossor* is the earliest-known burrowing mammal; its species name refers to its having a reduced number of phalanges and short but wide fingers adapted to digging; China, Late Jurassic.

**dodo**: see **Raphinae**.

***Doedicurus***: “pestle tail, a genus of xenarthran mammals in the subfamily Glyptodontinae; the largest glyptodont at 13 feet long and 5 feet high, *Doedicurus* is known only from southern South America, becoming extinct about 11,000 years ago; late Pleistocene to Holocene.

***Dokophyllum***: a genus of solitary rugose corals in the family Ketophyllidae; a rhizosessile horn coral, *Dokophyllum* produced root-like holdfasts that anchored it to the sediment; North America, Europe, and Asia; middle to late Silurian.

**Dolichothoraci**: a group of primitive arctolepid joint-necked fish (arthrodires), bottom fish characterized by long pectoral spines; see also **Brachythoraci**.

***Doliocaris ingens***: an enigmatic species of small arthropods, tentatively placed in the proposed group Thylacocephala; it was probably 5 to 8 inches long and is especially notable for its very large and complex eyes, each of which was about one-fourth of the body length; La Voulte-sur-Rhône, France, Middle Jurassic.



***Doliodus problematicus***: a species of bottom-dwelling shark; a specimen found in New Brunswick and dated at 409 Ma is the oldest intact shark fossil, earlier sharks being known mainly from their teeth; similar to the modern angel shark, but notable for a pair of inch-long bony spines on the front edge of the fins behind the head, reminiscent of the acanthodian fish of the Silurian; Canada, Early Devonian.

***Domeykosaurus chilensis***: see *Atacamatitan*.

***Dorudon***: a genus of archaeocete whales in the family Basilosauridae; like other basilosaurids, it was notable for a blowhole halfway to its eyes, an evolutionary step toward the crown cetacean blowhole on the top of the head; it was completely aquatic and had a rudimentary tail that was almost a caudal fluke; Egypt, late Eocene.

***Dorygnathus***: a genus of small, basal pterosaurs in the family Rhamphorhynchidae; it had heterodont teeth of different types and a wingspan of about 4 feet; known only from several sites in France and Germany, especially from complete skeletons of Holzmaden; Europe, Early Jurassic.

***Dorypterus***: “spear fin,” a genus of advanced palaeoniscid fish in the family Dorypteridae; 8 inches long and characterized by a high dorsal fin almost as long as its body; late Permian.

**Doushantuo Formation**: an important Ediacaran Konservat-Lagerstätte in Guizhou Province, Southern China; covering the period 600 to 550 Ma, the formation is notable for its exceptional preservation of Ediacaran phosphatic fossils and earlier Cryogenian acritarch fossils.

***Dracorex***: a proposed genus of ornithischian dinosaurs in the family Pachycephalosauridae; known from only one possibly juvenile specimen, a skull and several vertebrae; its flat, heavy skull and snout are covered with small spikes, and some have argued that these spikes are simply juvenile forms of a *Pachycephalosaur* skull; South Dakota, Late Cretaceous, 71–66 Ma.

***Dreadnoughtus schrani***: a species of titanosaurian sauropod dinosaurs known from two partially articulated specimens found in Patagonia in 2005 and described in 2014; up to 85 feet long and 30 feet tall, it may be the largest land animal known, but its weight is disputed, variously estimated at between 40 and 60 tons; Argentina, Late Cretaceous, 84–66 Ma.

***Drepanaspis***: “sickle-shield,” a genus of heterostracan fish in the family Psammosteidae; with wide-spaced eyes and a row of spines all along its spine from neck to tail, it was named for the sickle-shaped anterior outline of its flattened, semicircular head; well-known from the Hunsrück Slate of Germany, Early Devonian, 410 Ma.

**Drepanellidae**: a family of possibly paleocopid ostracods in the suborder Beyrichicopina; one of several index fossils in the family is *Drepanella crassinoda* of the Ordovician; late Cambrian to Late Ordovician.

**Drepanosauridae:** a family of unusual reptiles in the order Protorosauria; up to 2 feet long, drepanosaurs are characterized by a sickle-shaped structure at the tip of a prehensile tail, elongated limbs adapted to climbing, and a dorsal neural hump; although generally found in moist environments, specimens were discovered in 2013 in a site in Utah that in the Triassic was a desert oasis; North America, Late Triassic, 225–215 Ma.

**Dromaeosauridae:** “running lizard,” a family of feathered, carnivorous ornithischian dinosaurs of small to medium size but well-provided with weapons, including a long sickle claw on the hind feet that may have been used to disembowel or to simply grasp prey; global distribution, Middle Jurassic to Late Cretaceous.

**Dromaeosaurus:** a genus of theropod ornithischian dinosaurs in the family Dromaeosauridae; only 7 feet long and weighing just over 30 pounds, it was a small carnivore; known only from fragments, it has been reconstructed in museum casts from what is known of other dromaeosaurids; North America, Late Cretaceous, 77–75 Ma.

**Dromiceiomimus:** a possible genus of bird-like dinosaurs of the Late Cretaceous, generally considered synonymous with *Ornithomimus*, *q.v.*

**Dromomeron:** a genus of dinosauromorph archosaurs in the family Lagerpetidae; known from several fragmentary specimens from New Mexico and Argentina, it was lightly built, about 3 feet long and undoubtedly a fast runner; North and South America, Late Triassic, 220–210 Ma.

**Dryolestidae:** a family of small pantothere eutherian mammals; known in North America and Europe, Middle Jurassic to Late Cretaceous.

**Dryopithecus:** “oak-ape,” a genus of monkey-like primates in the family Hominidae; about 4 feet long, it closely resembled modern orangutans in its long arms, short legs, and curved fingers; Asia, Africa, and Europe; late Miocene, 12 Ma.

**Dryptosaurus:** a famous genus of primitive tyrannosaurid dinosaurs; known definitively from a partial skeleton of one individual, it is estimated to have been as much as 25 feet long; named “tearing lizard” by E.D. Cope because of the 8-inch claws on at least one of the three fingers on its forelimbs; the only known large carnivorous dinosaur of Eastern North America; Late Cretaceous, 67 Ma.

**Dunbarella:** a thin-shelled pectinoid bivalve characterized by numerous fine rays on the shell exterior; only 1.5 inches wide, it was similar to the modern scallop; its fossils sometimes occur in association with ammonoids, which undoubtedly preyed on it; North and South America, Europe, and Asia; Carboniferous.

**Dunbaria:** a genus of pterygote insects in the order Palaeodictyoptera; it had sucking mouth-parts and dragonfly-like wings with a wingspan of 1.25 inches; a specimen from Kansas shows veins and color bands in the wings; North America and Russia, early to middle Permian.

***Dunkleosteus***: a genus of very large arthrodire placoderms in the order Brachythoraci, one of many armored fish that became extinct at the end of the Devonian Period. Originally named *Dinichthys terrelli*, *Dunkleosteus* grew at least 20 feet long and weighed more than a ton, with some estimates much higher. Its posterior skeleton has not been preserved, probably because it was cartilaginous. Armed with very powerful jaws and bony plates instead of teeth, it preyed upon many marine animals. Cosmopolitan, Late Devonian.

**durophagy**: see **Mesozoic Marine Revolution** and *Globidens*.

***Dusignathus seftoni deméré***: a subspecies of Pleistocene walrus intermediate between its terrestrial ancestors and later walruses; characterized by a large bone crest on its head and short, tusk-like canine teeth; one of 24 species of walruses that evolved from bear-like land animals since the late Oligocene, with *Odobenus* being the only surviving species; see also *Valenictus*; Southern California, 3 Ma.

***Dyticonastis***: a monospecific genus of amphisbaenian reptiles; a burrowing limbless lizard, *D. rensbergeri* is known only from sites in central Oregon and is the only known amphisbaenian west of the Rocky Mountains; United States, late Oligocene to early Miocene.

# E

***Echinerpeton***: a poorly known monospecific genus of early synapsids; *E. intermedium* is known only from fragmentary remains found in Nova Scotia and its relationship to other synapsids is unclear; nevertheless, it may be the oldest known synapsid, dated between 311 and 308 Ma; one specimen may have borne neural spines; see also *Archaeothyris*; Canada, Late Pennsylvanian.

***Echinocorys***: a genus of irregular burrowing euechinoids in the family Holasteridae; subconical with a flattened base; North America, Europe, and Asia; Late Cretaceous to late Paleocene.

**Echinocystitidae**: a family of early echinoids in the subclass Perischoechnoidea; characterized by four columns of plates in each ambulacrum; Europe, late Silurian to Devonian.

**Echinodermata**: “spine skin,” a phylum of marine, mostly benthic animals known definitively from the late Precambrian to the present, with about 7,000 extant and 13,000 extinct named species; the largest phylum with no terrestrial or freshwater representatives; characterized by five-point radial symmetry and an internal skeleton of calcareous plates; includes starfish, sea urchins, sand dollars, sea cucumbers, and sea lilies.

**Echinoidea**: the sea urchins and sand-dollars, a class of echinoderms in the subphylum Echinozoa. Echinoids are characterized by a generally subspherical or spherical shape, moveable appendages, and a skeleton of interlocking calcareous plates. Most have a feeding apparatus called the lantern, which is composed of five pyramidal plates, each with a single calcitic tooth; those without the feeding lantern are referred to as atelostomate. Echinoids typically have an anal opening (periproct) in the upper surface; in regular genera the periproct is in the center, while in irregular genera it is located away from the center. Global distribution, Middle Ordovician to Recent.

**Echinoneoidea:** an order of irregular echinoids established in 2010 to include the Conulidea, Echinoneidae, *Cluniaster*, and *Mattsechinus*; North and South America, Europe, and Asia; Early Cretaceous to Pliocene.

**Echioceras:** a genus of evolute ammonoids in the order Ammonitida; generally 2 inches wide and strongly ribbed; *E. raricostatum* is an index fossil in the Early Jurassic; North America, Europe, and Asia; Jurassic.

**echolocation:** the ability to locate objects by biological sonar; notable terrestrially in bats and used to a lesser extent in some birds and small mammals; in marine environments, it was first developed in the Eocene by odontocete whales and became widespread in dolphins and porpoises of the Miocene.

**Echphora:** a large genus of predatory snails in the family Muricidae; the name “bearing out” is an architectural term going back to Vitruvius and refers to the distinctive T-shaped ribs protruding from the spiral shell; Eastern North America, late Eocene to Pliocene.

**Edaphosaurus:** “pavement reptile,” a genus of pelycosaurian synapsid reptiles in the order Pelycosauria and family Edaphosauridae. Perhaps the first large terrestrial herbivore, it is named for thick clusters of teeth in both the lower and the upper jaws. It is also characterized by the showy sail that more than doubled its skin surface, extending upward along its backbone on almost two dozen long, curving neural spines more than two feet long. *Edaphosaurus* was smaller than some of its spenacodontid cousins, such as the even more spectacular *Dimetrodon*. North America and Europe, late Pennsylvanian to early Permian.

**edentates:** see **Xenarthra**.

**edentulous:** lacking teeth.

**Ediacaran:** the final period of the Precambrian Eon and Neoproterozoic Era, 635–541 Ma; formerly called Vendian.

**Ediacaran biota:** a general term for late Precambrian assemblages of primitive organisms first found in the Ediacara Hills of Australia and later worldwide. Very difficult to identify and classify, they are mostly impressions in overlying strata. The Ediacarans include the first true multicellular animals: jellyfish, soft corals, worms, and other animals that have not been identified. Many seem likely to be evolutionary dead-ends that are unrelated to later taxa, but some of the world’s current animal body plans originated in the Ediacaran. Almost all of the other current body plans originated in the great radiation of species at the beginning of the Cambrian.

**Edmontosaurus:** a genus of late Maastrichtian hadrosaurs, duck-bill dinosaurs in the subfamily Saurolophinae; synonym: *Anatosaurus*. With a short neck but almost 40 feet long, some were among the largest hadrosaurids. Well-preserved skeletons of one species, *E. annectens*, show skeletal articulation and skin impressions. One was originally named *Trachodon annectens* and referred to as the “*Trachodon* mummy” because of its skin impressions and complete skeleton; and another called

“Dakota,” found in 1999, shows possible stripes on its fossilized skin. Although widespread across Western North America, *Edmontosaurus* was first discovered in the Horseshoe Canyon Formation of Southern Alberta. North America, Late Cretaceous, 74–66 Ma.

**Edrioasteroidea:** a long-lived class of stemless encrusting echinozoan echinoderms in the paraphyletic subphylum Pelmatozoa; they may have given rise to the crinoids in the Ordovician. The edrioasteroids are characterized by curved and sometimes spiral ambulacra. Although never numerous, they survived from the early Cambrian (possibly the Ediacaran) to the Permian. Global distribution.

**Effigia:** a famous example of convergent evolution, a genus of crocodylomorph archosaurs in the family Shuvosauridae. It was 6–8 feet long, edentulous but omnivorous, and primarily bipedal, closely resembling the theropod ornithomimid dinosaurs of the Early Cretaceous. But close examination showed that, like its close relative *Shuvosaurus*, it was more closely related to crocodylians. New Mexico, Late Triassic, 210–205 Ma.

**Egg Mountain:** a well-known site of a purportedly colonial dinosaur nesting ground in the Two Medicine Formation of Western Montana, where the first dinosaur eggs in North America were found. The site is notable especially for the *Maiasaura* nests with numerous eggs and possible indications of dinosaur parenting behavior. There are also specimens of *Orodromeus* and *Troodon*, as well as *Troodon* eggs. Late Cretaceous, 84–75 Ma.

**Eileanachelys:** a genus of early turtles known only from partial specimens found in Scotland; about a foot long and low-domed, it is similar to the Early Jurassic *Kayentachelys*; Middle Jurassic, 164 Ma.

**Einosaurus:** a medium-sized horned and plated herbivorous ceratopsian dinosaur, known only from Montana; about 20 feet long and weighing about 2 tons, *Einosaurus* looked like a small *Triceratops* except that it had a downward-curving horn extending forward from its nose; United States, Late Cretaceous, 75–73 Ma.

**Elasmobranchii:** “plated gills,” a subclass of chondrichthyan fish that includes the Batoidea (skates, rays, and sawfish) and the Selachii (sharks); characterized by small scales on the skin surface and by 5 to 7 pairs of gills with exposed slits; middle Silurian to Recent.

**Elasmosauridae:** a later, highly specialized group of plesiosaurs, notable especially for a very long neck; the type species *Elasmosaurus* at 46 feet was the longest plesiosaur; global distribution, Early to Late Cretaceous.

**Elephantidae** the elephants and mammoths, a still-extant family of large proboscidean mammals that split off from mastodons and the other proboscideans in the Pliocene and spread throughout the Northern Hemisphere; represented today by two monospecific genera, which are slightly smaller than some of the Pleistocene genera; see also **mammoths** and **Mammutoidea**; North America, Europe, Asia, and Africa; late Eocene to Recent.

***Elginerpeton***: a monospecific genus of early tetrapods, intermediate between fish and amphibians; *E. pancheni* was found in Upper Frasnian strata and dated at 375 Ma, 10 million years earlier than *Ichthyostega*; known from humerus, tibia, and jaw bones, it was about 5 feet long; Scotland, Late Devonian.

***Ellesmeroceras***: a genus of small nautiloid cephalopods in the order Ellesmerocerida; the shell is usually orthoconic but may also be curved; North America and Asia, late Cambrian to Early Ordovician.

**Elliot Formation**: a rock formation in South Africa that has produced many sauropodomorph specimens, such as *Massospondylus* and *Melanorosaurus*; Late Triassic to Early Jurassic.

**El Montsec Lagerstätte**: a site in Catalonia that has produced many fossils from the beginning of the Cretaceous, about 130 Ma, slightly earlier than the better-known Las Hoyas site of Eastern Spain. El Montsec is known for the only specimen of *Noguerornis*, several important specimens of early orb-weaving spiders, and many beetles and other insects. Spain, Early Cretaceous.

***Elrathia kingi***: a genus of medium-sized trilobites in the order Ptychopariida; one of the most common trilobites of North America, commercially exploited especially from the Wheeler Shale Formation of Utah; North America, Europe, and Asia; middle Cambrian.

**Embolomeri**: a contentious suborder of large, primitive fish-eating anthracosaurian amphibians. Although they have some reptilian features, they are probably not ancestral to reptiles. The embolomeres evolved from reptiliomorph amphibians in the Early Carboniferous, developing vertebral adaptations that facilitated undulatory swimming. They survived the end-Permian extinction and may have partially adapted to terrestrial life before becoming extinct. North America and Europe, Carboniferous to Early Triassic.

**Embrithopoda**: “heavy-footed,” an extinct order of large subungulate eutherian mammals, represented mainly by genera of the Paleocene and Eocene but known best by the latest embrithopod, *Arsinoitherium*, *q.v.*; despite their resemblance to the rhinoceros, the Embrithopoda are more closely related to elephants; Africa, Asia, and Europe; late Paleocene to early Oligocene.

**Emeidae**: a family of moas; see **Dinornithidae**.

**Emuellidae**: a family of early trilobites in the order Redlichiida; characterized generally by an elongated body with numerous thoracic segments, and by long genal and pleural spines; Australia and Antarctica, early Cambrian, 520–516 Ma.

***Enaliarctos***: a genus of early pinnipeds in the superfamily Otarioidea, probably ancestral to the desmatophocids; it had a short tail and retained the carnassial teeth of its terrestrial ancestors (possibly related to the ursids) but had flipper-like limbs; North America, late Oligocene to early Miocene.

***Enaliornis*:** “sea bird,” a genus of hesperornithine birds in the small family Enaliornithidae; the type genus *Enaliornis* is the oldest-known hesperornithine, dated between 100 and 94 Ma, near the beginning of the Late Cretaceous (Albian); about the size of a large pigeon, *Enaliornis* was a foot-propelled diver and probably nested near water; it is known from three partial skulls and many bone fragments; originally named *Pelagornis* but not closely related to that bird of the Miocene; England, Late Cretaceous.

**Enantiornithiformes:** an order of birds in the subclass Enantiornithes, known only from the Cretaceous. These “opposite birds” seem to have originated in the Early Cretaceous and to have achieved global distribution toward the end of the period; they may have been the predominant type of bird during the Cretaceous, but they were all extinguished in the crisis that marked the end of the Mesozoic era. The enantiornithines were more advanced than Jurassic birds in having enlarged breast bones, shortened tails, and a pygostyle; but they were less similar to modern birds than later genera such as *Ichthyornis* and *Hesperornis*. The sparrow-sized *Iberomesornis* (Spain, Early Cretaceous, 125 Ma) had a pygostyle but with a claw on each wing was one of the most primitive of the group. The type genus *Enantiornis* (Argentina, Late Cretaceous) was more advanced and seems to have been a good flyer. See also *Eoenantiornis* and **amber**. South America, Spain, and China; Early to Late Cretaceous.

***Enchodus*:** a genus of salmoniform neopterygian fish in the family Enchodontidae; up to 5 feet long and weighing 25 pounds, *E. petrosus* was a predatory fish with fangs more than 2 inches long; seven other species were smaller; global distribution, Late Cretaceous to early Eocene.

***Encrinurus*:** an important genus of pelmatozoan inadunate crinoids in the order Encrinida; encrinites are characterized by their unopened tulip shape, with a large cup from 1 to 2 inches long, at the top of a long stalk covered with ossicles; some Triassic formations are dominated by accumulations of encrinite stalks; Europe, Asia, New Zealand, and North America; Early to Middle Triassic.

***Encrinurus*:** a widespread genus of trilobites in the order Phacopida and family Encrinuridae; characterized by the large tubercles on its headshield which give it the appellation of “strawberry-headed”; global distribution, Middle Ordovician to Early Devonian.

**Endoceratidae:** a family of large, straight-shelled nautiloid cephalopods in the order Endocerida; the family includes possibly the largest known Paleozoic fossils, specimens of the giant *Cameroceeras* reaching a length of 20–25 feet; global distribution, Early Ordovician to Early Devonian.

**Endothyroidea:** an extinct superfamily of large benthic foraminiferans in the order Fusulinida; index fossils in the Late Devonian and Early Carboniferous; global distribution, Devonian to Late Triassic.



**Ensifera:** the crickets and katydids, a suborder of stridulatory chewing insects in the order Orthoptera, among the earliest flying insects; global distribution, Late Carboniferous to Recent.

**Enteletoidea:** a superfamily of punctate articulate brachiopods in the order Orthida; global distribution, Middle Ordovician to Early Triassic.

**Entelodontidae:** a family of large, primitive artiodactyl mammals in the superfamily Entelodontoidea; although long assigned to the Suina, they are now considered closer to whales and hippopotamuses than to pigs; they are characterized by bony flanges or bumps on each side of the jaw, so that they superficially resemble warthogs; North America, Europe, and Asia; middle Eocene to early Miocene.

**entognathous:** of insects, having the mouth parts retracted below the surface of the head; a group of proto-insects in the subphylum Hexapoda are sometimes referred to as the Entognatha.

**Entomoconchacea:** a superfamily of large ostracods in the suborder Myodocopa; characterized by the absence of a rostrum above the permanent aperture; Europe, Devonian to Permian.

**Eoabelisaurus:** a genus of ceratosaurian theropod dinosaurs in the family Abelisauridae; described in 2012 and dated at about 170 Ma, it is now the earliest (by 40 million years) and most complete skeleton of an abelisaurid; Patagonia, Middle Jurassic.

**Eoalulavis:** a monospecific enantiornithine genus, the only species being *Eoalulavis hoyasi*; found at Las Hoyas, it is the earliest-known bird with an alula, a tuft of small feathers attached to the base of the thumb, improving maneuverability in flight; Spain, Early Cretaceous, 125 Ma.

**Eoandromeda:** an Ediacaran genus of possible animals of an uncertain nature; circular and up to 1.5 inches wide, they have 8 spiral arms that seem to be tubular; known only from slightly different specimens from Australia and China, they may be stem-ctenophores, but widely different interpretations have been advanced; 580–550 Ma.

**Eobasileus:** a genus of dinoceratan mammals in the family Uintatheriidae; the largest of the uintatheres, it was the size of a modern rhinoceros at 4 tons, 13 feet long, and 7 feet high at the shoulder; armed with two short tusks and three pairs of blunt horns, *Eobasileus* closely resembled its cousin, the more widespread *Uintatherium*; North America, middle to late Eocene.

**Eocarcharia dinops:** a species of large dinosaurs in the family Carcharodontosauridae; characterized by a massive brow ridge above the eyes, hence its species name, “fierce-eyed”; may have been as long as 20–26 feet; Niger, Early Cretaceous, 112 Ma.

**Eocene:** the second epoch of the Cenozoic Era, from 56 to 34 Ma. The earliest orders of modern mammals were present by the end of the epoch, and modern birds

diversified throughout. At the end of the Eocene, modern grassland ecosystems had spread, along with modern moths and butterflies as well as the larger grazing mammals. Lower world temperatures occurred toward the end of the period, introducing minor glaciations.

**Eocrinoidea:** a paraphyletic class of pelmatozoan echinoderms in the subphylum Blastozoa, ancestral to several other classes; the earliest-known stalked, arm-bearing echinoderms; Europe, North America, and China; early Cambrian to late Silurian.

**Eodalanitina:** a genus of phacopid trilobites in the family Dalmanitidae; from 1 to 2 inches long, it is notable for its raised, crescent-shaped, schizochroal eyes; it had more than a dozen thoracic segments and the small pygidium ended in a short spine; Europe, Middle Ordovician, 461–458 Ma.

**Eoderoceratidae:** a family of ammonoids in the order Ammonitida; characterized by an evolute shell and small spines; South and North America, Europe, and Africa; Early Jurassic, Sinemurian to Pliensbachian.

**Eodiscina:** a suborder of trilobites in the order Agnostida; they are isopygous and very small, less than an inch long; early Eodiscina genera are notable for their abathochroal eyes, but later genera are eyeless; global distribution, Cambrian to Silurian.

**Eodiscoidea:** a superfamily of trilobites generally considered part of the order Agnostida; see also **Pagetia**; global distribution, early to late Cambrian.

**Eodromaeus:** “dawn runner,” a basal genus of theropod saurischian dinosaurs about 4 feet long but weighing only about 11 pounds; a possible common ancestor of all other dinosaurs; Argentina, Late Triassic, 230 Ma.

**Eoenantiornis:** a monospecific genus of enantiornithine birds known from one specimen found in the Yixian Formation; dated at the beginning of the Aptian Stage, 125 Ma, *E. buhleri* was about 5 inches long; it is one of the most primitive and oldest of the known enantiornithine birds; Jehol biota, China, Early Cretaceous.

**Eognathacantha ercainella:** a possible early species of chaetognaths, known only from a whole-body specimen found in the Maotianshan Shales; China, early Cambrian, 520 Ma.

**Eohippus:** a genus of perissodactyl ungulates in the family Equidae; formerly synonymous with *Hyracotherium*, it is now considered a separate monospecific genus; *E. angustidens* was the size of a medium-sized dog; North America, early Eocene.

**Eolympia:** See **Ceriantharia**.

**Eomaia:** an enigmatic, monospecific genus of early mammals; dated at 125 Ma and known from one complete skeleton, *E. scansoria* was only about 6 inches long nose to tail; although it had several features common in placental mammals, including fur, it lacked several features common to all placentals; it also had an epipubic bone, a marsupial character; Jehol biota, China, Early Cretaceous, 125 Ma.

***Eomanis***: a genus of pangolins in the suborder Eupholidota; the earliest-known pangolin from Europe, it was only 20 inches long and had scales only on its body; Messel Shale Pit, Germany; early Eocene.

**Eomoropidae**: a primitive family of perissodactyl ungulate mammals in the suborder Ancylopoda, related and possibly ancestral to the chalicotheres; although they bore claws on their feet, they were sheep-sized grazers or browsers; Asia and North America, early Eocene.

**Eomyidae**: a family of rodents in the suborder Castorimorpha and superfamily Geomyoidea; the family includes the earliest gliding squirrel (*Eomys quercyi*) and a variety of small and middle-sized genera; North America, Europe, and Asia; middle Eocene to Pleistocene.

***Eophalangium***: see **Opiliones**.

***Eophrynus***: a genus of spider-like arachnids in the order Trigonotarbida; characterized by numerous dorsal knobs and half a dozen ventral ridges, unable to spin silk; Europe, Late Carboniferous.

***Eoraptor***: a 1992 discovery in Argentina of one of the earliest dinosaurs, dated at 231.4 Ma. A primitive saurischian close to the ancestry of both sauropodomorphs and theropods, *Eoraptor* was the size of a greyhound, about 3 feet long. It was probably mainly carnivorous but more primitive than *Herrerasaurus* and other early theropods in having no jaw-hinge, and its degree of bipedality is unclear. It had curved and serrated teeth and three-fingered hands adapted to tearing flesh. Argentina, Late Triassic.

***Eosimias***: a genus of extremely primitive anthropoid primates, significant because it seems to represent a transitional figure between the higher and lower primates. *Eosimias* is characterized especially by a deep chin and dagger-like canine teeth similar to those of many modern monkeys. Smaller than expected for an intermediate form between the upper and lower primates, it is the size of a shrew; the largest of the four species so far described weighed only 10 ounces. China, middle Eocene, 40–45 Ma.

**Eosuchia**: a polyphyletic group formerly considered an order of diapsid reptiles, now discarded except as an informal term; once considered numerous, the eosuchians are now restricted to the small family **Younginidae**, *q.v.*

***Eothele***: see **Palaeothele**.

***Eotitanops***: a genus of brontotheres, perissodactyl grazing mammals; the earliest accepted brontothere, *Eotitanops* was less than 2 feet high and resembled a small modern tapir; it had 5 digits on the manus and 3 on the pedes; North America and Asia, early to middle Eocene.

***Eotitanosuchus***: a genus of basal therapsids, placed tentatively in the suborder Biarmosuchia although significantly different from other biarmosuchians; known

from a single partial skull, it is estimated to have been about 9 feet long; Russia, middle Permian.

***Eotragus***: a genus of early ruminants in the family Bovidae; the size of a gazelle, about 40 pounds, and characterized by two vertical horns, *Eotragus* was a browser in open and wooded grasslands; the earliest-known bovid, it evolved in Eurasia around 20 Ma and appeared in Africa soon after; Asia, Europe, and Africa; early to late Miocene.

***Eozostrodon***: a contentious genus of early cynodont mammals tentatively placed in the family Morganucodontidae; known only from disarticulated fragments, mainly teeth, it is considered by some to be synonymous with *Morganucodon*; found in England near the boundary of the Triassic and Jurassic.

**Ephemeroptera**: the mayflies, an extant order of palaeopteran insects; they are aquatic and are characterized by the primitive characters of long tails and wings that cannot be folded over their abdomen; global distribution, Late Carboniferous to Recent.

***Epidendrosaurus***: a genus of sparrow-sized saurischian dinosaurs in the suborder Theropoda; notable for extreme elongation of the forelimb digits and other adaptations to a tree-dwelling habit; synonym: *Scansoriapteryx*; China, Late Jurassic, 160 Ma.

**epifaunal**: referring to benthic organisms that live on the surface of a sea or lake bed, either attached or free-moving, as opposed to infaunal organisms, which burrow into the sea bed or construct burrows or tubes.

***Epigaulus***: see *Ceratogaulus*.

**epi-planktic**: of marine organisms attached permanently to a floating substrate.

***Epithyris***: a genus of articulate terebratulid brachiopods in the family Postepithyrididae; punctate with a short loop; Europe and Africa, Middle to Late Jurassic.

***Eporeodon***: a genus of oreodonts in the family Merycoidodontidae and subfamily Eporeodontinae; herbivorous artiodactyls with four digits and weighing 200–300 pounds, they are related to camels; not numerous and restricted to Western North America, early Oligocene to early Miocene.

**Equidae**: the horses, a family of perissodactyl mammals in the suborder Hippomorpha and the superfamily Equoidea. The palaeothere *Hyracotherium*, from the middle Paleocene, had long been considered the first horse but is no longer considered ancestral to the Equidae. The earliest unquestioned Equidae are *Eohippus* and *Protorohippus*, fox-sized animals of the early Eocene. Early horses increased in size very slowly from the late Paleocene to the late Oligocene, but then diversified rapidly in the early and middle Miocene. From the late Miocene to the Pleistocene, their size continued to increase, with smaller species becoming extinct. The line of descent of the later Equidae is well-documented, from *Miohippus* (Oligocene),

*Hypohippus* (Miocene), *Merychippus* (Miocene), and *Dinohippus* (Miocene to Pliocene) to the earliest-known species of the genus *Equus*, *E. simplicidens* (late Pliocene to Pleistocene). *Equus* quickly migrated to Eurasia and Africa but became extinct in North America about 12,000 years ago.

***Equisetum*:** a still-extant genus of horsetails in the class Equisetopsida; they appeared in the Devonian and became widespread in the Carboniferous; there are about 25 extant species of *Equisetum*; global distribution.

**Equisetopsida:** a still-extant class of plants now considered a relative of the ferns and assigned to the Pteridophyta; formerly called Sphenopsida or Sphenophyta; global distribution, Late Devonian to Recent.

**Eramosa Lagerstätte:** a fossil locality in Ontario, Canada, that has produced well-preserved autochthonous specimens of eurypterids and other arthropods, annelid worms, conodonts, and fish from the middle to late Silurian.

***Erbenochile*:** an unusual genus of phacopid trilobites in the family Acastidae; notable for its two straight-sided eyes extending perpendicularly above the body; each eye had up to 500 lenses, and the largest species had 360-degree vision; North Africa, 403–393 Ma.

***Eremotherium*:** a genus of large ground sloths in the subfamily Megatheriinae; from 18 to 20 feet long and weighing 3 tons, it could sit at least partially erect; almost toothless, it was unusually sexually dimorphic, males being almost 50 percent larger than females; it appeared about 5 Ma and became extinct about 11,000 years ago; North and South America, Pleistocene.

***Eritherium*:** a proposed genus of proboscideans described in 2009, considered a basal proboscidean, much earlier than *Moeritherium* (late Eocene) and other ancestral proboscidean genera; known only from a partial skull, jaw, and teeth; Morocco, Paleocene, 60 Ma.

***Eryops*:** “drawn-out face,” a monospecific genus of semi-aquatic temnospondyl amphibians in the family Eryopidae; perhaps the largest land animal of its time at 5–10 feet long and 200 pounds, *Eryops* is one of the best-known temnospondyls; its muzzle is almost as long as that of an alligator, and its ribs are unusually short and straight; North America, Late Pennsylvanian to early Permian.

***Erythrosuchus*:** a genus of thecodont reptiles, close to the ancestry of the last common ancestor of the archosaurs; *Erythrosuchus* was 16 feet long and one of the largest predators of the Middle Triassic, competing with therapsids in Southern Africa in the period of time before they disappeared; restricted to Southern Africa, 250–230 Ma.

***Essexella*:** see Scyphozoa.

**Euarchonta:** a proposed grouping of primates, tree shrews, colugos, and the extinct Plesiadapiformes; early Paleocene to Recent.

**eucynodonts:** the clade of cynodont therapsids that includes the ancestors of mammals; global distribution, Early Triassic to Recent.

**Euechinoidea:** a subclass of echinoids that includes all post-Paleozoic echinoids; global distribution, Late Triassic to Recent.

**Eugeneodontida:** an order of holocephalic fish; distinguished by a tooth-whorl of sharp teeth in the lower jaw; poorly known although numerous; global distribution, Early Carboniferous to Early Jurassic.

**Euhoplites:** “well-armored,” a genus of small ammonitid ammonoids; characterized by strong ribbing of the shell, which was covered with tubercles and other bumps; North and South America and Europe, Early Cretaceous, 110–100 Ma.

**Eukaryota:** the domain of organisms whose complex cells have a distinct nucleus surrounded by a membrane; they range from microscopic amoebae to the largest plants and animals; although the oldest eukaryote fossils are about 1.7 billion years old, genetic evidence points to an age of about 3 billion years; see also **Archaea** and **Bacteria**.

**Eulipotyphla:** an order of small insectivorous mammals that became widespread toward the end of the Cretaceous and is still represented by the shrews, hedgehogs, and moles; see for example **Zalambdalestidae** and **Asioryctitheria**; global distribution, Late Cretaceous to Recent.

**Eumalacostraca:** the subclass of crustaceans that includes most of the modern crustaceans, such as crabs, lobsters, shrimp, crayfish, and sow bugs; global distribution, Cambrian to Recent.

**Eunotosaurus:** a genus of broad-bodied reptiles that may be an intermediate form between turtles and their Paleozoic ancestors; known from relatively rare but well-described specimens, they have a broad body with several flattened ribs and turtle-like vertebrae; see also **Pappochelys** and **Kayentachelys**; South Africa, middle to late Permian.

**Euomphalus:** a widespread genus of marine gastropods in the family Euomphalidae, generally about 2 inches wide; the closely coiled shells are usually planispiral but occasionally have a slightly raised spire; Silurian to middle Permian.

**Eupantotheria:** an order now considered obsolete; its members, generally small therian mammals between the Middle Jurassic and the Early Cretaceous, probably include the ancestors of the later marsupials and placentals; they are being reclassified into separate groups.

**Euparkeria:** a genus of primitive reptiles in the possibly monogeneric family Euparkeriidae; known primarily from the Karoo Basin in South Africa, it is close to the ancestry of the archosaurs; about 3 feet long but only 10 pounds, characterized by recurved teeth, forelimbs slightly shorter than the hindlimbs, and a row of osteoderms down the spine and tail; Africa, Early to Middle Triassic.

***Europasaurus***: a genus of small sauropod dinosaurs in the family Brachiosauridae; estimated at between 5 and 20 feet long, *Europasaurus* seems to represent an example of island dwarfism; Germany, Late Jurassic.

***Europejara olcadesorum***: a species of pterodactyloid pterosaurs in the family Tapejaridae; the oldest tapejarid known and the first found in Europe, it is a relatively small species, with a wingspan of 7 feet; dated between 130 and 125 Ma, it was discovered in 2012 in a Lower Cretaceous formation in Spain.

**Euryalida**: the basket stars, a still-extant order of asterozoan echinoderms in the class Ophiuroidea; their numerous arms grow up to 2 feet long and can branch in any direction, so that they often resemble a small, bushy plant; they have a poor fossil record; global distribution, Carboniferous to Recent.

**euryapsids**: a polyphyletic group of early Mesozoic marine reptiles including the ichthyosaurs; noted for a single temporal fenestra near the top of each side of the skull, higher than in the synapsids.

**euryhaline**: tolerant of a wide range of salinity; bivalves are more euryhaline than trilobites, which became extinct at the end of the Permian, and brachiopods, which have declined since the Paleozoic; dinoflagellates are also generally euryhaline.

**Eurymylidae**: a family of basal rabbit-like mammals, possibly ancestral to all later rodents; Mongolia, late Paleocene to middle Eocene.

**Eurypterida**: an extinct order of sea scorpions, arthropods in the class Chelicerata; they had gills, and most were less than 12 inches long, but some were larger than a man (see *Jaekelopterus* and *Pentecopterus*); they generally had more than one pair of walking legs, the last of which was larger and used for swimming; they probably gave rise to the Arachnida, but the horseshoe crab is their closest modern relative; global distribution, Ordovician to late Permian.

***Eurypterus remipes***: “wide wing oar-foot,” the first eurypterid to be discovered and the most common, a species of chelicerates in the family Eurypteridae; generally less than a foot long, but individuals as long as 4 feet are known; *E. remipes* had the spiny chelicerae and walking legs, distinctive broad paddles, and spiked telson that are characteristic of the order; North America and Europe, late Silurian.

***Eusthenopteron***: a genus of large rhipidistian fish, possibly stem-tetrapods; differences in its teeth, spine, skull, and especially the bones of its swimming fins may have led to the lobe-finned sarcopterygians and the labyrinthodont amphibians such as *Ichthyostega*; see also *Acanthostega* and **Tetrapoda**; Canada, Middle Devonian.

***Euthacanthus***: a genus of edentulous acanthodian fish in the family Climatidae; England and Scotland, Early Devonian.

**Eutheria**: the subclass of mammals that includes all living and extinct placental mammals. The earliest eutherians arose in the Early Cretaceous or perhaps Late Jurassic, and diversified slowly until the beginning of the Paleocene, when they began a very rapid radiation of species into the many ecological niches that became



available after the end-Cretaceous extinction. There are fourteen orders in the subclass, in some classifications grouped as four large clades: Afrotheria, Euarchontoglires, Laurasiatheria, and Xenarthra. Early Cretaceous to Recent.

**Euthycarcinoidea:** an obscure group of arthropods with affinities to both insects and crustaceans; about an inch long, they had a cephalon with small antennae, an abdomen with many legs, and a terminal tail spine; their fossil record is sparse but widespread: Australia, North America, Scotland, Germany, and France; Silurian to Middle Triassic.

*Euthycarcinus* “straight crab,” a genus of obscure arthropods in the subclass **Euthycarcinoidea**, *q.v.*; known from Germany and France, Carboniferous to Triassic.

**Eutriconodonta:** an enigmatic order of primitive mammals of the Mesozoic; formerly called Triconodonta, a polyphyletic grouping, but now restricted to a monophyletic assemblage of a dozen carnivorous or omnivorous genera; they include the largest Mesozoic mammals: the badger-size *Repenomamus* (3 feet long and weighing 30 pounds) and *Jugulator amplissimus*, somewhat larger; Middle Jurassic to Late Cretaceous.

**evolute:** “unrolled,” especially of ammonoids, loosely coiled, with successive whorls barely overlapping earlier ones, so that all whorls are visible.

**evolutionary adaptation:** the process by which a taxon, in the course of many generations, accommodates itself to its environment, eventually giving rise to new species as a result of the changes it undergoes.

**Exogyra:** a large genus of marine bivalves, oysters, in the still-extant family Gryphaeidae and extinct subfamily Exogyrinae; characterized by a very thick shell and a spirally twisted left valve; global distribution but declining after the Cretaceous; Jurassic to Miocene.

**extinction:** the global disappearance of a taxon resulting from its failure to produce surviving direct descendants. A marked decrease in the amount of life on Earth is referred to as a mass extinction. Background extinctions are those that occur continuously between the periods of mass extinction. The extinctions at the end of the Ordovician, Devonian, Triassic, Permian and Cretaceous periods are considered mass extinctions, and it is likely there were other mass extinctions before the Phanerozoic.



# F

**Fabaceae:** the principal family of plants in the order Fabales; the most prominent subfamilies are the Papilionoideae and Mimosoideae, important for their role in fixing atmospheric nitrogen in concert with symbiotic bacteria such as the Rhizobiales; the earliest-known fossil specimens have been found in Paleocene strata, but the family's roots go back to the radiation of angiosperms in the Early Cretaceous; global distribution, Paleocene to Recent.

***Falcarius utahensis:*** a primitive therizinosaurid saurischian dinosaur, known only from a find near the Green River in Utah. About 13 feet long and 4 feet tall, it is named for its large, sickle-shaped claws. *Falcarius* is notable for its herbivorous characteristics — small teeth adapted for shredding leaves, large gut, stout legs, and a long neck — all of which contrast with its smaller and faster carnivorous ancestors and seem to connect *Falcarius* with the later therizinosaurs, which were large herbivores. Early Cretaceous, 126 Ma.

***Falcatus:*** a genus of very small early sharks; characterized by an unusual dorsal fin that hung over the head of the male; also by a tall and strongly forked tail, and by very small pectoral and pelvic fins; North America, Middle Mississippian to Early Pennsylvanian.

**faunal succession:** the principle that groups of fauna and flora change over time, each succeeding group above the previous group in sedimentary rock strata that are often characteristic of certain intervals of time; established by William Smith, it is the basic concept of biostratigraphy.

**faunal zone:** a period of time or a stratigraphic unit that is characterized by the presence of a unique assemblage of fossils known as a guide fauna.

**faunule:** a small fauna, especially a small group of animal fossils found only in a single stratum.

**Favositidae:** a family of colonial corals in the extinct order Tabulata; the tightly packed corallites are long, thin tubes with punctate walls pierced by mural pores;

the type genus *Favosites*, called honeycomb coral, is especially important in petroleum geology; global distribution, Late Ordovician to Late Triassic.

**Fenestella:** a large genus of stenolaemate bryozoans in the family Fenestellidae; fan-shaped colonies with a net-like surface; especially widespread from the Middle Devonian to the late Permian; global distribution, Middle Ordovician to Late Triassic.

**Fenestellidae:** a large family of stenolaemate bryozoans in the order Fenestrada; the colony's skeleton consists of many stiff branches connected by crossing arms, resulting in a fenestrate, fan-shaped net; the shape, position, and orientation of the zooecia, used to identify different species, vary greatly; global distribution, Ordovician to Late Triassic.

**fenestra:** in biology, a hole or small opening in an organism's body; in paleontology, fenestrae are important usually as slits or holes in the skull, often behind the orbits (as in diapsids and synapsids), or in an individual bone (as in a neck frill); the root *fenestr-* also appears in many names of organisms with net-like structures.

**Fermeuse Formation:** one of several formations on the Avalon Peninsula in Newfoundland containing fossils of the Ediacaran **Mistaken Point** assemblage, *q.v.*

**Fezouata Formation:** a Tremadocian Konservat-Lagerstätte in Morocco, discovered in the 1990s, that has produced very well-preserved fossils from a period between the Lagerstätten of the Cambrian and the Soom Shale of the Late Ordovician; among the described species are the sponge *Pirania auraeum* and a possible marrellomorph tentatively named *Furca mauretunica*; North Africa, Early Ordovician, 480–477 Ma.

**Filicopsida:** the ferns, a class of plants in the division Tracheophyta; formerly called Pteridophyta and Polypodiopsida; the origins and the classification of ferns are unclear; global distribution, Devonian to Recent.

**First Family Site:** the location in Hadar, Ethiopia, of a cluster of finds of *Australopithecus afarensis*, including some nearly complete skeletons, the most famous called “Lucy”; most of these specimens are dated between 3.2 and 3.4 Ma.

**Fistuliporidae:** a large and diverse family of stemless marine bryozoans in the class Stenolaemata and extinct order Cystoporata; the colonies were initially encrusting, and later genera became dendroid; Silurian to Late Triassic.

**flatfish:** fish with the unusual pleuronectiform character of having both eyes on the top side of the body; this trait has made flatfish important in the history of evolution, research on some transitional species showing gradual movement of one eye toward the upper side; see *Amphistium*, *Gerrothorax*, and *Heteronectes*.

**Flexibilia:** a small subclass of stalked or creeping crinoids; characterized by a flexible tegmen with open ambulacral grooves, the calycal plates being loosely united; global distribution, Middle Ordovician to late Permian.

**Florissant Fossil Beds National Monument:** an important site in Central Colorado for insects and plants in lacustrine deposits of volcanic ash laid down at the boundary of the Eocene and Oligocene; it contains large petrified stumps of sequoia-like trees, the finest fossil insects of North America, and many angiosperms; North America, late Eocene.

**Florissantia:** a genus of sterculioid angiosperms in the family Malvaceae; its 1-inch-wide five-petaled flowers have been found throughout North America, especially in Oregon and the Florissant Fossil Beds of Colorado; North America, Eocene to Oligocene.

**Fontchevade Man:** name given to two hominin specimens found at Fontchevade, France; bearing characteristics of both *H. sapiens* and *H. neanderthalensis*, they were first dated as Pliocene and interpreted as a surprisingly early appearance of modern humans in Europe, antedating Neanderthals; but research in 2007 dated them as Pleistocene, when *H. sapiens* and *H. neanderthalensis* co-existed.

**Foraminifera:** a class of one-celled organisms in the phylum Retaria, almost all aquatic and mostly marine. They are usually less than 2 mm but range up to several centimeters long. These one-celled organisms are mostly benthic, living on or under the sea floor, while a few are planktic. Most foraminiferans develop a calcitic test, often in several concentric layers, so that many are important index fossils. Planispiral taxa are coiled, in either an evolute or an involute manner. Almost 9000 extant and almost 2000 extinct species are known. Cambrian to Recent.

**Fordilla:** the earliest-known bivalve, a widespread genus of small, primitive bivalves in the order Fordillida; suboval, about one-tenth of an inch long; only three species of *Fordilla* are currently recognized, all from the early Cambrian, about 520 Ma; see also *Pojetaia*.

**form genus:** a biological classification of a part of an organism, used when the relationship of the part to the whole organism is unclear, and mainly for plants because they seldom fossilize whole; also referred to as a parataxon.

**Formicidae:** the ants, a family of hymenopteran insects in the superfamily Vespoidea; ants evolved from primitive wasps between 130 and 100 Ma, along with the flowering plants; they became the ecologically dominant insect by the end of the Paleocene, and 10 percent of the species known from the Eocene are still present; Early Cretaceous to Recent.

**form taxonomy:** a taxonomic system based primarily on morphology rather than on phylogeny (biological relationship).

**Fort Union Formation:** a formation in the Powder River Valley in Wyoming and Montana that straddles the period between the end of the Cretaceous and the beginning of the Paleocene; it contains many important fossils, such as a still-unnamed ornithurine bird that may have survived the extinction, the taeniodont mammal *Alveugena*, and plant fossils such as *Cercidiphyllum*; 66–64 Ma.

**fossil:** There are two primary types of fossils. Body fossils are parts of an organism preserved by carbonization or permineralization, or as casts or molds. Trace fossils, such as worm and mammal tunnels or tracks, are records of some action of an organism. Fossils are typically found in sedimentary strata but may be found deformed in metamorphic deposits. Mud flows, lahars, and even igneous lava flows also often preserve many types of fossils.

**fossiliferous:** fossil-bearing, referring to any deposit or stratum of rock that contains the fossilized remains of an organism.

**fossorial:** adapted to digging and living in burrows, typical of many rodents but also badgers and some bees and wasps.

**fossoriality:** the habit of living in burrows underground; known in many instances since the Paleozoic but increasingly important as a lifestyle for small animals as open grassland increased globally during the Miocene.

***Fractofusus misrai:*** an Ediacaran rangeomorph fossil known only from the Mistaken Point assemblage; Newfoundland, Canada, 575–560 Ma.

***Fronidularia:*** a genus of foraminifera in the family Lagenidae; generally leaf-shaped; global distribution, Triassic to Recent.

***Fruitadens haagarorum:*** a species of ornithischian dinosaurs in the family Heterodontosauridae; only about 4 inches high, between 2 and 3 feet long, and weighing less than 2 pounds, it is the smallest known ornithischian; like modern birds, it ate fruit and insects; closely related to horned, duck-billed, and armored dinosaurs; United States, Late Jurassic, 150 Ma.

***Fruitafossor:*** a monospecific genus of small burrowing mammals; known only from a complete skeleton found in Fruita, Colorado, *F. windscheffeli* was only 4 inches long but has several adaptations for fossoriality and probably fed mainly on termites; it is a striking example of convergent evolution, being unrelated to any other known animals with similar habits; United States, Late Jurassic.

**fullerenes:** the term for a molecule of carbon in a hollow sphere or other shape. They form closed carbon lattices found in rocks, and because they may trap atmospheric gases at the time the rocks are formed, they have been used since the 1990s to investigate atmospheric changes in different geological time periods. For example, some investigators claim that fullerenes from some end-Permian rocks display noble-gas isotope ratios that are typical of meteorites, not Earth; these ratios are possibly evidence of a meteorite impact that may have contributed to the end-Permian extinction.

**furcula:** generally, the wishbone of birds and some dinosaurs, but see also **Collembola**.

**Fusulinida:** an extinct order of foraminiferans, important as index fossils between the Devonian and the end of the Permian; the order contains three superfamilies —

the Endothyroidea, Fusulinoidea, and Parathuramminoidea; global distribution, early Silurian to late Permian.

**Fusulinidae:** a family of large, spindle-shaped foraminiferans in the superfamily Fusulinoidea; mostly about the size of a grain of wheat but some as long as 2 inches; global distribution, Early Pennsylvanian to late Permian.

**Fusulinoidea:** a superfamily of foraminiferans in the extinct order Fusulinida; it comprises the families Fusulinidae, Ozawainellidae, Schwagerinidae, Staffellidae, and Verbeekinidae; global distribution, generally considered extinct at the end of the Permian.

***Futalognkosaurus:*** a genus of herbivorous sauropod dinosaurs; known from three partial specimens, it was found near Lake Barreales in Argentina in 2000; one of the largest dinosaurs known, it is estimated to have been at least 90 feet long; Late Cretaceous, 88–86 Ma.

# G

**Galeritidae:** a family of irregular echinoids in the superfamily Conulidea; characterized by simple ambulacral plating, they appeared about 70 Ma and became extinct at the end of the Cretaceous; Europe and Asia.

**Galliformes:** the order of birds that includes chickens, pheasants, turkeys, Guinea fowl, and grouse. The galliforms probably arose in the late Cretaceous, but few Cretaceous candidates have been proposed; one is *Vegavis iaai*, a possible anseriform bird found in Antarctica. The galliform family Phasianidae is represented by several genera that appeared in the Eocene. Global distribution, Cretaceous to Recent.

**Gamponychidae:** a family of primitive crustaceans in the extinct order Palaeocaridacea, possibly related to the eurypterids; Carboniferous.

**ganoid scales:** fish scales with a bony, enamel-like surface, common in sturgeon and gar; generally diamond-shaped and non-overlapping but linked together at joints.

***Gansu yumenensis*:** a species of Cretaceous ornithomorph birds found in Gansu and Liaoning Provinces; known from several partial specimens, it seems to be close to the ancestry of modern birds; similar in various ways to *Hesperornis*, loons, and ducks; China, Early Cretaceous, about 120 Ma.

**Garstang's Hypothesis (of vertebrate origins):** an early twentieth-century theory of chordate evolution that proposed an alternative route for chordate evolution from echinoderms; Garstang opposed Ernst Haeckel's theory, based on the principle that ontogeny recapitulates phylogeny, which is now discredited; most aspects of Garstang's theory are now accepted.

***Gasparinisaura cincosaltensis*:** a species of herbivorous ornithomorph dinosaurs; about 6 feet long, it weighed about 40 pounds; Argentina, Late Cretaceous, 85–82 Ma.

***Gastonia***: a genus of basal ankylosaurian dinosaurs, generally classified in the family Nodosauridae; from 15 to 20 feet long and about 1 ton, *Gastonia* had a strong set of spikes, scutes, and plates; Utah, United States, Early Cretaceous, 126–123 Ma.

***Gastornis***: a genus of large flightless birds in the order Anseriformes; they had massive skulls and legs and were probably good runners; although they are quite similar to the South American phorusrhacids of the Miocene, the two groups are not related; the largest species, *G. giganteus* and *Diatryma*, grew to almost 7 feet high and were about the size of the largest moas; researchers still dispute whether they were herbivorous, carnivorous, or both; North America and Europe, late Paleocene to Eocene.

***Gastrioceras***: a genus of goniatitid ammonoids in the family Gastrioceratidae; characterized by a wide umbilicus and a globose shell with a goniatitic (simple and relatively smooth) suture pattern; widespread in the Middle to Late Pennsylvanian, several species are index fossils; North America and Europe, Late Carboniferous, possibly to Permian.

**Gastropoda**: “stomach foot,” the class of mollusks that includes land, marine, and freshwater snails and slugs; the most speciose class of mollusks, originating in the late Cambrian; see *Chippewaella* and *Strepsodiscus*.

***Geiseltaliellus***: a genus of lizards in the family Iguanidae; see *Palaeopython*; Europe, Eocene to Oligocene.

**Gelocidae**: a family of hornless ungulate mammals, possibly polyphyletically related to the Pecora; among the earliest ruminants but more advanced than the Hypertragulidae; North America, Europe, Asia, and Africa; Eocene and Miocene.

***Geminiiraptor suarezorum***: a species of raptor-like dinosaurs in the family Troodontidae, found in Utah in 2010. Its head was large, as in raptors; but since it is known only from a partial jaw bone, its relationship is uncertain. It is dated between 130 and 125 Ma, almost 50 million years earlier than the numerous North American raptors of the Late Cretaceous. United States, Early Cretaceous.

***Gemündina***: a monospecific genus of rhenanid placoderms in the family Asterosteidae; its flattened body and very large, wing-like pectoral fins gave it a shape similar to that of rays (see **Batoidea**), which evolved 200 million years later in the Triassic; *G. stuerzi* is known from several exceptional specimens from the Hunsrück Lagerstätte; notable for the absence of the characteristic placoderm tooth-plates; Germany, Early Devonian.

**generalized**: of an organism: having few specific adaptations to its ecological niche.

***Geniohyus***: a genus of primitive hyraxes in the extinct family Pliohyracidae and subfamily Geniohyinae; Egypt, known only from the early Oligocene.

**Geologic Time Scale** (simplified for this book’s purposes): **Precambrian Eon**, up to 541 Ma, ending in the Neoproterozoic Era, which consists of the Tonian,

Cryogenian, and Ediacaran Periods. **Phanerozoic Eon** (541 Ma to the present), consisting of three eras: **Paleozoic Era**, Cambrian, Ordovician, Silurian, Devonian, Carboniferous (for North America, divided into Mississippian and Pennsylvanian Epochs), and Permian; **Mesozoic Era**, Triassic, Jurassic, and Cretaceous; and **Cenozoic Era**, divided into the Paleogene Period (Paleocene, Eocene, and Oligocene Epochs), Neogene Period (Miocene and Pliocene Epochs) and Quaternary Period (Pleistocene and Holocene Epochs). The Phanerozoic periods are divided into epochs, and the epochs into shorter spans called stages. For a more detailed list, see the ICZN's International Chronostratigraphic Chart.

***Georgiacetus***: a genus of protocetid whales in the suborder Archaeoceti; its pelvis was not attached to its spine, representing the loss of functional hindlimbs in whales' evolution from terrestrial ancestors; Southeastern United States, middle Eocene, 40–37 Ma.

***Geosaurus***: a genus of marine crocodylomorphs in the clade Thalattosuchia, family Metriorhynchidae, and subfamily Geosaurinae; up to 10 feet long, its classification is contentious because of small differences in specimens; probably related to *Dakosaurus*, *Cricosaurus*, and *Rhacheosaurus*; South America and Europe, Late Jurassic to Early Cretaceous.

***Gerrothorax***: a probably monospecific genus of stereospondyl amphibians in the family Plagiosauridae; about 3 feet long and extremely flattened, *G. pulcherrimus* was pleuronectiform, with both eyes on the top of its broad head; it retained its larval gills, so that it could remain underwater indefinitely, probably lying on the bottom awaiting prey; Europe, Middle to Late Triassic.

**Ghost Ranch**: a Konzentrat-Lagerstätte in New Mexico that is known for thousands of specimens of dinosaurs from the end of the Triassic; the best-known discovery was the first *Coelophysis*; United States, Late Triassic, 220–202 Ma.

***Giganotosaurus***: one of the largest known carnivores, a genus of carcharodontosaurid dinosaurs; up to 43 feet long and weighing up to 14 tons, *Giganotosaurus* was almost as large as *Spinosaurus*; known only from a skull, femur, lower jaw, and other fragments; the type species is *G. carolinii*; Argentina, Late Cretaceous, 99–96 Ma.

***Gigantopithecus***: a genus of hominoid primates in the family Pongidae, known from partial skeletons and teeth of the Pliocene in India and the Pleistocene in China, as recent as 100,000 years ago; they stood as high as 10 feet and weighed up to 1200 pounds; the largest known ape, *Gigantopithecus* was primarily herbivorous.

***Gigantoproductus***: a genus of large brachiopods in the order Productida and the family Monticuliferidae; up to 12 inches wide, *G. giganteus* is the largest brachiopod known; global distribution, Carboniferous.

**Gigantopteridales**: a diverse group of large spermatophyte trees at the end of the Paleozoic. Among the most advanced plants of the Paleozoic, they are possible



ancestors of later plant forms, including angiosperms. They had many characteristics of flowering plants but are not known to have flowered themselves; in fact, their mode of reproduction is unclear. They appeared near the end of the Permian and flourished in Asia and North America for 10 million years, briefly surviving the great extinction before disappearing in the Early Triassic.

***Gigantoraptor xu***: a species of theropod dinosaurs in the bird-like family Caenagnathidae; dated at 85 Ma but possibly younger, it had no teeth but had large claws and probably a large beak; not well-known, it is estimated to have been about 25 feet long and 2 tons in weight; see also ***Anzu***; Mongolia, Late Cretaceous, Campanian.

***Gigatitan***: a genus of large predatory insects in the order Titanoptera; notable for fluting on the wings that could produce stridulation when rubbed by the hindlegs, in the manner of modern crickets; it had a 16-inch wingspan and stout spines on the forelegs; Madygen Formation, Kyrgyzstan; Late Triassic, 230–225 Ma.

***Ginkgoites***: a form genus of the leaves of the Ginkgoales, with indented but not deeply divided fan-shaped leaves; global distribution in the late Mesozoic.

**Ginkgophyta**: a division of gymnospermous plants that first appeared in the late Permian but is now represented by only one genus, *Ginkgo biloba*, in the order Ginkgoales; the ginkgos are known in the fossil record primarily by their distinctive lobed and veined leaves.

***Giraffatitan***: a genus of titanosaurian sauropodomorph dinosaurs in the family Brachiosauridae; known from partial skeletons found in Tanzania, *Giraffatitan* is closely related to *Brachiosaurus*; it is estimated to have been more than 70 feet long and to have weighed up to 80 tons; Africa, Late Jurassic.

***Girtyocoelia***: a genus of Permian calcareous sponges in the subclass Ceractinomorpha. An important reef builder late in the Permian, especially in the economically important Permian reef complex of Texas, it seemed to be extinct in the Early Triassic but then reappeared in the Middle Triassic. Close relatives appear earlier, in Ordovician strata, but it is unclear whether they are *Girtyocoelia* itself. North America, Middle Pennsylvanian to Permian or Triassic.

***Girvanopyge***: a genus of deep-ocean trilobites in the order Asaphida and family Cyclopygidae; characterized by an unusual cylindrical thorax and a very broad glabella; Europe, Middle to Late Ordovician.

**glabella**: the convex axial segment of the cephalon in trilobites, usually bulbous on the anterior end; the animal's major organs lie beneath the glabella, which is covered by a solid cephalic shield, the carapace.

***Glabrocingulum***: a genus of low-spired marine snails in the family Gosseletinidae; United States, Carboniferous.

***Glacialisaurus***: a genus of relatively small massospondylid dinosaurs of Antarctica, one of several sauropodomorphs found in the Hanson Formation; known only from fragments of two specimens; Early Jurassic.

**Gliridae**: a still-extant family of sciuriform rodents in the superfamily Gliroidea, descended from the Ischyromyidae; the family includes the modern dormice; Europe, Asia, and Africa; early Eocene to Recent.

**Global Boundary Stratotype Sections and Points**: Markers selected by the International Commission on Stratigraphy on which the International Chronostratigraphic Chart is based. The choices are based principally on stratigraphic first appearances of particular fossils, with a few extinctions also noted. The list also includes some markers based on paleomagnetic and climatic data. See for example *Cardioceras*, *Iapetognathus*, *Marsupites*, and *Monograptus*.

***Globidens***: a genus of small mosasaurs known for its rounded teeth, specialized for durophagy — crushing turtles, ammonoids, and other hard-shelled animals; North America, Africa, and Asia; Late Cretaceous, 85–66 Ma.

**Globigerinida**: still-extant order of globose planktic foraminiferans, important as an index fossil in the Cretaceous. Simple but multi-chambered foraminiferans, the globigerines seem to be unusually resistant to mass extinctions. The genus *Globigerina*, which appeared in the Eocene, now dominates, and large areas of ocean floor worldwide are covered by the bodies of various species in the order, constituting what is called a *Globigerina* ooze. In reference to the end-Cretaceous extinction, see also *Guembelitra*. Global distribution, Jurassic to Recent.

**glossopterid flora**: an important group of pteridospermatophyte plants found in Permian and Early Triassic strata laid down in Gondwana; the absence of glossopterids in northern land masses was important early evidence of the existence of the southern supercontinent; Antarctica, Australia, New Zealand, Southern Africa, India, and South America.

***Glossopteris***: a genus of seed ferns in the extinct order Glossopteridales; characterized by a tongue-shaped leaf with a prominent midrib and veins, arranged spirally around the ends of the branches; it was a dominant plant in the Permian glossopterid flora but is rare in Triassic and Jurassic deposits; Australia, Antarctica, India, Asia, Southern Africa, and South America; Permian to Jurassic.

**Glyphocyphidae**: a family of epifaunal sea urchins, irregular echinoids in the still-extant superorder Echinacea and order Camarodonta; South America, Africa, Europe, and Asia; Early Cretaceous to Eocene.

**Glyptocrinina**: a suborder of camerate crinoids in the order Monobathrida; large, one-inch thecae in some families; Middle Ordovician to Permian.

**Glyptodontinae**: a subfamily of large, heavily armored xenarthran mammals in the still-extant order Cingulata and family Chlamyphoridae. Their striking armor consisted of a dome-shaped covering of scutes over the whole body and skull.

The type genus, *Glyptodon*, was about 11 feet long and almost 5 feet high, and weighed up to 2 tons; the southern genus *Doedicurus* was slightly larger. Living in South America for 20 million years, they entered North America in the Pliocene by migrating across the newly formed Panama land bridge. They were probably hunted to extinction by the first humans to arrive in the Americas. South and North America, early Miocene to Pleistocene.

***Glyptops*:** a genus of cryptodire turtles in the family Pleurosternidae; the type species, *G. plicatulus*, is about a foot long and is well-represented in the Morrison Formation; restricted to North America, Late Jurassic to late Cretaceous.

***Glyptostrobus*:** a still-extant genus of trees in the family Cupressaceae; related to the modern bald cypress and still represented by the Chinese swamp cypress, *Glyptostrobus* bears a cone at the tip of a branch covered with scale-like leaves and grew as high as 115 feet; North America, Europe, and Asia; Cretaceous to Recent.

***Gnathobelodon*:** a genus of proboscideans in the family Gomphotheriidae, characterized by a projecting jawbone that resembled a shoe horn; similar to *Amebelodon* and *Platybelodon* except for having no lower tusks but simply the long jawbone; North America, middle to late Miocene.

**Gnathodontidae:** a family of conodonts in the order Ozarkodinida; widespread in the early Carboniferous, they declined rapidly and became extinct in the early Permian.

**Gnathostomata (echinoids):** a superorder of irregular sea urchins that possess a feeding lantern; lower Jurassic to Recent.

**Gnathostomata (vertebrates):** “jaw-mouthed,” a superclass or infraphylum of jawed vertebrates. The gnathostomes appeared in the Middle Ordovician, derived from agnathans that had developed pectoral and pelvic fins as well as enlarged anterior gill arches, which folded over forward in some species, gradually becoming upper and lower jaws. Jaws gave such an advantage in predation that the gnathostomes became the dominant vertebrates in the oceans from the Silurian through the Early Devonian. By the end of the Devonian, almost all agnathans had become extinct. The gnathostomes were the ancestors of almost all modern vertebrates, descending through placoderms or osteichthyans. Middle Ordovician to Recent.

**Gnetales:** an unusual, still-extant order of Mesozoic gymnosperms in the class Gnetophyta, probably related to the Bennettitales; the Gnetales had a vascular system similar to that of angiosperms and have been considered possible ancestors of the flowering plants; still-extant genera include *Welwitschia*, *Gnetum*, and *Ephedra*; widespread in the Cretaceous, but possible specimens are known from the Permian, Triassic, and Jurassic; Australia, Antarctica, Africa, and North and South America.

**GOBE:** the Great Ordovician Biodiversification Event; see **Ordovician**.

**Gobiatherium:** a genus of large ungulates in the extinct suborder Dinocerata; unlike its ungulate relatives, *Gobiatherium* had no tusks, horns, or knobs on its low skull; China, middle Eocene.

**Gobipteryx:** a genus of early toothless enantiornithine birds; until 1995, when *Confuciusornis* was discovered, *Gobipteryx* was the earliest-known beaked bird; Mongolia, Late Cretaceous, 75–70 Ma.

**Gogia:** a genus of mainly North American echinoderms in the class Eocrinoidea; a common middle Cambrian eocrinoid, the plate-covered *Gogia* was one of the earliest stalked echinoderms, dating back to the late early Cambrian and disappearing toward the end of the period; North America and Spain.

**Gogo Formation:** an Upper Devonian (Frasnian) site in Western Australia, a Konservat-Lagerstätte containing exceptionally well-preserved soft-tissue fossils. Among its notable specimens are three species of armored placoderm fish that seem to have been viviparous: *Austroptyctodus gardineri*, *Materpiscis attenboroughi*, and *Incisoscutum ritchiei*. Two specimens of the latter species show evidence of fertilization of eggs inside a female fish occurring as much as 30 million years earlier than previously thought, around 380 Ma. Since the fish evidently gave birth to live young, the two fossils represent the earliest-known vertebrate mothers. The specimen of *Materpiscis* contains a fetus and an umbilical cord.

**Gomphos elkema:** the oldest complete skeleton of a rabbit-like mammal, found in the Nemegt Basin of Mongolia; closely related to both lagomorphs and rodents, it supports the idea that the two groups shared a common ancestor that lived near the end of the Cretaceous; it also indicates that lagomorphs appeared no earlier than 65 Ma; Mongolia, 55–50 Ma.

**Gomphotheriidae:** a diverse family of proboscideans in the suborder Gomphotherioidea; the largest species weighed up to 7 tons and were about 10 feet high at the shoulder; most species had four tusks and may have had elephant-like trunks; the last of the gomphotheres became extinct about 9000 years ago; global distribution except Australia and Antarctica, late Oligocene to Holocene.

**Gomphotherium:** a genus of proboscideans in the family Gomphotheriidae; 8 feet high at the shoulder and weighing 5 tons, it had four tusks; North America, Europe, Asia, and Africa; early Miocene to early Pleistocene.

**Gondwana:** the Paleozoic southern supercontinent, named for the Gondwana geological system (dated from the Carboniferous to the Jurassic) in the region of India where early *Glossopteris* investigations occurred. Located in the lower part of the Southern Hemisphere, Gondwana included what is now South America, Africa, Madagascar, India, Antarctica, Australia, and New Zealand. See also **paleogeography**.

**Gondwanatheria:** a group of primitive mammals known from fragmentary specimens from the Late Cretaceous through the Miocene, related to haramiyidans and

multituberculates; a discovery in 2010 of *Vintana sertichi*, an almost complete skull of a 20-pound gondwanatherian, greatly expanded knowledge of the group.

**Goniatitida:** a large order of Paleozoic ammonoids; characterized by goniatitic sutures, with a simple pattern of smooth lobes and saddles; widespread from the Devonian to the end of the Permian.

**Goniopholis:** a genus of Late Jurassic medium-sized crocodylomorphs in the clade Thalattosuchia and family Goniopholididae; 6–9 feet long, *Goniopholis* was very similar to modern crocodiles and is considered a neosuchian; possibly the earliest goniopholidid is *Calsoyasuchus*, known from a partial skull found in Arizona and dated at 196.5 Ma; cosmopolitan, Late Jurassic to Early Cretaceous.

**Goniopora:** a still-extant genus of scleractinian corals in the family Poritidae; a large and diverse group, generally massive but some species branching; global distribution, Early Cretaceous to Recent.

**Gorgonopsidae:** a family of theriodont therapsids; early gorgonopsians were dog-sized and some later species were the size of a large bear; they had some mammalian characters but are not considered in the direct line of descent, which goes through their cousins the cynodonts; Africa and Europe, middle to late Permian.

**Gorgosaurus:** a genus of tyrannosaurid dinosaurs in the subfamily Albertosaurinae; bipedal, as long as 30 feet and weighing almost 3 tons, it was smaller than *Tyrannosaurus* or *Tarbosaurus*; Canada, Late Cretaceous, 77–75 Ma.

**Graeophonus:** a genus of whip spiders in the order Amblypygi and family Paracharontidae; about half an inch long, three species of *Graeophonus* are known from Carboniferous sites in Nova Scotia, Illinois, and England.

**Grande Coupure:** a term used for the great turnover of mammalian faunas in Europe at the boundary of the Eocene and Oligocene, marked especially by the migration into Europe of many new Asian taxa.

**Graptolithina:** the graptolites, a class of colonial marine invertebrates in the subphylum Hemichordata, probably related to the still-extant pterobranchs. A graptolite colony is called a rhabdosome and has a varying number of stipes (branches); the individual zooids were housed in thecae on the stipes. Very little is known about the structure, morphology, or feeding habits of the zooids (see **Psigraptus**). The largest zooids were about an eighth of an inch long, and they probably could not leave the theca. Graptolites evolved from bottom-encrusting to sessile forms in the Cambrian, with the earliest sessile order, the Dendroidea, persisting to the Carboniferous. It gave rise to the planktic Graptoloidea, which diversified rapidly worldwide during the Ordovician. Graptolites are important as index fossils of the early and middle Paleozoic Era because of their global occurrence and their rapid evolution and radiation into many different species; the strata of the Ordovician and Silurian have been divided into graptolite biozones of about one million years each. The anisograptid, dichograptid, diplograptid, leptograptid, and monograptid faunas

are the most important. See also *Chaunograptus*. Middle Cambrian to Carboniferous, global distribution in the Ordovician and Silurian.

**Graptoloidea:** an order of graptolites and the only completely planktic group; generally characterized by a smaller number of stipes than the Dendroidea; they appeared early in the Ordovician and became the most prominent planktic animals worldwide until their extinction in the Devonian; Early Ordovician to Early Devonian.

**grasses:** the Poaceae (or Gramineae). The earliest-known grass fossils go back to the time of the dinosaurs, with phytoliths from grasses known in dinosaur coprolites toward the end of the Early Cretaceous. Changing environmental conditions in the Paleocene may have encouraged the spread of grasses, but the first grasslands seem to have appeared only much later, in the middle Eocene, and then to have evolved in conjunction with the rise of ungulate mammals in the Eocene. Since the Eocene, grasses have spread globally and are the most common of all plants today. See also **fossoriality** and **ungulates**.

**Great American Biotic Interchange:** the mingling of animal populations between South and North America that was made possible by the rise of the Isthmus of Panama about 3 million years ago, joining the two previously separated continents. Only a few terrestrial animals had moved from one continent to the other until the late Pliocene. The interchange resulted in many regional changes, notably the extinction of several South American groups because of the introduction of large new predators from the North.

**Great Oxygenation Event:** term referring to the production of oxygen by organisms, mainly cyanobacteria; although the timing and causes are debatable, significant oxygen production began around 2400 Ma and resulted in levels of atmospheric oxygen sufficient for complex oxygen-breathing and sexually reproducing organisms sometime in the Neoproterozoic Era, between 1000 and 600 Ma.

**Green River Formation:** a lower Eocene formation of the Western United States with significant outcroppings in Colorado, Utah, and Wyoming, including Fossil Butte National Monument; the formation has produced large numbers of fish, especially in finely varved lacustrine strata; other important fossils are early bats, the North American crocodylian *Borealosuchus*, and many stingrays, turtles, snakes, plants and insects; Eocene, 54–49 Ma.

***Greererpeton burkemorani*:** a genus of stem-tetrapod amphibians in the family Colosteidae. Almost 5 feet long, its body was eel-like, with a flattened skull 7 inches long. The short limbs had five digits but were used mainly for steering in the water. It was almost completely aquatic, remaining in rivers and lakes while other stem-tetrapods were moving ashore in the Carboniferous. North America, Late Mississippian.

**Grès à Voltzia:** a Middle Triassic Konservat-Lagerstätte in northeastern France, dated about 243 Ma. Its brackish-water deposits were laid down in a deltaic environ-

ment similar to that of the Carboniferous Mazon Creek site. The finely laminated clay rock of the Grès à Meules stratum contains very well-preserved specimens of terrestrial and aquatic fossils, including plants, millipedes and other arthropods, brachiopods, crustaceans, and insects. Fish (see *Dipteronotus*) and amphibians, mainly capitosaurid temnospondyls, are also represented.

**Groeberiidae:** a small family of South American marsupials, rodent-like but with a skull architecture and dentition different from any other mammals; late Eocene to early Oligocene.

**Groenlandaspis:** a genus of arthrodiran placoderm fish; ranging from 3 to 19 inches long, it had small toothplates and strong, pyramid-shaped thoracic armor; global distribution, Late Devonian.

**Gryphaea:** a genus of bivalves in the order Ostreoida and family Gryphaeidae. The distinctively convoluted *Gryphaea* is characterized by prominent growth bands in the thick, twisted upper valve. It was considered in the first half of the twentieth century to be a possible example of orthogenesis because of an erroneous interpretation of its coiling growth pattern, disproved by Anthony Hallam and Stephen Gould. Global distribution, Late Triassic to Eocene.

**Gryphaeidae:** a still-extant family of bivalves, sometimes called “foam oysters,” in the order Ostreoida; global distribution, Middle Triassic to Recent.

**Gryposaurus monumentensis:** a genus of herbivorous dinosaurs in the family Hadrosauridae; a duckbill, *Gryposaurus* probably ate many kinds of vegetation, having as many as 800 teeth set in a powerful jaw; North America, Late Cretaceous, 83–74 Ma.

**GSSP:** see **Global Boundary Stratotype**.

**Guaibasauridae:** an early family of saurischian dinosaurs; first proposed in 1999, its makeup is still in flux; see *Panphagia*, *Chromogisaurus*, *Agnosphitys*, and *Saurischia*; Argentina and Brazil, Late Triassic, 231–208 Ma.

**Gualicho shinyae:** a species of allosaurid theropod dinosaurs similar but not closely related to *Tyrannosaurus rex*; also described as similar to *Deltadromeus* but with much shorter forelimbs. Known from a partial skeleton found in the Huincul Formation of Argentina and described in 2016, it was about 16 feet long and weighed half a ton. Like *T. rex*, *Gualicho* had a two-digit manus on forelimbs the size of those of a human child, a result of convergent evolution. Argentina, Late Cretaceous, 95 Ma.

**Guanlong wucaii:** a species of theropod saurischian dinosaurs in the superfamily Tyrannosauroidea, perhaps the earliest basal tyrannosauroid, dated at 160 Ma. Known from two specimens described in 2006, *G. wucaii* was only about 4 feet high and 10 feet long, with three fingers on its strong forelimbs. It bore a large but fragile crest on its forehead, stretching from behind the nostrils to just behind the eyes and about 3 inches high. The function of the crest is not known, but it would appear to



be a liability in combat, since it is only as thick as a tortilla. Western China, Late Jurassic.

***Guembelitra cretacea***: a species of planktic foraminiferans in the order Globigerinida and family Guembelitriidae. Known as an opportunistic “disaster species” because, although rare at the end of the Cretaceous, it is the most common of several foraminiferans that survived into the Paleocene. Abundant in the earliest Paleocene strata, it evidently thrived in the environmental conditions following the extinction of many other species. See also **Globigerinida**. Europe, Australia, Asia, and; South America; Cretaceous to Oligocene.

**guide fossil**: see **index fossil**.

***Guildayichthys***: a genus of early marine actinopterygian fish in the order Guildayichthyiformes; only about 2 inches long, it had short, conical teeth; its disc-shaped body and robust pectoral, dorsal, and anal fins gave it good maneuverability; see also ***Discoserra***; North America, Early Carboniferous.

***Guiyu oneiros***: a species of sarcopterygian fish, the earliest-known articulated specimen of an osteichthyan; about a foot long, with ganoid scales, it was found in Yunnan Province near the site where the similar but slightly later *Psarolepis* was found; China, Early Devonian, 419–418 Ma.

**gundi**: see **Ctenodactylidae**.

***Gunflintia***: a genus of cyanobacteria that is among the earliest-known bacteria; around 2 billion years ago, it and similar photosynthetic organisms began to increase the oxygen content of the atmosphere to levels that supported more complex life forms; first found in the 1950s in the Gunflint Chert of Canada and later in Australia, Proterozoic to Cambrian.

***Gurbanodelta kara***: a species of basal metatherian mammals described in 2016, probably in the order Deltatheroidea, the latest-known deltatheroidan; known only from a jaw fragment, it was a scansorial omnivore; dated 10 million years later than the previously known deltatheroidans, it may be a Lazarus taxon if confirmed; Xinjiang, China, late Paleocene.

***Gymnarthridae***: a family of tuditanomorph lepospondyl amphibians in the order Microsauria; distinguished from other microsaurians by its single row of conical teeth; North America and Europe, Late Carboniferous to early Permian.

***Gymnocodiaceae***: an enigmatic family of small algal fossils characterized by irregular tubes with perforate walls; sometimes classified as rhodophytes and sometimes as chlorophytes; Europe, North and South America, Asia, and Africa; Permian to Cretaceous.

***Gymnolaemata***: a class of bryozoans that includes most living bryozoans; global distribution, Middle Ordovician to Recent.



**gymnosperms:** a group of seed-bearing plants that includes cycads, conifers, and ginkgos; characterized by “naked” seeds not enclosed in an ovary or seed-case as with angiosperms; they appeared in the Late Devonian and rapidly spread worldwide.

***Gyracanthus:*** a genus of acanthodian fish in the family Gyracanthidae; 2–3 feet long, *Gyracanthus* is notable for its fin spines, which were 18 inches long; global distribution, Early Carboniferous.

**Gyrogonites:** the fossil cast of the nucule, the female reproductive structure, of charophytes. The worldwide distribution and spiral ornamentations of these small, nut-like casts make them important index fossils in some freshwater deposits. Gyrogonites appear in the fossil record as far back as the Silurian.

# H

***Haasiophis***: a monospecific genus of marine snakes in the family Simoliophiidae; about 3 feet long, *H. terrasanctus* is especially notable for its hindlimbs; known from an almost complete skeleton, it figures in the ongoing debate about the origins of snakes; Israel, Late Cretaceous, 94 Ma.

**Haast's eagle**: see *Harpagornis moorei*.

***Habrohagla***: a genus of katydid-like orthopteran insects in the family Prophalangopsidae, which was formerly called Haglidae; *H. curtivenata* was 4–5 inches long and was very similar to the larger species of modern katydids; also called *Parahagla*; China and Russia, Early Cretaceous.

***Hadrocodium wui***: a species of mouse-like primitive mammal that has the earliest-known example of several mammalian ear and brain features; known only from a single skull, from which the body is estimated to have been about 1 inch long; China, Early Jurassic, 195 Ma.

**Hadrosauridae**: a family of ornithischian duck-billed dinosaurs; one of the most successful dinosaur families, persisting from 86 to 66 Ma; descendants of the iguanodontids, the hadrosaurs are divided into five subfamilies, the largest of which are the Lambeosaurinae and the Saurolophinae; middle-sized herbivores, hadrosaurs ranged in length from 18 to 54 feet; North and South America, Europe, Asia, and Antarctica; Late Cretaceous, 90–66 Ma.

**Hagerman Fossil Beds**: an important late Pliocene site in South-Central Idaho, in cliffs on the southwest bank of the Snake River. The site contains many mammals and other remains from the period about 3.2 to 3.7 Ma, notably the Hagerman horse, *Equus simplicidens*, which resembled a small zebra, about 4 feet high at the shoulder and weighing about 900 pounds. United States, Pliocene.

***Haikouella***: a genus of primitive animals, found in the Chengjiang biota; considered a probable chordate, it is similar to *Yunnanozoon* and to *Pikaia* of the Burgess Shale; China, early Cambrian.

***Haikouichthys***: a monospecific genus of primitive proto-vertebrate animals from the early Cambrian; about an inch long, it resembles a narrow *Mylokunmingia*; China, early Cambrian.

**Halitheriinae**: a subfamily of sirenian mammals in the family Dugongidae; the type genus is *Halitherium*, which is very similar to modern dugongs; North and South America, Africa, and Europe; early Oligocene to Miocene.

***Halkieria***: a genus of enigmatic Cambrian organisms tentatively considered mollusks; in appearance like an armored slug, the halkieriids somewhat resemble *Wiwaxia*; they are generally 2–3 inches long and flattened, and have the shape of an elongated oval; known primarily from *H. evangelista* of the Sirius Passet site in Greenland; North America, Europe, Asia, and Australia; early to middle Cambrian.

***Hallopora***: a large genus of “branching twig” stenolaemate bryozoans in the extinct order Trepostomata and family Halloporidae. The *Hallopora* are characterized by their dendroid habit, large pores, and many diaphragms in some branches. Bushy zoaria up to a foot across are seldom preserved intact, but the branches are important constituents of some reefs, especially Ordovician. Several species are index fossils. Global distribution, Ordovician to Devonian.

***Hallucigenia***: one of the famous genera of the Burgess Shale, now known also from cousins in China and elsewhere; possibly related to modern velvet worms (Onychophora) and to *Collinsium ciliosum*, a late Cambrian worm reported in 2015 (517 Ma), but considered by some a basal arthropod; *Hallucigenia* is notable for 14 spikes on its back, 14 limbs, and a bulbous head with two eyes and a mouth encircled by a ring of small stiffening spikes; there are also teeth farther down its throat; North America, Europe, and Asia; early to middle Cambrian.

**Halysitidae**: a family of chain corals in the order Tabulata; colonies ranged from 2 inches to several feet wide, with the corallites connecting to each other in a strikingly chain-like pattern; global distribution, Early Ordovician to Early Devonian, 472–412 Ma.

***Hamites***: a paraphyletic genus of heteromorph ammonoids in the order Ammonitida and suborder Ancyloceratina; named for the hook shape of most species, with a very evolute, spirally shaped shell; a relatively weak swimmer because of the drag created by the open shape; global distribution, Early to Late Cretaceous.

***Hamulina***: a genus of heteromorph ammonitid ammonoids in the family Hamulinidae; it has an unusual crook-shaped shell; Caribbean and Europe, Early to Late Cretaceous.

**Hangenberg Event**: an extinction event dated at about 359 Ma, at the end of the Famennian, the final stage of the Devonian, characterized by widespread anoxia in the oceans.

***Haootia quadriformes***: a species of early cnidarians, the earliest-known animal with muscles; described in 2014 and dated at 560 Ma, its body has a four-sided

symmetry and is composed of bundles of muscles stacked horizontally, with short extensions from the corners; Newfoundland, Canada, Ediacaran.

***Haplocheirus sollers***: a species of avetheropod dinosaurs that seems to be the earliest-known member of the lineage of dinosaurs that led to birds. Known from only one specimen, it is the earliest and largest known of the superfamily Alvarezsauridae. About 7 feet long in the body, it had a long tail, powerful biceps and forelimbs, and three long digits on the manus. Xinjiang, China; Late Jurassic, 160 Ma.

***Haplohippus***: a genus of horses in the still-extant family Equidae and the subfamily Hyracotheriinae; a perissodactyl ungulate, *Haplohippus* was a forest browser; North America, known from Oregon and Texas, late Eocene.

**haploid**: single or simple. Haploid cells are gamete (reproductive) cells that contain one set of chromosomes rather than the two sets of diploid cells. In fertilization, haploid gametes combine to make a diploid, producing a zygote, a fertilized ovum.

***Haplolepis***: a genus of small palaeoniscid actinopterygian fish in the family Haplolepididae; like its relative *Canobius*, a smaller ray-finned fish of the Early Carboniferous, it had vertical jaw suspension and a large gape; North America and Europe, Late Carboniferous.

**Haplorrhini**: “simple nose,” a suborder of primates that includes humans, apes, monkeys, and tarsiers, as well as their extinct primate ancestors; the Haplorrhini are actually called “dry-nosed” in reference to their lacking a rhinarium, the moist area around the nostrils of the Strepsirrhini and most other mammals; Paleocene to Recent.

**Haramyidae**: an enigmatic family of proto-mammals of the Late Triassic. *Haramiyavia* is a possible species based on jawbone and teeth fragments in a specimen of limestone from about 210 Ma, 30 to 40 million years earlier than the earliest proven mammals. Research in 2015 seems to show that the haramyids were not true mammals but part of a side-branch of mammaliaform animals that became extinct. North America, Europe, Asia, and Africa; Triassic to Cretaceous.

**hard parts**: mineralized or otherwise hardened structures of an organism that fossilize easily, such as shells, bones, horns, bills, teeth, cuticles, claws, and scales.

***Harpagornis moorei***: Haast’s eagle, a large predator of New Zealand that became extinct only 500 to 700 years ago, after the arrival of humans on the two islands. Weighing 22 to 40 pounds, it had a 9-foot wingspan and was at least 30 percent larger than the largest extant bird of prey. Genetic research indicates that it is most closely related to a very small bird of prey, the two-pound *Hieraaetus* eagle of Australia and New Guinea. The probable common ancestor of Haast’s eagle and *Hieraaetus* is a two-pound species that lived between 1.8 and 0.7 Ma, so that Haast’s eagle represents one of the most rapid instances of evolution from a very small to a very large species. Before the arrival of humans, the only mammals in New Zealand were three species of bats, but there were 250 species of birds. *Harpagornis*

dominated the food chain, hunting the 400-pound moas (*Dinornithidae*); both went extinct within a century of the arrival of humans and accompanying rats, which multiplied in the absence of natural predators and ate the eggs of many birds.

**Harpetida:** an order of trilobites in the subclass *Librostoma*; characterized by an unusual brim around the cephalon; probably a feeding apparatus, the brim kept the animal from enrolling tightly; also characterized by very small eyes and flat genal prolongations; global distribution, late Cambrian to Late Devonian.

**Harpoceras:** a genus of ammonoids in the family *Hildoceratidae*; generally thin-shelled and flattened laterally, the various species range widely in size, from 5 inches up to 18 inches wide; global distribution, Early to Late Jurassic.

**harvestman:** see *Opiliones*.

**Hatzegopteryx:** a genus of very large azhdarchid pterosaurs in the suborder *Pterodactyloidea*, known from fragments found in Romania in 2002; estimated to be as large as *Quetzalcoatlus*, to which it is similar, both of them having a wingspan of about 40 feet; Late Cretaceous, 66 Ma.

**Heidelberg man:** see *Homo heidelbergensis*.

**Helaletes:** a genus of lophiodont tapirs in the superfamily *Tapiroidea* and extinct family *Helaletidae*; derived from *Homogalax* and close to the ancestry of the modern tapir, *Helaletes* was small and agile, and looked like a small horse; North America and Asia, early Eocene, 50–46 Ma.

**Helcionelloida:** an early Paleozoic class of small marine mollusks; characterized by rugose, cap-shaped shells, conical and sometimes coiled; global distribution, early Cambrian to Early Ordovician.

**helens:** a pair of long, curved, calcareous extensions often found connected to the operculum of hyoliths; the function is unclear, perhaps as supporting structures; named for C.D. Walcott's wife and daughter.

**Heliconiinae:** a still-extant subfamily of butterflies in the superfamily *Papilionoidea* and family *Nymphalidae*; famous for examples of Batesian and Müllerian mimicry; Miocene to Recent.

**Helicoplacus:** a genus of early Cambrian echinoderms in the class *Helicoplacoidea*. It is one of the earliest echinoderms but is represented by only two genera and very few specimens. *Helicoplacus* was cigar-shaped and 2–3 inches high, with spirally arranged plating on three ambulacra, different from other echinoderms in lacking any radial symmetry. The only complete specimen was found in the White Mountains of California, but fossil plates have been found across North America.

**Helicoprion:** a genus of eugeneodontiform holocephalian fish in the family *Agassizodontidae*. Shark-like and estimated at 12–30 feet long, it is known only from heterodont teeth and partial skulls since the cartilaginous body disintegrated soon after death. Notable for its dentition, with a tooth-whorl as a cutting plate in

the lower jaw and simple crushing teeth in the upper jaw; the tooth whorl contains as many as 150 teeth. Global distribution, middle Permian, 285–270 Ma.

***Heliobatis radians*:** “sun ray,” a genus of rays in the order Myliobatiformes and family Dasyatidae; its generic name refers to the circular outline of its pectoral fin discs; known from many specimens found in the Green River Formation, it was generally 1–2 feet long; it had a long tail with numerous spines and up to three stingers, and its diet was primarily small fish, crayfish, and mollusks; Wyoming, United States, early Eocene, 54–48 Ma.

***Heliolites*:** a genus of tabulate colonial corals in the family Heliolitidae; circular corallites, smooth or surrounded by 12 oval segments; cosmopolitan, Middle Ordovician to Middle Devonian.

***Heliomedusa*:** a monospecific genus of early brachiopods in the family Disciniidae; circular and less than an inch in diameter, *H. orientalis* was first thought a jellyfish, but it is now known from dozens of specimens in the Chengjiang biota that show the lophophore and the growth lines of the shell; China, early Cambrian.

**Hell Creek Formation:** a very important North American formation that comprises strata from the end of the Cretaceous and beginning of the Paleocene, dated roughly 70–66 Ma. With the Frenchman Formation of Saskatchewan, it extends over a circular area 500 miles in diameter, centered in northeastern Montana. It is best-known for dinosaur fossils, including the most complete hadrosaur skeleton ever found. But it has also produced fossils of invertebrates, plants, fish, reptiles, amphibians, and birds. Near its boundary with the overlying Fort Union Formation, there are exposures of the iridium-enriched stratum that marks the end of the Mesozoic Era.

**Helodontidae:** an enigmatic family of holocephalic fish, grouped with the Chimaeriformes, possibly related to sharks; the type genus is *Helodus*; they are characterized by a heterocercal tail fin and the absence of toothplates; instead they have a series of flattened tooth elements in each jaw; Australia, North America and Europe; Late Devonian to Permian.

**Helohyidae:** “marsh pig,” a family of small palaeodont artiodactyl mammals, similar to the Raoellidae and possibly close to the ancestry of whales; Asia and North America, late Eocene to late Oligocene.

***Hemicidaris*:** a genus of echinoids in the order Hemicidaroida and family Hemicidaridae; Europe, Africa, and North America; Middle Jurassic to Early Cretaceous.

**Hemicidaroida:** a paraphyletic order of sea urchins, regular echinoids in the subclass Euechinoidea; cosmopolitan, Late Triassic to Late Cretaceous.

***Hemicyclaspis*:** a genus of osteostracan fish in the order Atelaspiformes, closely related to *Cephalaspis*; 4–5 inches long, it is pleuronectiform and is characterized by paired pectoral fins, a low dorsal fin, a row of low dorsal spines, a single nostril,

and a bony headshield that was almost circular in cross-section; North America and Europe, Early Devonian.

**Hemicyoninae:** a subfamily of carnivorous ursid mammals that probably includes the ancestors of modern bears; the later species, such as *Hemicyon*, ranged from 4 to 7 feet long and were generally digitigrade; North America, Europe, and Asia; late Oligocene to late Miocene.

**Hemipneustes:** a sea urchin, a genus of large irregular euechinoids in the order Holasteroidea and family Holasteridae; characterized by a high-domed test and a deeply sunken anterior ambulacrum; the largest echinoid of the Cretaceous; Europe and Asia, Early to Late Cretaceous.

**Hemipsalodon:** “semi-shearing teeth,” a genus of creodonts in the family Hyaenodontidae; a scavenging carnivore, *H. grandis* was 6–7 feet long and weighed about 250 pounds; the first and second molars were modified for slicing meat; Western North America, late Eocene.

**Hemizonida:** an order of echinoderms in the class Asterozoa, primitive sea-stars; North America and Europe, early Silurian to Late Carboniferous.

**Heptodon:** a genus of perissodactyl placental mammals in the superfamily Tapiroidea and family Heleptidae; known in North America soon after the beginning of the Eocene, it was about 3 feet long and closely resembled the modern tapir; British Columbia, early Eocene, 50–49 Ma.

**Hercynian orogeny:** see **Variscan orogeny**.

**Herefordshire Nodules:** a late Silurian assemblage of carbonate nodules from a volcanic ash stratum dated at 425 Ma, found in Western England in 1996. The nodules contain exceptionally preserved calcitic fossils of organisms of a shallow epicontinental sea, including brachiopods, polychaete worms, mollusks, crustaceans (see *Colymbosathon*), and echinoderms. Since the fossils cannot be separated from their matrix, many have been digitally recorded by a complex process of serial thin sectioning that preserves fine detail.

**Herpetotherium:** a genus of marsupials in the family Herpetotheriidae, widespread in North America from the early Eocene to early Miocene; *Herpetotherium* was a small ground-dwelling omnivore, closely related to modern marsupials; North America, Eocene to Miocene.

**Herrerasauridae:** a family of early saurischian dinosaurs; they are traditionally considered theropods, but 2017 research argues that their similarities may be simply the result of convergent evolution rather than phylogenetic relationship; the carnivorous herrerasaurids are relatively small dinosaurs, generally less than 15 feet long; South and North America, Late Triassic, 231–215 Ma.

**Herrerasaurus:** a genus of early saurischian dinosaurs in the carnivorous family Herrerasauridae; the type species, *H. ischigualastensis*, is dated at 231 Ma; lightly

built, its length is estimated at between 10 and 15 feet and its weight up to 700 pounds; Argentina, Late Triassic.

***Hesperornis***: the best-known member of the hesperornithine birds, a more advanced early group than the enantiornithines; *Hesperornis* was a large, flightless, diving sea-bird, almost 6 feet long; North America and Asia, Late Cretaceous, 85–75 Ma.

***Hesslerides***: a genus of trilobites in the family Proetidae; characterized by a large glabella comprising most of the cephalon, with crescentic eyes set near the rear of the cephalon; North America, Early Carboniferous.

**Heteractinida**: a probably paraphyletic Paleozoic order of sponges in the still-extant class Calcarea with six- or eight-pronged calcareous spicules; global distribution, early Cambrian to Carboniferous.

**heterocercal**: referring to an asymmetrical tail fin, generally with the upper part extending farther than the lower part, seen especially in sharks; on the other hand, the Anaspida and mosasaurs are characterized by a reversed heterocercal tail fin.

**heterochrony**: a genetic shift in the evolutionary development of tissue or an anatomical part, causing it to develop at an abnormal time relative to an ancestor; the change can then be inherited by the offspring; for example, the adults of some later species of the Jurassic bivalve genus *Gryphaea* exhibit traits that were juvenile in an earlier species.

**Heterocorallia**: an order of late Paleozoic corals in the subclass Zoantharia; it has one family, the Heterophyllidae; solitary and elongate, possibly related to the Rugosa but with a different arrangement of septa; global distribution, Middle Devonian to Early Carboniferous.

***Heterocraniarhyniensis***: a species of arthropods in the subclass **Euthycarinoidea**, *q.v.*; Scotland, Early Devonian.

**heterodont dentition**: having more than one type of teeth, evidence of specialization in feeding.

**Heterodontosauridae**: a basal family of ornithischian dinosaurs; a long-lived and widespread group known from sparse specimens on all continents except Australia and Antarctica; they were as long as 6 feet, including a long tail, and are characterized by long, grasping forelimbs; also characterized by their heterodont dentition (the trait they were named for), having three different types of teeth; probably herbivorous but may also have preyed on small animals; only *Heterodontosaurus* is known from a complete skeleton, but see also ***Abriktosaurus***; Late Triassic to Early Cretaceous.

***Heterodontosaurus***: a monospecific genus of basal ornithopod dinosaurs; known from several specimens but primarily from an articulated skull and skeleton dated between 210 and 190 Ma; it was up to 6 feet long, had three different types of teeth,



and had five digits on the manus and four on the pedes; South Africa and North and South America, Late Triassic to Early Jurassic.

**Heteromyidae:** a still-extant family of rodents in the superfamily Geomyoidea; widespread in North America in the Oligocene, the family's range has shrunk, but the kangaroo mouse and kangaroo rat are two of many surviving genera; North and Central America, Oligocene to Recent.

**Heteronectes:** a genus of flatfish showing a transitional stage in the development of flatfish asymmetry; known only from Italy, Eocene; see also **flatfish**.

**Heterosoricinae:** a proposed subfamily of insectivores in the family Soricidae (the shrews); North America, Europe, Africa, and Asia; Eocene to Pliocene.

**heterosporous:** the production of two types of spores differing in size and sex; known in several types of terrestrial plants such as *Archaeopteris* and the club-mosses in the Devonian.

**Heterostraci:** "different shield," a diverse subclass of jawless, armored fish-like vertebrates; generally small (5–9 inches) and benthic, they evolved during the time when the mineralized skeleton first appears in the fossil record; the group includes principally the cyathaspid and their descendants the pteraspids; the family Psammosteidae was the last of the heterostracans, extinguished at the end of the Devonian; global distribution, late Cambrian to Late Devonian.

**Hexactinellida:** a class of glass sponges, characterized by 4-, 5-, and 6-rayed siliceous spicules; formerly called Hyalospongiae; more common as fossils than demosponges because their siliceous spicules fossilize easily; global distribution, Cambrian to Recent.

**Hexanchiformes:** a still-extant order of primitive sharks in the superorder Squalomorphii; characterized by 6 or 7 gills, one dorsal fin, and a heterodont dentition; well-known from the Middle Jurassic through the Cenozoic, but teeth resembling those of hexanchiforms are known as far back as the Devonian; the extant families are the Hexanchidae and the Chlamydoselachidae, and extinct families are the Crassonotidae, Mcmurdodontidae, and Orthacodontidae; Devonian? to Recent.

**Hexapoda:** a subphylum of arthropods that includes true insects and the entognathous proto-insects: the Collembola (springtails), Protura, and Diplura; the group has also traditionally included myriapods, but genetic evidence may exclude them; global distribution, Early Devonian to Recent.

**Hexathelidae:** see *Rosamygale*.

**Heymonsicambria scandica:** one of several important discoveries of fossil pentastomes showing that the parasitic **Pentastomida** (*q.v.*), tongue-shaped worms, date back to the Cambrian; Canada, late Cambrian.

**Hiemolora:** a poorly known genus of Ediacaran fossils, known at least from the Mistaken Point fauna and possibly elsewhere; it is a tentacular medusoid, with 12–20 arms radiating from a 2-inch circular body; Canada, Ediacaran, 575–560 Ma.

***Hildoceras***: a genus of ammonoids in the order Ammonitida and family Hildoceratidae; characterized by a narrow, discoidal, and evolute shell; *Hildoceras* is named for St. Hilda, the founding abbess of Whitby Abbey in Yorkshire, England, who legendarily turned all the snakes into stone, creating the ammonoids; Europe and Japan, Middle Jurassic.

***Hindeodus parvus***: a species of conodonts in the family Anchignathodontidae; its first appearance marks the beginning of the Mesozoic Era and the Triassic Period at 252.17 Ma; China.

**Hippuritoida**: the rudists, an order of euryhaline bivalve mollusks in the class Heterodonta; flourishing in the warm, saline water of the Cretaceous, they became the basis of the most prominent reefs of the period, cementing themselves together in tropical reefs several hundred feet high, running for hundreds of miles along some Cretaceous coastlines; the individuals took various tube and conical shapes, the latter sometimes as long as 40 inches; see for example ***Radiolites***; cosmopolitan, Late Jurassic to the end of the Cretaceous.

**holarctic**: referring to the Holarctic Region, the temperate areas of Europe, Asia, North America, and to North Africa, from the Jurassic to the present.

**holaspis**: the final ontogenetic phase of trilobites, followed by several molts that merely increased body size and added segments; see also **meraspis** and **protaspis**.

**Holasteroida**: an order of Mesozoic sea urchins, heart-shaped atelostomate echinoderms; several species are important in biostratigraphy, with a few genera still extant; Cretaceous to Recent.

**Holectypidae**: a family of irregular echinoids in the order Holectypoida; the group includes some of the earliest and most primitive irregular echinoids, similar to the Pygasteridae; global distribution, Early Jurassic to Late Cretaceous.

**Hollinoidea**: a superfamily of dimorphic paleocopid ostracods in the extinct order Beyrichicopina; some forms with sulci and lobation; North America and Europe, Devonian to Permian.

**Holocene**: the most recent epoch of the Cenozoic Era, the last 11,700 years.

**Holocephali**: a still-extant subclass of cartilaginous fish in the class Chondrichthyes; known as far back as the Devonian but only from scattered teeth; the only surviving order is the Chimaeriformes, the ghost sharks; Devonian to Recent.

**holochroal**: the type of compound eye in most trilobites, with thousands of tightly packed lenses covered by a single cornea.

**Holoptychiidae**: a family of sarcopterygian fish in the order Porolepiformes; these lobe-finned fish included at least one genus that may have been amphibian, *Laccognathus*; North America and Europe, Middle Devonian to Early Pennsylvanian.

**Holothuroidea**: the sea cucumbers, a still-extant class of echinoderms in the sub-phylum Echinozoa. Their body is generally cylindrical, with five ambulacra and a leathery skin which contains ossicles of different types and sizes. They are generally

6–12 inches long, but the longest known (*Synapta maculata*) grows to 10 feet. The fossil record is poor since there is no integrated skeleton, but ossicles and elements of the calcareous ring around the mouth are known from as early as the Silurian, and body specimens are known from the Devonian and later. Global distribution, Silurian to Recent.

**holotype:** a single physical specimen of the type species of a taxon, designated as the defining type of the taxon at the time when it is formally described and established as a formal group; the holotype anchors specific physical characters to the name of the taxon.

**Holuridae:** a family of palaeonisciform chondrosteian fish; characterized by an ossified exoskeleton and robust rhombic scales; Europe, Carboniferous to Permian.

**Holzmaden Shale:** a Lower Jurassic Konservat-Lagerstätte in Southern Germany, where several limestone and shale quarries have produced exceptionally preserved specimens of shallow-sea taxa from the Lower Jurassic *Posidonia* Shale, dated at 185–183 Ma. Of the vertebrate fossils, the most common are the ichthyosaurs, including the first to clearly show *Stenopterygius* with a dorsal fin and an upper lobe of the tail. Many of these specimens show stomach contents, and there is a high percentage of juveniles and females with unborn fetuses, indicating that the area was probably a spawning ground. Other vertebrates include teleosaurid crocodiles (see *Steneosaurus*), pterosaurs, and fish. Cephalopods such as the ammonoid *Harpoceras* are common, and other invertebrates include crinoids and bivalves. One of four Lagerstätten dated near 183 Ma; see also **Strawberry Bank** and **Ya Ha Tinda**.

**Homacodontidae:** a paraphyletic family of palaeodont mammals in the superfamily Dichobunoidea; among the earliest and most generalized artiodactyls; North America, Asia, and Europe; Eocene.

**Homalozoa:** a controversial group of early Paleozoic animals traditionally considered a subphylum of echinoderms; some consider them a separate class called Carpoidea; also called calcichordates or stylophorans by some, they may even have an evolutionary link with chordates; characterized by a calyx with a short stem, projecting arm and tail-like structures, and a lack of any symmetry; global distribution, middle Cambrian to Early Devonian.

**hominid:** term referring to the family Hominidae, which includes all modern great apes (*i.e.*, modern humans, gorillas, chimpanzees, and orangutans) and their immediate ancestors; early Miocene to Recent.

**hominin:** term referring only to modern humans, extinct members of the genus *Homo*, and their immediate ancestors, such as *Australopithecus*, *Paranthropus*, and *Ardipithecus*; late Miocene to Recent.

**Hominoidea:** the apes, a superfamily of haplorrhine primates consisting of the families Hominidae and Hylobatidae; Oligocene to Recent.

***Homo erectus***: a species of primates more advanced in several ways than *H. habilis* and probably ancestral to *H. sapiens*. Remains of *H. erectus* have been found in Java, China, Africa, Europe, and Western Asia, some as old as 1.75 million years and some possibly as young as 70,000 years ago. *Homo erectus* was on average about 5 feet tall and had a cranial capacity slightly less than *H. sapiens*. Although it was long thought to be the first hominin to walk upright, other species, notably *Au. afarensis*, now seem to have done so as early as 3.4 Ma. A find of a jawbone and two skullcaps found in the Republic of Georgia in the late 1990s may be *H. erectus*, and its age is thought to be about 1.7 Ma; it is similar to a jawbone from Kenya from 1.6 Ma and is possible evidence of early migration of the species from Africa. Some authorities now divide *H. erectus* into three separate species in Africa, Europe, and Asia. See also **Denisovans**, **Neanderthals**, and **Ngandong fauna**.

***Homo erectus pekinensis***: a form of *H. erectus* characterized by a massive brow ridge and a cranial capacity of 900–1200 cc; tools and the remains of modern humans have also been found at the site; Northern China, Pleistocene, about 750,000 years ago.

***Homo ergaster***: the group of hominins considered by some to be the branch of *H. erectus* that gave rise to *H. sapiens* in Africa; see also **Turkana Boy**; southeastern Africa, 1.9 to 1.3 Ma.

***Homo floresiensis***: a species of hominins known from partial skeletons of nine individuals found on the Indonesian island of Flores; between 2 and 4 feet tall, the specimens have generated intense debate, some claiming that a disease caused their diminutive size; the emerging consensus, however, is that they do represent a separate species; dated between 200,000 and 50,000 years ago.

***Homo habilis***: possibly the earliest-known representative of its genus, *H. habilis* lived from about 2 million years ago to about 1.75 million years ago, with most specimens found in Africa and Asia; possibly ancestral to *H. erectus*, with a cranial capacity (around 650–700 cc), slightly more than that of the australopithecines but less than that of *H. erectus*.

***Homo heidelbergensis***: a disputed species of hominins; considered by some to represent the branch of *H. erectus* ancestral to Neanderthals and modern humans; Europe, Africa, and possibly Asia; 600,000 to 120,000 years ago.

**Homoioostelea**: a controversial class of early biradial echinoderms, generally placed in the subphylum Homalozoa; characterized by a feeding arm and a stem consisting of a series of plates; cosmopolitan, Cambrian to Devonian.

**homologous structures**: body parts of different organisms that have anatomical features in common but that perform different functions. For example, bats' wings and human hands have homologous bone structures, but only bats can fly. The hindlimbs of whales may seem homologous with those of hippopotamuses; but since they are no longer functional, the whales' hindlimbs are considered vestigial. See also **analogous structures** and **vestigial structures**.

***Homo naledi*:** the name given to a species of hominins known only from a deposit of bones in a cave north of Johannesburg, South Africa, probably a burial site. Found in loose soil and unaccompanied by other fauna, they are difficult to date, with estimates ranging from 2.5 to 0.9 Ma. The bones represent parts of at least 15 individuals, and there are multiple examples of almost every bone in the body, so that the skeleton constructed from them is more complete than any previously known hominin specimen. This discovery seems to be an early stage of hominin development, having a brain the size of an orange but also having other more advanced characteristics.

***Homo neanderthalensis*:** see **Neanderthals**.

***Homo rhodesiensis*:** the name given to several pre-modern hominin specimens found in the twentieth century in East and North Africa; dated between 400,000 and 120,000 years ago, the group is thought by some to be an African version of *H. heidelbergensis* and probably in the direct line of descent to *H. sapiens*; whether it should be called *H. sapiens rhodesiensis* is in question.

***Homo sapiens sapiens*:** modern humans, the only surviving member of the genus *Homo*; see also **Cro-Magnon, Denisovans, and Neanderthal**; middle Pleistocene to Recent.

***Homotherium*:** a genus of large felids in the subfamily Machairodontinae. Its canines were longer than those of *Machairodus* but shorter than some other saber-toothed cats. *Homotherium* was about the size of a modern male lion, but its elongated forelimbs and short tail give it a hyena-like appearance. Its last representatives seem to have been those in Europe, which disappeared about 28,000 years ago. Global distribution except Australia and Antarctica, Pliocene to Pleistocene.

**honeycomb coral:** see **Tabulata**.

***Hoplitoplacenticeras*:** “heavily armed Placenticeras,” a Late Cretaceous ammonoid in the order Ammonitida; its shell can be 3 feet across and so strongly ribbed that it has a spiky appearance; important stratigraphically in the Campanian, it is the latest representative of the Placenteratidae, found worldwide into the Maastrichtian.

***Hoplopteryx*:** a genus of teleost actinopterygian fish in the still-extant family Trachichthyidae; almost a foot long, it had relatively small fins, but the dorsal fin was supported by a row of strong spines; in an evolutionary advance, a series of uroneural bones in the tail supported the fin rays and made *Hoplopteryx* a strong swimmer; related to the modern roughy; global distribution, Late Cretaceous, 90–70 Ma.

**horizon:** in paleopedology, a layer of soil; the upper layers lie generally within 1.5 feet of the surface (labeled horizons A and E) and the subsurface horizon lies within 7 feet of the surface (labeled horizon B).

**horned dinosaur:** see **Ceratopsia**.

**horseshoe crab:** see *Limulus*.

**House Range:** see **Wheeler Shale**.

**Hunsrück Slate:** Several quarries in this Konservat-Lagerstätte of the Early Devonian (about 407 Ma) contain well-preserved soft-tissue pyritization fossils. Important examples include fish (especially *Drepanaspis* and *Gemündina*), echinoderms (crinoids, asteroids, and ophiuroids), mollusks, and several arthropods (especially the malacostracan crustacean *Nahecaris* and the pycnogonid sea-spider *Palaeoisopus*). Germany, Early Devonian, Pragian to Emsian Stages.

**Hurdia:** a genus of stem-arthropods in the order Radiodonta. Known first from the Burgess Shale assemblage and at first misidentified, it was correctly described in 2009 and seen to be related to *Anomalocaris*. Between 8 and 20 inches long, it is characterized especially by large gills attached to its sides and by a thin, pointed carapace extending forward. North America, Europe, and Asia; middle Cambrian.

**Hyaenodon:** a short-lived but diverse genus of creodonts in the extinct family Hyaenodontidae; the largest species, *H. gigas*, was about 10 feet long and weighed half a ton; *Hyaenodon* was cat-like and walked on its toes; not a direct ancestor of the modern hyenas; North America, Europe, Africa, and Asia; late Eocene to early Miocene.

**Hyalospongiae:** see **Hexactinellida**.

**Hybocrinida:** an order of early crinoids in the polyphyletic class Inadunata; characterized by a monocyclic cup and circular stem; North America and Europe, Late Ordovician and possibly early Silurian.

**Hybodontiformes:** “hump tooth,” a long-lived suborder of euselachian sharks, named for their compressed conical teeth; dominant Mesozoic predators, hybodonts were 6–7 feet long; prominent genera include *Hybodon* and *Ptychodus*, the type genera of the large families Hybodontidae and Ptychodontidae; global distribution, Early Carboniferous to Late Cretaceous.

**Hydnoceras:** a genus of glass sponges in the class Hexactinellida; horn-shaped and about 8 inches long, it is an index fossil in the Late Devonian; North America and Europe, Devonian to Mississippian.

**Hydrodamalis gigas:** Steller’s sea cow, a genus of sirenians in the family Dugongidae; as long as 30 feet, it was toothless and fed entirely on seaweed; with a very thick layer of blubber, it may have been unable to dive; hunted to extinction in the middle of the eighteenth century; North Pacific Ocean, Pliocene to Holocene.

**Hydrozoa:** a class of cnidarians in the subphylum Medusozoa. Mostly soft-bodied, predatory marine animals, solitary or colonial, they include the Portuguese man-of-war but are separate from the jellyfish (see **Scyphozoa**). They probably date back to the Precambrian, but fossils are rare. Three groups — fire corals, milleporines, and stylasterines — have a stony growth that fossilizes; they appeared in the Cretaceous and are widespread through the Cenozoic.

**Hyeniales:** an order of primitive shrubs with short, forked leaves in whorls; *incertae sedis* between sphenophytes and pteridophytes; global distribution, Devonian.

**Hylobatidae:** the gibbons, classified with humans and the Cercopithecidae in the superfamily Hominoidea and infraorder Catarrhini; Southeast Asia, late Miocene to Recent.

**Hylonomus:** a monospecific genus of anapsid reptiles, placed tentatively in the Romeriida; the earliest-known unquestioned reptile, known from Nova Scotia about 312 Ma, *H. lyelli* was 9 inches long and had a long tail; Canada, Middle Pennsylvanian.

**Hymenoptera:** an order of insects that includes bees, wasps, and ants; global distribution, Early Triassic to Recent.

**Hyalolitha:** “u-bone,” a group of enigmatic Paleozoic animals, long considered probable mollusks but in 2017 shown to be lophophorates, related to brachiopods. Up to 1.5 inches long, they are similar in some ways to annelids, the segmented worms. They have conical calcareous shells with an operculum closure at the large end and two curved extensions called helens protruding, along with short feeding tentacles. The shell generally appears triangular or u-shaped when crushed flat. There are two orders, the Hyolithida and the problematic smaller group Orthothecida. Widespread in the Cambrian, their numbers declined through the Devonian, but a few persisted to the end of the Permian.

**Hyopsodontidae:** a family of small, primitive ungulate mammals, possibly related to horses; dachshund-like in appearance, they were generally insectivorous and herbivorous; they were unspecialized, having clawed toes and a generalized dentition; North and South America, Europe, Asia, and Africa; early Paleocene to Eocene.

**Hypacrosaurus:** a duospecific genus of large hadrosaurid dinosaurs in the subfamily Lambeosaurinae. Similar to *Corythosaurus* but with a higher and wider crest and with very high neural spines, for which one species is named *H. altispinus*. The other species, *H. stebingeri*, is especially important for the discovery of a great number of hatchlings and embryos in eggs the size of a small soccer ball. Research on the embryos has shown, among other things, that their relatively long incubation time was almost six months, much longer than in birds. Two Medicine Formation, North America, Late Cretaceous, 86–71 Ma.

**Hypertragulidae:** a family of small artiodactyl ungulate mammals, among the earliest ruminants; weighing only 5–9 pounds, they resemble very small deer; Europe, Asia, and North America; Eocene to Miocene.

**Hyphalosaurius:** a genus of choristoderan reptiles in the family Hyphalosauridae. Very common in the Jehol biota, it reached a length of almost 3 feet, with a very long neck and tail. Some specimens show skin impressions, and *Hyphalosaurius* may have been viviparous. China, Early Cretaceous, about 125 Ma.



***Hyphantoceras***: a genus of heteromorph ammonitid ammonoids in the superfamily Turrilitaceae; it has a loose, helically coiled shell that stretches out to 4–5 inches long; cosmopolitan, Late Cretaceous.

**Hypochilidae**: a still-extant family of araneomorph spiders in the superfamily Paleocribellatae; there are no definitive known fossil specimens, but the body plan of the modern lamp-shade spider *Hypochilus* seems to be a mosaic of primitive and derived characters; found only in China and North America.

***Hypsilophodon foxii***: a species of herbivorous ornithischian dinosaurs in the suborder Ornithopoda, the only generally accepted hypsilophodont. Known only from several specimens found on the Isle of Wight in the nineteenth century, *H. foxii* was 5–6 feet long and lightly built, weighing less than 50 pounds; it had a stiff tail, five long fingers on weak forelimbs, and four toes on its hindfeet. Its name refers to a frill along its spine, not to its dentition. England, Late Jurassic to Early Cretaceous.

**Hypsilophodontidae**: a large, probably paraphyletic family of small ornithischian dinosaurs in the suborder Ornithopoda; from 3 to 6 feet long and lightly built, generally bipedal; global distribution, Middle Jurassic to Late Cretaceous.

**hypsodont dentition**: high-crowned teeth with a flattened surface for chewing tough vegetation, with enamel extending the length of the tooth and past the gum line, and with cementum between the lophs of the tooth.

***Hyrachyus***: a genus of ceratomorph mammals in the family Hyrachyidae; 4–5 feet long and related to the Lophiodontidae, it is known from hundreds of specimens; it is generally considered to be related to the tapirs but has rhinoceros-like dentition; holarctic distribution, Eocene.

**Hyracodontidae**: a family of perissodactyl ungulates in the superfamily Rhinocerotoidae; initially small and tapir-like, the later hyracodontids include the largest known terrestrial mammals, the Indricotherinae (see *Paraceratherium*); North America, Europe, and Asia; early Eocene to early Miocene.

**Hyracoidea**: a still-extant order of superficially rabbit-like mammals; in the Eocene the hyracoids ranged from cow-sized to mouse-sized and were widespread in Africa; related to sirenians and elephants; Africa, Europe, and Asia, early Eocene to Recent.

***Hyracotherium***: a genus of palaeotheres in the family Palaeotheriidae, close to the ancestry of Equidae and brontotheres. It had four toes on its forelimbs and three toes on its hindlimbs but is considered the earliest-known perissodactyl. Its teeth were low-crowned and it weighed up to 50 pounds. *Hyracotherium* had a global distribution in the early Eocene, as evidenced by whole fossil skeletons found in Europe and North America and partial ones elsewhere. See also *Eohippus*. Early to middle Eocene.

**Hystricospherida**: an enigmatic group of spiky and spherical protist microfossils, one-celled marine algae; not well-known but possibly related to the zygotes of freshwater chlorophytes or to dinoflagellates; global distribution, Paleozoic to Recent.



# I

***Iapetognathus fluctivagus***: a species of denticulate conodont elements in the family Cordylodontidae; its first appearance (currently considered to be 485.4 Ma) marks the GSSP for the beginning of the Early Ordovician in Newfoundland, Canada; the species is also known from the United States, Asia, and Australia.

***Iberomesornis***: see **Enantiornithiformes**.

***Ibyka***: a poorly known genus of early plants tentatively placed in the order Iridopteridales; Middle to Late Devonian.

***Icaronycteris***: a genus of early microchiropteran bats in the family Icaronycteridae; the earliest-known bat, it was about 6 inches long, had a wingspan of 15 inches, and probably used echolocation; North America, Asia, and possibly Europe; early Eocene.

**ICBN**: International Code of Botanical Nomenclature; in 2011 the Eighteenth International Botanical Congress changed the name to *International Code of Nomenclature for algae, fungi, and plants*.

**icehouse conditions**: periods of extensive cooling on Earth, referring to periods of lower global temperatures and glaciation. They are associated with low levels of carbon dioxide, relatively calm volcanic eruptions, and low sea levels. The most recent, the Pleistocene glaciations, are well-documented, but the earlier cool periods are not. The Karoo Ice Age was a period of cooling toward the end of the Carboniferous, extending into the early Permian; evidence for it has been found especially in Southern Africa and South America, but its extent and effects are not well-known. A cool period at the end of the Ordovician, roughly 450–420 Ma, is sometimes referred to as the Andean-Saharan Glaciation. Two longer periods of more severe cooling occurred in the Cryogenian Period, before the Ediacaran. Dated at 650–635 Ma, the Marinoan Glaciation ended the Cryogenian after a warm span of about 25 million years; and the long Sturtian Glaciation, from 717 to 660 Ma, marked the first part of the Cryogenian. Another long stretch of global cooling,

probably the most severe but least understood, is called the Huronian Glaciation, occurring between 2400 and 2100 Ma.

**ichnology:** see **paleoichnology**.

**Ichthyodectidae:** “fish biters,” a family of Mesozoic teleost actinopterygian fish in the still-extant superorder Osteoglossomorpha and extinct order Ichthyodectiformes; most were between 3 and 16 feet long, and they preyed on smaller fish; Late Jurassic to Late Cretaceous.

***Ichthyolestes:*** a genus of archaeocete whales in the family Pakicetidae, fish-eating but mainly terrestrial; Pakistan, early to middle Eocene.

**Ichthyopterygia:** a superorder or subclass of diapsid marine reptiles including ichthyosaurs and their smaller ancestors; predatory and strong swimmers, they had a relatively short neck and porpoise-like body; Europe and Asia, Early Triassic to Late Cretaceous.

***Ichthyornis:*** a genus of early toothed birds in the order Ichthyornithiformes, dated between 95 and 84 Ma; notable for its rows of sharp teeth, similar to those of mosasaurs, and for its vertebrae, which are fish-like, concave on both sides; strongly keeled, it was probably a good flyer; similar to a small tern, it is closer to modern birds than are more archaic groups like the enantiornithines; North America, Late Cretaceous.

**Ichthyosauria:** an order of specialized diapsid marine reptiles in the superorder Ichthyopterygia, characterized by an elongated snout and a fish-shaped body; their ancestors may have been diapsids that returned to the sea; ichthyosaurs ranged in length from 3 feet to more than 50 feet, and they were viviparous; Early Triassic to Late Cretaceous.

***Ichthyostega:*** a genus of primitive labyrinthodont amphibians in the clade Tetrapodomorpha; close to the early ancestry of all terrestrial vertebrates and among the first to adopt an amphibian habit; its pedes had 7 digits, but a fossil manus has not been found; the skull was broad and flattened, and some species attained lengths of 3 feet; see **Tetrapoda**; North America and Europe, Late Devonian.

**ICSN:** International Code of Stratigraphic Nomenclature, the generally accepted authority for the names assigned to rock strata.

**Ictidosauria:** see **Tritheledontidae**.

**ICZN:** International Code of Zoological Nomenclature, the generally accepted authority for animal nomenclature; the current 4th edition was issued in 1999, and a 5th edition is planned for 2018.

***Iguanodon:*** a genus of bulky ornithischian dinosaurs in the suborder Ornithopoda; one of the largest animals of its time, the herbivorous *Iguanodon* ranged from 30 to 40 feet long and weighed about 3 tons; with long arms, it could shift easily from quadrupedality to bipedality; the genus has seen many revisions and reassignments

of species, but *I. bernissartensis*, one of the earliest dinosaur discoveries, is the type species; its manus is distinctive, with a prominent thumb spike and a prehensile fifth finger; it was named for its set of iguana-like teeth; Europe, North America, and probably Asia and Africa; Early Cretaceous, 126–125 Ma.

***Illaenus*:** a genus of medium-sized isopygous trilobites in the family Illaenidae and order Corynexochida; *Illaenus* grew as large as 2 inches, its cephalon had a high profile, and it had two short and recurved genal spines; the Illaenidae persisted from the Early Ordovician to the late Silurian; Europe and North Africa, Middle Ordovician.

**impunctate:** see **punctate**.

**Inadunata:** a class or subclass of stalked crinoids that recent research identifies as polyphyletic; the members of its three orders (Cladida, Disparida, and Hybocrinida) are being reassigned; global distribution, Early Ordovician to Middle Triassic.

**inarticulate:** see **articulate**.

***incertae sedis*:** of uncertain classification.

***Incisoscutum ritchiei*:** see **Gogo Formation**.

**index fossil:** a morphologically distinctive fossil taxon that characterizes a particular time period or biozone, usually found in a limited number of strata; it is abundant and widespread but short-lived, so that its presence in a stratum makes it possible to correlate widespread occurrences of the stratum; also referred to as guide fossil or zone fossil.

***Indocetus*:** a genus of archaeocete cetaceans in the family Protocetidae, one of the earliest ancestral whales. Its four sacral vertebrae are fused to each other and to its pelvis, so that it may have been able to support its weight on land. It probably used its hindlimbs rather than its tail in swimming. India, early Eocene.

***Indohyus*:** a genus of artiodactyl mammals in the family Raoellidae; *Indohyus* was deer-like in shape and about the size of a raccoon; several distinctive features show that it may be closely related to whales; India, middle Eocene.

***Indricotherium*:** see ***Paraceratherium***.

**infaunal:** see **epifaunal**.

**Iniopterygiformes:** an unusual order of holocephalic fish in the class Chondrichthyes, distantly related to the modern Chimaeriformes, the ghost sharks; they ranged from 6 to 18 inches long and had a cartilaginous skeleton; they are named “nape wing” for the distinctive pair of wing-like fins high on their back; a specimen from Kansas was found in 2009 to have a fossilized brain inside its intact skull; North America, Devonian to Carboniferous.

***Inkayacu paracasensis*:** a species of large penguins that lived in Peru in the late Eocene; very similar to modern penguins except that it was about five feet tall,

weighed about 120 pounds, and had a long beak; the specimen found in the Paracas National Reserve in Peru in 2009 is also notable for having well-preserved feathers that may have been brown and gray.

***Inoceramus***: a very large genus of deeply ribbed bivalves in the order Praecardioida and subclass Cryptodonta; some species were over 3 feet in diameter; the inoceramids were declining gradually for at least 10 million years before disappearing about 1.5 million years before the end of the Cretaceous; global distribution, Early Jurassic to Late Cretaceous.

**Insecta**: a class of arthropods in the subphylum Hexapoda; the largest class of animals, with almost a million named species. Insects' most basic apomorphies are a chitinous exoskeleton, six jointed legs, and compound eyes. The only invertebrates that have achieved flight, most groups of insects have four wings presently or had them at an earlier stage of their evolution (see also **Pterygota**, **Diptera** and **Coleoptera**). Insects first appeared in the Early Devonian, but their fossil record is very sparse through the Devonian and Carboniferous. The oldest known insect is a springtail from the Devonian Rhynie Chert of Scotland (see **Rhyniognatha**), and the first definitive flying insects appeared in the Late Carboniferous (see **Ensifera**).

**Insectivora**: an abandoned name for a grouping of the many small mammals that became widespread in the Cretaceous, preying mainly on insects; see **Eulipotyphla**.

**invertebrate**: an informal term for all non-vertebrate metazoan animals.

**involute**: especially of ammonoids, tightly coiled, with successive whorls overlapping and often covering most of the surface of earlier ones.

**Iridopteridales**: one of the widespread but enigmatic orders of early vascular plants called cladoxyloids; the whole-plant concept is unclear because its trunk and branch connections are not known; global distribution, Middle to Late Devonian.

***Isanosaurus***: a monospecific genus of sauropod saurischian dinosaurs; *I. attavipachi* is important as one of the earliest sauropods, but it is poorly known from fragments of one skeleton, dated at about 210 Ma; Thailand, Early Triassic.

***Isastraea***: a genus of scleractinian corals in the subclass Hexacorallia; it lived in warm, clear, shallow water; North America, Europe, and Africa; Jurassic to Cretaceous.

***Ischadites***: a contentious genus of benthic marine organisms currently classified as algae in the obscure family Receptaculitidae; its globose body resembles a sponge, with spiral rows of interlocking plates; North America and Europe, Middle Ordovician to Early Devonian.

***Ischnacanthiformes***: an order of acanthodian fish; they were slender, lightly armored nektic predators, characterized by two dorsal fins and stout spines; larger than other acanthodians, the larger species grew as long as 6 feet; North America and Europe, late Silurian to Carboniferous.

**Ischyromyidae:** a basal family of sciuriform rodents; known from France to North America through the Eocene, they gave rise to the Gliridae and other modern rodents; probably scansorial and probably competitive with early scansorial primates (see also **Paramyidae**); North America, Europe, and Asia; Paleocene to Oligocene.

**Isectolophidae:** a family of perissodactyl ceratomorph mammals in the superfamily Tapiroidea; probably descended, along with the Helaletidae, from *Homogalax*, an early Eocene tapiroid of Asia and North America; also related to the ancestral horse *Hyracotherium*; North America, Europe, and Asia; early to late Eocene.

**Isisaurus:** a genus of titanosaurian sauropodomorph dinosaurs; about 60 feet long and 20 feet high, it is characterized by unusually long forelimbs and a thick, vertically directed neck; probably a high browser; India, Late Cretaceous, 71–69 Ma.

**island dwarfism:** a process resulting in reduced size in a population of animals isolated on islands from other populations of the same species; see *Bubalus*, *Europasaurus*, and *Homo floresiensis*.

**Isoptera:** the termites, a suborder of insects in the order **Blattodea**, *q.v.*

**isopygous:** of trilobites, having a cephalon and pygidium of approximately the same size.

**Isotelus rex:** the largest known trilobite, a species in the order Asaphida and family Asaphidae; characterized by its isopygous shape and its size: 28 inches long, 3 inches high, and 16 inches wide; North America, Middle to Late Ordovician.

**Itagnostus:** a genus of agnostid trilobites in the family Peronopsidae; isopygous and in some species with a thorax narrower than the cephalon and pygidium; known only from Marble Canyon in British Columbia; Canada, middle Cambrian.

**Ixodida:** the ticks, an order of arachnids, divided into two main families, the Ixodidae and the Argasidae; poorly known but in the fossil record at least since 99 Ma; they have thrived along with browsing mammals since the spread of grasslands in the Eocene; also called Metastigmata; North America and Asia, Cretaceous to Recent.

# J

***Jamoytius kerwoodi***: a lamprey-like jawless fish with long paired fins running the length of its body; formerly considered an anaspid ostracoderm, its classification is still in dispute; it is now tentatively placed in the disputed class Hyperoartia; Scotland, known only from the Silurian.

***Janassa bituminosa***: the type species of the family Janassidae, poorly known cartilaginous fish in the family Petalodontidae; known primarily from teeth; North America and Europe, Mississippian to Permian.

***Janjucetus***: a stem mysticete whale in the family Mammalodontidae; about 11 feet long, it is notable for its short skull, its large eyes, and especially its large teeth; it had no baleen, a principal character of modern mysticetes; Australia, known only from one well-preserved specimen of the late Oligocene.

**Java Man**: a set of fossil bones discovered at Trinil, Java, about 60 miles from Ngandong, where the Solo Man remains were found; first classified as *Pithecanthropus* or a sub-genus *Javanthropus*, it is now considered *Homo erectus*; Pleistocene, about 1.5 million years ago.

**Jehol Biota**: “hot river,” a fossil community seen in several Konservat-Lagerstätten of Liaoning Province in China, found in the Lower Cretaceous Jiufotang and Yixian Formations, an area known for numerous hot springs. The species are dated between 133 and 110 Ma, the dates sometimes being uncertain because of problems dating the hundreds of fine-grained volcanic lake deposits that have preserved very detailed structures in the fossils; most of the important fossils are dated between 130 and 120 Ma, in the Yixian Formation. The most striking are a range of feathered dinosaurs such as *Jeholornis* and *Sinosauropteryx* and protobirds such as *Confuciusornis*, but there are also significant mammals (see *Repenomamus* and *Eomaia*), reptiles (see *Hyphalosaur*), insects, and some of the earliest angiosperms. See also *Caudipteryx*, *Protarchaeopteryx*, *Beipiaosaurus*, and *Sinornithosaurus*.

***Jeholornis***: one of the many bird-like feathered dinosaurs found in China since the 1970s. Like *Archaeopteryx* and other proto-birds, it is notable for its long, bony tail with feathers at the end rather than the pygostyle tail of modern birds. Omnivorous, eating insects and seeds of various plants, *Jeholornis* was about the size of a turkey, almost 3 feet long from beak to tail. While the type species is *J. prima*, found in 2002, other species with varying dentition, such as *J. palmapenis*, have been found since. Hebei province, China; Early Cretaceous, about 120 Ma.

***Jeholosaurus***: a monospecific genus of ornithischian dinosaurs in the family Thescelosauridae, *J. shanyuagensis* is known from two partial juvenile specimens from the Yixian Formation, dated. about 125 Ma; it was bipedal and probably herbivorous; China, Early Cretaceous.

***Jianfengia multisegmentalis***: a species of early arthropods known only from the Chengjiang biota; about half an inch long with many short legs and at least two anterior appendages, it is morphologically similar to *Opabinia*; China, late Cambrian, 530–515 Ma.

***Jinzhouosaurus***: a genus of ornithischian dinosaurs in the Jehol biota; about 25 feet long, it is known from a complete skeleton from the Yixian Formation and is tentatively considered a hadrosaurid on the basis of a spike-like thumb and a small crest at the top of the head; China, Early Cretaceous, 122 Ma.

**Jiufotang Formation**: a Lower Cretaceous (Aptian) Lagerstätte in Liaoning Province; important for many feathered dinosaur specimens as well as pterosaurs, birds, insects, and arachnids; preservation of fine detail was possible especially because of fine volcanic ash deposits; taxa from the formation are an important part of the Jehol biota; China, Early Cretaceous.

**Joggins Formation**: a Lower to Middle Pennsylvanian site in Nova Scotia whose strata record an area of swamps and periodically flooded forests; important especially for an early terrestrial vertebrate fauna, including the temnospondyl *Dendrotriton*; Canada, Late Carboniferous, 315 Ma.

**John Day Fossil Beds**: a series of Eocene, Oligocene, and Miocene Konzentrat-Lagerstätten in Central Oregon near the towns of Fossil, Mitchell, and Dayville. Several formations represent one of the most complete sequences of Cenozoic strata in the world, covering a period of more than 40 million years and including a great variety of animal and plant specimens. Some of the notable mammals from the three sites are the predatory feliforms *Nimravus*, *Dinaelurus*, *Patriofelis*, and *Pogonodon*; bison-sized entelodonts, such as *Archaeotherium* and *Daeodon*; the rhinoceros *Diceratherium*; the chalicothere *Moropus oregonensis*; the dwarf brontothere *Xylotitan*; the mouse-deer *Hypertragulus*; and amynodonts. See also **Clarno Nut Beds** and **Painted Hills**. North America, middle Eocene to late Miocene.

***Josephoartigasia***: a genus of the largest known rodents, in the family Dinomyidae; related to the modern pacarana, it is estimated at about 1 ton and 10 feet long; known only from a very large and almost complete skull; South America, Pliocene to early Pleistocene.

***Jugulator***: a monospecific genus of North American eutriconodont mammals in the proposed family Volaticotheria; slightly larger than *Volaticotherium*, *J. amplissimus* was probably also a glider; it is known only from teeth and jaw fragments from the boundary between Early and Late Cretaceous.

***Juramaia***: a genus of basal therian mammals known from an almost entire skeleton found in 2011; the type species, *J. sinensis*, is dated at 160 Ma and is important in determining the date when marsupials diverged from placental mammals; China, Late Jurassic.

**Jurassic**: the second period of the Mesozoic Era, 201 to 146 Ma, divided into Early, Middle, and Late Epochs. As the supercontinent Pangaea continued to separate into northern and southern halves, more coastline appeared globally. The arid climate of the Triassic gave way to an almost “greenhouse” climate worldwide, with sea level rising and rain forests replacing deserts in many places. Gymnosperms diversified widely, including conifers and many tropical genera. The separating land masses were dominated by dinosaurs and pterosaurs, which had appeared in the Late Triassic. The stem-mammaliaforms of the Late Triassic developed slowly at first but then diversified rapidly in the Middle Jurassic. Almost unnoticed, the first birds appeared near the end of the period. In the seas, plesiosaurs, ichthyosaurs, and sharks were dominant large predators, and the largest fish known (such as *Leedsichthys*) were among their prey. Marine invertebrates, especially ammonoids, also proliferated during the period.

***Juravenator***: a monospecific genus of small, feathered theropod dinosaurs; similar to *Compsognathus* but only 1–2 feet long, *J. starki* bore some feathers but had scaly dinosaur skin on its tail; Germany, Late Jurassic.



# K

**Kaiparowits Formation:** a sandstone and mudstone formation in Southern Utah, comprising layers dating between 76.6 and 74.5 Ma. One of the most productive sites for plants and animals of the Campanian age, it has yielded crocodiles, turtles, and especially herbivorous horned dinosaurs such as *Kosmoceratops richardsoni* (found only here) and *Nasutoceratops titusi*. Hadrosaurs, also herbivores, are common, as well as several other very large species. The tyrannosaurids *Teratophoneus curriei* and *Lythronax argestes* are among the predators in the formation. Many of the specimens are complete, such as several whole dinosaur skeletons and a turtle that died with many eggs in her body.

**Kangaroo Island:** a South Australian site that has produced several fossils similar to those of the Burgess Shale and the Chengjiang biota, including *Anomalocaris* and *Tuzoia*; it is dated at 520 Ma, intermediate in time between the two more famous localities.

**Kaprosuchus saharicus:** a species of crocodiles in the family Mahajangasuchidae, characterized by three sets of large upper and lower tusks on each side of its jaws; these boar-like tusks worked like scissors to slice the flesh of prey, possibly dinosaurs; variously estimated between 11 and 20 feet long; Niger, Early Cretaceous.

**Karanisia:** a genus of lorisid primates found in 2002 in the Fayum Depression; the genus includes at least one undisputed species, *K. clarki*, which seems to have a toothcomb similar to modern lemurs; *Karanisia* represents the earliest evidence of anthropoid radiation; Egypt, middle Eocene, about 40 Ma.

**Karaurus:** “Karatau tail,” a monospecific early genus of salamanders in the family Karauridae; known from one complete specimen found in the Karatau Mountains of Kazakhstan, *K. sharovi* was about 7 inches long, with a broad, frog-like head, a short body and tail, and sturdy legs; Kazakhstan, Late Jurassic, 155 Ma.

**Karkenian:** the form genus of seeds associated with the Ginkgophyta; global distribution, Jurassic to Eocene.

**Karoo Ice Age:** see **icehouse conditions**.

**Karoo Supergroup:** an extensive series of formations spanning about 100 million years, important especially for the formations from the time between the Permian mass extinctions and the Early Triassic; South Africa, Late Carboniferous to Middle Jurassic.

**Kayentachelys:** a genus of stem-turtles either in the order Testudines or in a more primitive classification of its own; it seems to be a link between the primitive *Odontochelys* and modern turtles; about a foot long, it possessed both a plastron and a carapace; found in the Kayenta Formation of Utah and Arizona, Early Jurassic.

**Kayentatherium:** a genus of Early Jurassic cynodont mammalianomorphs in the family Tritylodontidae; known from some anterior skeletal bones and several complete skulls found in Arizona; United States, Early Jurassic.

**Keichousaurus:** a genus of sauropterygian marine reptiles in the suborder Pachypleurosauria; up to about 9 feet long, with a long neck and tail; may have been viviparous; Guizhou Province, China; Early to Late Triassic, 249–236 Ma.

**Keilor skull:** a skull found in 1940 in a late Pleistocene site in southern Australia, classified as *Homo sapiens*; the skull, between 13,000 and 15,000 years old, led to the discovery of human habitation in the area about 31,000 years ago; the site is among the earliest locations of human habitation in Australia.

**Kelenken:** the largest of the phorusrhacids, a monospecific genus of large flightless predatory birds; between 7 and 10 feet tall and weighing up to 500 pounds, *K. guillermoi* had the largest head of any known bird; Argentina, middle Miocene; see also *Andalgalornis*.

**Kellwasser event:** the extinction event that marks the boundary between the Frasnian and Famennian Stages near the end of the Devonian.

**Kem Kem beds:** a site in southeastern Morocco that has produced many fossils from the Late Cretaceous, including several crocodylomorphs, pterosaurs, and turtles, and especially several large dinosaurs such as *Carcharodontosaurus* and *Spinosaurus*.

**Kennalestes:** a genus of shrew-like eutherian mammals in the order Leptictida, known from several specimens found in Mongolia; China, Late Cretaceous, 75 Ma.

**Kentrosaurus:** an African genus of ornithischian dinosaurs in the family Stegosauridae; about 15 feet long but only 1 ton, the herbivorous *Kentrosaurus* was armored by several pairs of plates and spikes along the spine, as well as a large spike projecting from each shoulder; Tanzania, Late Jurassic.

**Kenyanthropus platyops:** the name tentatively given to poorly known fossils, a skull and fragments of a hominin found in the late 1990s by Meave Leakey; Lake Turkana, Kenya, 3.5 to 3.3 Ma; see also **Lomekwian industry**.

***Kenyapithecus***: a middle Miocene hominoid primate, known from only a few East African fossils. Although similar to *Sivapithecus* and other Asian pithecines, *Kenyapithecus* is now thought more likely to be in the direct line of descent to the Hominidae. *Kenyapithecus* fossils date to around 16 million years ago, about 12 million years earlier than any presently recognized hominins, and the fossil record in between is incomplete.

**keratin**: a fibrous protein, similar to chitin, that is an important protective material found in hooves, nails, skin, horns, feathers, beaks, claws, and whale baleen. It is also the basic material of mammalian hair and is considered an important evolutionary contributor to the rise of mammals. Keratin has uncertain origins; a 2008 genetic study claims that keratin genes originated in an unknown reptile ancestor from about 300 Ma.

**key bed**: a thin but widely occurring stratum of sedimentary rock composed primarily of a particular, easily identifiable material, sometimes of fossils; the prolific nautiloid *Orthoceras*, for example, forms key Ordovician beds in several places; the key bed most often referred to is the iridium layer that marks the end of the Mesozoic Era.

***Kimberella***: an enigmatic genus of Ediacaran bilaterian animals; benthic and slug-like, it is generally considered a primitive mollusk; known from hundreds of oval specimens dated between 558 and 555 Ma, it ranged from less than an inch long to 6 inches; Australia and Eurasia, Ediacaran.

***Kirkbyoidea***: a small superfamily of reticulate, straight-hinged Paleozoic ostracods; Devonian to Middle Permian.

***Kirkidium***: a genus of articulate brachiopods in the family Pentameridae; 3–4 inches long, biconvex and astrophic, with a large pedicle valve; North America and Europe, Silurian.

**Kirtland Formation**: an important sedimentary formation of the Late Cretaceous, located in the San Juan Basin of New Mexico and Colorado; it is known for many specimens of dinosaurs of the Campanian, including *Kritosaurus* and *Alamosaurus*, as well as many other vertebrates; United States, 75–73 Ma.

**Kloedenelloidea**: a large superfamily of Paleozoic ostracods in the extinct order Palaeocopa; global distribution, Ordovician to Triassic but less abundant in the later Paleozoic.

***Knightsia***: a genus of clupeiform fish in the family Clupeidae; generally from 4 to 8 inches long and herring-like, *Knightsia* occurs in great numbers in the Green River Formation of Wyoming and is the most common fish fossil in shops around the world; North and South America, early Eocene.

***Knightsconus antarcticus***: a species of monoplacophoran mollusks in the order Archinacelloidea; it had a chambered, conical shell and is a possible ancestor of the Cephalopoda; known only from Antarctica, middle Cambrian.

***Koilops herma***: a species of tetrapods described in 2016 as similar to *Greererpeton*; Scotland, Early Carboniferous (Tournaisian).

***Koolasuchus***: a genus of temnospondyl amphibians in the suborder Stereospondyli and family Chigutisauridae; known from several fragmentary specimens, it is estimated to have been about 15 feet long, with a large, flat, triangular head; one of the last temnospondyls; Australia, Late Cretaceous, 125–115 Ma.

***Kosmoceras***: a large genus of ammonitid ammonoids in the superfamily Stephanocerataceae; most species characterized by a combination of ribs and tubercles; global distribution in Callovian deposits, Middle Jurassic.

***Kosmoceratops richardsoni***: an ornithischian dinosaur in the family Chasmosaurinae, notable for the 15 horns and spikes on its head and ornate neck-frill; a herbivore dated at 75 Ma and about 15 feet long, it had a skull almost 6 feet long; known from only two specimens found in the Kaiparowits Formation of Southern Utah, it seems to be closely related to a Canadian dinosaur, *Vagaceratops irvinensis*; North America, Late Cretaceous.

***Kritosaurus***: a genus of poorly known hadrosaurid ornithischian dinosaurs in the subfamily Saurolophinae; first found in the Kirtland Formation and also known from fragments found in Montana, Alberta, and Mexico; North America, Late Cretaceous, 75–70 Ma.

***Kryptops***: “hidden face,” a proposed monospecific genus of carnivorous saurischian dinosaurs in the clade Ceratosauria, known from fragmentary remains described in 2008; *K. palaios* was about 20 feet long and is possibly one of the earliest abelisaurids; some researchers believe, however, that it may be a chimera since some fragments were found 50 feet from others and may belong to a different dinosaur; Ténéré Desert, Niger, Early Cretaceous, 110 Ma.

***Kuehneosauridae***: a family of gliding, lizard-like lepidosauromorph diapsids in the order Eolacertilia; lateral sails on either side of the body enabled them to glide in the air, but they could not fly; North America and Europe, Early to Late Triassic.

***Kuehneotherium***: a genus of primitive shrew-sized mammals in the family Kuehniotheriidae, known from abundant tooth, dental, and mandible specimens but no complete skeletons; weaker jaws than the Morganucodonts, probably subsisting on small insects and worms; Europe and Greenland, Late Triassic to Early Jurassic.

***Kulindroplax perissokomos***: a species of mollusks in the class Aplacophora, known only from a specimen found in England in 2012; the first unambiguous aplacophoran with chiton-like armor, for the first time connecting the generally shell-less Aplacophora with the Polyplacophora (chitons); its underside has a fine covering of small spicules; late Silurian.

***Kunmingella***: a genus of Cambrian crustaceans in the order Bradiriida; one of several crustaceans in the Chengjiang biota with a bivalved carapace over head and abdomen; known only from China, early Cambrian.

***Kutchicetus***: a monospecific genus of slender ancestral whales in the family Remingtonocetidae; *K. minimus* was about 8 feet long and weighed between 200 and 400 pounds; its four short, gracile limbs would give it only slight mobility on land, while its elongated and robust tail vertebrae indicate that it used caudal undulation for swimming, a transitional feature in the evolution of whales; however, it did not have tail flukes; Pakistan and India, early Eocene.

**Kutorginata**: a small class of primitive brachiopods, one of the three extinct classes in the subphylum Rhynchonelliformea; global distribution, early to middle Cambrian.

**Kutorginida**: an order of brachiopods in the class Kutorginata; smooth, biconvex calcareous shells and primitive articulation are similarities to early Cambrian mollusks and hyoliths; early Cambrian.

# L

**La Brea Tar Pits:** a Konzentrat-Lagerstätte in Los Angeles that has produced many complete specimens of mammals and birds of the late Pleistocene. The bones are impregnated by asphalt, with little degradation of bone structure or proteins; very little soft tissue is preserved, however. More fossil birds have been produced here than anywhere else. United States, dated between 38,000 and 11,000 years ago.

**labyrinthodonts:** a paraphyletic group of early amphibian tetrapods; they descended from the rhipidistian fish and were probably ancestral to all later amphibians; characterized by a labyrinthine infolding of the dentine with conspicuous fangs; global distribution, Early Devonian to Early Cretaceous.

**Laccognathus:** “pitted jaw,” a genus of lobe-finned sarcopterygian fish in the extinct order Porolepiformes and family Holoptychiidae; characterized by three large fossae on the jaw, of unknown function; probably amphibian; North America and Europe, Middle to Late Devonian.

**Laganosuchus thaumastos:** a 20-foot-long crocodile notable for its 3-foot-long flat head and snout; like modern crocodiles, its short legs extending to the side kept it from moving well on land; Niger, Cretaceous, 110 Ma.

**Lagenida:** an order of benthic foraminiferans characterized by finely perforate monolamellar walls; global distribution, late Silurian to Recent.

**Lagerpeton:** a monospecific genus of dinosauriform archosaurs in the family Lagerpetidae; known from fragmentary specimens, *L. chanarensis* is estimated to have weighed only 10 pounds; a possibly lagerpetid ichnogenus from a trackway in Poland indicates that the genus may have originated in the Early Triassic; see also **Dromomeron**; Argentina, Middle Triassic.

**Lagerstätte:** a German mining term commonly used for a fossil location that contains an exceptionally large number of specimens. Konzentrat-Lagerstätten contain many specimens which are not notably well-preserved but are important for their sheer numbers (such as nesting areas, bone beds, cave deposits, and coquinas).

Konservat-Lagerstätten, on the other hand, are noted for quality rather than quantity, containing significant numbers of fossils preserved in exceptional detail, sometimes in three dimensions and sometimes showing soft tissue and fragile appendages. Lagerstätten are especially useful in understanding the development and evolution of fossil ecosystems.

**“Laggania”:** see *Anomalocarididae*.

**Lagosuchus:** a genus of small archosaurian reptiles of the Triassic. Although it is incompletely known from only one partial specimen, it may be significant in having an unreptilian hinged ankle joint that allowed it to walk erect with its legs under its body, a characteristic of dinosaurs. Therefore, *Lagosuchus* may fit somewhere in the ancestral line leading to dinosaurs. Argentina, Middle Triassic, about 235 Ma.

**Lambdaotherium:** a contentious genus of perissodactyl mammals formerly placed in the Brontotheriidae but now considered only a close early relative; although poorly known, it was smaller than the earliest accepted brontothere, *Eotitanops*; North America, early Eocene.

**Lambeosaurinae:** a sub-family of later duck-billed ornithomimid dinosaurs in the family Hadrosauridae. Ranging in length from 25 to 35 feet, the lambeosaurs are characterized especially by a large, hollow cranial crest; *Lambeosaurus lambei* also had a backward-pointing spike behind the hollow crest. They were herbivorous and could move both bipedally and quadrupedally. Other genera include *Corythosaurus*, *Hypacrosaurus*, and *Olorotitan*; North America and Asia, Late Cretaceous, 86–66 Ma.

**Lamnidae:** a still-extant family of sharks, including the great white shark, *Carcharodon carcharias*, and its extinct larger ancestor *C. megalodon* (Miocene to Pleistocene); global distribution, Cretaceous to Recent.

**Lance Formation:** a stratigraphic unit of the Maastrichtian Stage in Western North America, coextensive in places with the Hell Creek Formation; it contains an important group of dinosaurs and smaller vertebrates from between 69 and 66 Ma, just before the end-Cretaceous extinction.

**lancelets:** see *Cephalochordata*.

**land plants:** evidence of the earliest true land plants is found in fossilized spores from the Ordovician, and in possible spores from the Cambrian; the earliest fossil plant specimens are known from the Silurian (see *Cooksonia*).

**lantern:** see *Echinoidea*.

**Laramidia:** the name given to the western part of North America which existed as a narrow island continent in the Late Cretaceous, when North America was split by tectonic activity and the rising water level of the oceans; the strata laid down in the resulting Western Interior Seaway are rich with Cretaceous fossils.

**Las Hoyas Lagerstätte:** a site in Eastern Spain dated at 126–125 Ma in the late Barremian Stage of the Early Cretaceous; Las Hoyas is well-known for the only known specimens of the enantiornithine birds *Eoalulavis* and *Iberomesornis*, important in establishing the development of flight in birds; the thin-bedded limestone strata, probably laid down in a freshwater environment, have also produced a great variety of fish, spiders, insects, and plants.

**Latimeria:** an extant genus of lobe-finned fish in the order Coelacanthiformes and family Latimeriidae. The coelacanths were long considered extinct since the Cretaceous until the discovery of modern latimerians in the twentieth century. A specimen of *L. chalumnae* was discovered in 1938 near the Comoros Islands, and several others have been found along the East African coast since then; a second modern species of coelacanth, *L. menadoensis*, was discovered in Indonesia in 1997. The latimerians have fleshy lobe fins and are up to 6 feet long. Their fossil record is unclear, but some researchers believe they originated in the Triassic. See **Coelacanthidae** and **Tetrapoda**. Triassic? to Recent.

**Laugiidae:** a family of sarcopterygian fish in the subclass Actinistia, related to the modern coelacanths of *Latimeria*; Europe, Greenland, and China; Early Triassic to Late Jurassic.

**Laurasia:** A term referring to the northern land masses that are now North America, Europe and Northern Asia; see **paleogeography** for dates.

**Laurasiatheria:** a clade of placental mammals that appeared in the northern supercontinent Laurasia in the Cenomanian, at the beginning of the Late Cretaceous; it includes the carnivorans, ungulates, shrews, bats, whales, and pangolins; see also **Eutheria**; Cretaceous to Recent.

**Laurentia:** the name given to the early North American land mass when it was a separate continent from the Cambrian to the Silurian.

**La Voulte-sur-Rhône:** a marine Konservat-Lagerstätte of the Callovian that is notable especially for the number of soft-bodied cephalopods preserved by pyritization, such as *Doliocaris ingens*; see also *Ophiopinna*; France, upper Middle Jurassic.

**Law of the Unspecialized:** see **Unspecialized Descent**.

**Lazarus taxon:** a taxon whose fossil record shows one or more significant gaps, with no morphological change between the first and last specimens.

**Leaellynasaura:** “Leaellyn’s lizard,” a monospecific genus of small herbivorous ornithischian dinosaurs in the order Ornithopoda. It was 7 to 10 feet long with a very long tail, but only 2 feet tall. Dated between 118 and 110 Ma, *L. amicagraphica* is known from two almost complete specimens found at **Dinosaur Cove** in Australia, which was close to the South Pole in the middle of the Cretaceous. It is notable for large optic lobes in its brain which indicate good night vision. Australia, Early Cretaceous.



***Lebachia***: a genus of tall cone-bearing trees in the order Coniferales, of the late Paleozoic and possibly Mesozoic; similar in appearance to the modern *Araucaria*, it is related to the earlier Cordaitaceae and may be ancestral to modern conifers; global distribution, Late Pennsylvanian to Permian or Triassic.

**lectotype**: when the type of a taxon is identified by a set of syntypes, a single name-bearing specimen may at some point be designated as the lectotype, a later-selected holotype.

***Leedsichthys problematicus***: a species of actinopterygian fish in the extinct family Pachycormidae; possibly the largest fish known, this filter-feeding giant is estimated to have been more than 70 feet long; the pachycormids have only partly calcified skeletons, making their fossils sometimes difficult to interpret; Europe and Chile, Middle Jurassic.

***Leehermania***: see **Staphylinidae**.

***Leioceras***: a genus of ammonoids including *L. opalinum* and *L. lineatum*; the first appearance of the assemblage marks the beginning of the Middle Jurassic at 174.1 Ma; Spain.

**Lemuroidea**: a still-extant superfamily of strepsirrhine primates that includes at least the lemurs, and in some classification schemes the lorises and galagos also; their origins are still disputed, but they probably arose from adapiforms or lorisoids in the Eocene; Africa, Eocene to Recent.

***Lenticulina***: a large genus of foraminiferans in the family Nodosariidae; global distribution, Permian to Miocene.

**Leperditicopida** an order of paleocopan ostracods; from 1 to 2 inches long, thick-shelled and straight-backed; global distribution, Cambrian to Devonian.

***Lepidocaris rhyniensis***: the only species in the branchiopod order Lipostraca; possibly related to the similar modern fairy shrimp in the order Anostraca, this small (0.12 inches) crustacean is the most common arthropod in the Rhynie Chert but is known only there, where it lived in ephemeral pools created by hot springs; Scotland, Middle Devonian.

***Lepidodendron***: “scale branch,” a genus of tree-like lycopodiophytes related to the club mosses, in the order Lepidodendrales. One of the most common fossils in the coal beds of the Pennsylvanian, they probably reached heights of 100 feet and diameters of about 4 feet, with narrow, grass-like leaves as long as 3 feet. The surface of the branches was a mat of closely spaced squares, and the branches ended in spore-producing cone structures that grew 1–3 inches in diameter and up to a foot in length. Global distribution, Early to Late Carboniferous.

***Lepidophylloides***: a form genus of the leaves of *Lepidodendron*; Carboniferous.

**Lepidosauria**: a large subclass of reptiles that includes the orders **Rhynchocephalia** and **Squamata**, q.v.

**Lepidostrobus:** a form genus of the large cones (strobili) of *Lepidodendron*, *q.v.*

**Lepidotes:** a genus of semionotid actinopterygian fish; generally about a foot long, some were as long as 3 feet; they were covered with diamond-shaped ganoid scales and preyed on mollusks; Europe and South America, Early Jurassic to Early Cretaceous.

**Lepospondyli:** a diverse subclass of small tetrapods, generally considered amphibians; the lepospondyls include five orders: Adelospondyli, Aistopoda, Lysorophia, Microsauria, and Nectridea; distinguished from the labyrinthodonts by spool-shaped centra in the vertebrae, the lack of fangs, and the lack of infolded dentine in the teeth; the group almost disappeared early in the Permian, with only one species surviving to the late Permian; Pennsylvanian to late Permian.

**Leptaena:** a genus of articulate brachiopods in the extinct order Strophomenida and family Raphinesquinidae; its shells are notable for a high degree of wrinkling and ornamentation; Ordovician to Early Carboniferous.

**Leptictida:** a possibly paraphyletic order of small eutherian mammals, presenting an unusual combination of primitive and specialized characters; one of the earliest branches from basal eutherians, they may be distantly related to the Euarchontoglires (rodents and related groups); North America, Europe, and Asia; Late Cretaceous to Oligocene.

**Leptictidium:** a genus of small mammals in the order Leptictida. It was 2–3 feet nose to tail but weighed only about 5 pounds. *Leptictidium* had a tail longer than the body; short, weak forelimbs; and strong, elongated hindlimbs. Its cranium and dentition are archaic, and it was omnivorous. Among the few completely bipedal mammals besides humans, it used its tail for balance. Best-known from the Messel Shale Pit; Europe, early to late Eocene.

**Leptochoeridae:** a family of early artiodactyl mammals in the superfamily Dichobunoidea, related to and possibly ancestral to the Entelodontidae; North America, middle Eocene to middle Oligocene.

**Leptocleididae:** “slender clavicle,” a family of small plesiosaurs in the clade Leptocleidia; generally 8–10 feet long with a round body and short tail, they swam in shallow seas worldwide; Early Cretaceous, 140–115 Ma.

**Leptocyon:** “slender dog,” a genus of fox-like mammals in the family Canidae and subfamily Caninae, weighing about 7 pounds; see also *Mesocyon*; North America, Oligocene through Miocene.

**Leptodus:** a genus of productid articulate brachiopods in the family Lyttoniidae; characterized by an unusually thin and flattened brachial valve and an oyster-like pedicle valve that was cemented to the substrate or other shells; global distribution, Permian.

**leptograptid fauna:** an important fossil assemblage of the Ordovician that includes the slender planktic graptoloid *Leptograptus*, extinct at the end of the Ordovician; see **Graptolithina**.

**Leptolepis:** “thin scale,” a long-lived genus of actinopterygian fish in the family Leptolepidae. It was one of the earliest teleosts, with a skeleton made up completely of bone, as opposed to the combination of bone and cartilage in *Pholidophorus* and some other early teleosts. *Leptolepis* is named for its thin scales, which lacked the dentine or cosmine covering of most earlier fish. The combination of bony skeleton and thinner scales improved swimming ability. Global distribution, Middle Triassic to Early Cretaceous.

**Leptomeryx:** a genus of ungulate mammals in the family Leptomerycidae; it was a small deerlike ruminant, weighing between 20 and 30 pounds, and is thought to be one of the earliest cervids; North America, late Eocene to early Miocene.

**Lesothosaurus:** a monospecific genus of small, herbivorous ornithischian dinosaurs; about 3 feet long, with small forelimbs and manus, *L. diagnosticus* was evidently a fast runner; Lesotho, South Africa, Early Jurassic.

**Lewisuchus:** a genus of early archosaurian dinosauriforms in the clade Dinosauriformes and family Silesauridae; related to *Pseudolagosuchus*; about 3 feet long, it is known from several partial specimens dated at about 247 Ma; Argentina, Middle Triassic.

**Liaoceratops:** a monospecific genus of early ceratopsian dinosaurs; *L. yanzigouensis* is known only from two possibly juvenile horned skulls found in the Yixian Formation; *Liaoceratops*, estimated to have weighed only 7 pounds, is dated at 130 Ma and thought to be a basal neoceratopsian, near the time when the neoceratopsian branch of Ceratopsia diverged from the parrot-beaked Psittacosauridae; China, Early Cretaceous.

**Liaoning:** see **Jiufotang Formation**.

**Lias:** a term long used for a 20-million-year series of strata in Northwest Europe dated between the Rhaetian Stage of the Triassic and the Toarcian of the Jurassic; the term also came to be used for that period of time, roughly the Early Jurassic; modern dating revealed the inaccuracy of the references, and the term is now seldom used.

**Libellulium:** a well-known genus of flying insects in the family Petaluridae; distantly related to the modern dragonfly and sometimes classified in its order, the Odonata; wingspan 5–7 inches; North America and Europe, Jurassic.

**Lichida:** an order of spiny trilobites of the middle Paleozoic; the surface of the exoskeleton was grainy, even tubercular; some spines were long, but most were short and thick; Early Ordovician to Late Devonian.

**Liliensternus:** a genus of Late Triassic theropod dinosaurs; synonym *Halticosaurus*; known from several fragmentary specimens found in Germany and Switzerland, *Liliensternus* was a bipedal predator, about 17 feet long with strong hindlimbs and

shorter forelimbs; in appearance it resembles an intermediate between the smaller *Coelophysis* and the larger *Dilophosaurus*; Europe, Late Triassic, 228–201 Ma.

***Limulus*:** “looking sideways,” one of two surviving genera of horseshoe crabs, chelicerates in the order Xiphosurida and family Limulidae. Horseshoe crabs are notable as an example of evolutionary stasis, the still-extant species being almost identical to their earliest known ancestors. The genus *Tachypleus* is found on the coast of Asia and *Limulus polyphemus* lives on the Atlantic Coast of North America. More closely related to spiders than to crabs, the Limulidae have survived since the Early Ordovician.

***Limusaurus*:** a monospecific genus of slender theropod dinosaurs in the family Noasauridae; bipedal with short arms and about 6 feet long, *L. inextricabilis* is notable especially because hatchlings were born with several dozen teeth but lost them and did not replace them; in the nineteen specimens known, adults were completely toothless, showing only traces of the tooth sockets; no other dinosaurs or reptiles are known to follow this pattern, although many replace and increase the number of their teeth as they grow older; China, Late Jurassic.

***Linguatula serrata*:** an extremely simplified pentastome, among the important discoveries in the 1990s of early Paleozoic specimens of this tongue worm, which is common today as a dog parasite; phosphatized specimens were found in the upper Cambrian strata of the Orsten Lagerstätten; it is roughly cone-shaped, with the mouth and attachment hooks at the large end; Sweden, late Cambrian.

***Lingula*:** a well-known genus of marine intertidal brachiopods in the order Lingulida; about 2 inches long, with a 6-inch pedicle, *Lingula* has existed worldwide and essentially unchanged in shape since the middle Cambrian.

***Lingulella*:** an extinct genus of inarticulate brachiopods in the order Lingulida and family Obolidae; *L. waptaensis* appears in the Burgess Shale; North America, middle Cambrian to Late Ordovician.

**Lingulida:** a still-extant order of inarticulate brachiopods in the class Lingulata; the most conservative of brachiopod orders, lingulids burrow in sediment, attached by a long pedicle; characterized by an oval, biconvex shape and a shell of calcium phosphate; middle Cambrian to Recent.

***Lingulina*:** a genus of generally tongue-shaped foraminiferans in the family Nodosariidae; Permian to Miocene.

***Liopleurodon*:** a genus of large but short-necked marine plesiosaurs in the family Pliosauridae; *L. ferox*, the largest species, probably weighed between one and two tons and grew to about 20 feet long, although some estimates are much higher; the predatory *Liopleurodon* was a strong swimmer; Europe, Middle to Late Jurassic.

**Lipostraca:** a monospecific order of freshwater branchiopods in the subclass Phyllopoda, containing the fairy shrimp *Lepidocaris rhyniensis*, known only from the Rhynie Chert of the Early Devonian, one of the earliest preserved freshwater crustaceans.

***Liriodendron***: a still-extant genus of trees in the family Magnoliaceae, known globally from the Cretaceous through the Eocene; its range shrank during periods of late Cenozoic glaciation; also known in the form genus of the leaf, *Liriophyllum*; Middle Cretaceous to Recent.

**Lissamphibia**: a subclass of amphibians that includes all living members of the class: frogs, toads, salamanders, and caecilians; Early Triassic to Recent.

**Lithistida**: a still-extant polyphyletic group of demosponges whose massive skeleton of fused siliceous spicules is often preserved; global distribution, Cambrian to Recent.

***Lithostrotion***: a genus of colonial rugose corals in the suborder Stauriida and family Lithostrotionidae; especially important in Early Carboniferous North American biostratigraphy; global distribution, Early Carboniferous to Permian.

**Litopterna**: an order of superficially horselike South American ungulate mammals in the superorder Meridiungulata, possibly descended from condylarths; widespread from the Paleocene to the Pliocene and present in South America in the late Pliocene when true horses first appeared there; one family of litopterns, the Macraucheniiidae, survived into the Pleistocene.

***Littorina littorea***: the common periwinkle, a still-extant species of gastropods in the superfamily Littorinoidea and family Littorinidae; global distribution, Eocene to Recent.

**Littorinoidea**: a superfamily of gastropods previously placed in a supposed order Mesogastropoda but now simply considered part of the very large clade Caenogastropoda; Eocene to Recent.

***Livyatan***: a genus of odontocete whales in the superfamily Physeteroidea; *L. melvillei* is known from a middle-Miocene skull and mandible discovered in the Pisco Formation of Peru in 2010; a powerful predator, it had some teeth more than a foot long, longer than any other animal known; it was about the size of a sperm whale, and its skull may have in fact contained a reservoir of spermaceti; a tooth found in Australia in 2016 is thought to belong to the genus and was dated at 5–6 Ma; Miocene to Pliocene.

**lizard-hipped dinosaur**: a general term referring to the saurischian dinosaurs.

**lobe-fins**: see **Sarcopterygii**.

**Lomekwian industry**: the name given to primitive tools found in Kenya near Lake Turkana, dated about 3.3 Ma and evidently made by ancestors of the species *Homo*, such as Australopithecines or the uncertainly identified *Kenyanthropus platyops*.

**London Clay**: a lower Eocene formation in Southern England that has produced a large and diverse fauna and flora which indicate a tropical to subtropical climate in the early Eocene; younger strata in the area, through the Eocene into the Oligocene, clearly show a cooling of the climate.

**Longisquama:** “long scales,” a monospecific genus of small four-legged reptiles that bore long shafts, possibly feathered, on both sides of its body. Since it lived around 225 Ma, shortly after the appearance of the earliest dinosaurs, it may be evidence that birds did not descend from dinosaurs. The shafts of *L. insignis* (tentatively called “non-avian feathers”) may not actually be feathers, and whether *Longisquama* is related to birds is unknown. It is certainly not a dinosaur, but it does have a wishbone identical to *Archaeopteryx* (150 Ma) and similar to that of modern birds. Most authorities believe it is probably an ambiguous diapsid with no bearing on the origin of birds. Madygen Formation, Kyrgyzstan, Middle to Late Triassic.

**Lonsdaleia:** a genus of colonial rugose corals in the order Stauriida, characterized by their cerioid structure and the star-burst shape of the individual polyps; Asia, Europe, and North America; Late Devonian to Permian.

**Lophialetidae:** an Asian family of ceratomorph perissodactyl mammals in the superfamily Tapiroidea; the manus is tridactyl, as in the other Asian family, the Deperetellidae; middle to late Eocene.

**Lophodontidae:** a European family of perissodactyl ceratomorph mammals in the superfamily Tapiroidea; early to late Eocene.

**lophodont:** “crested tooth,” having molar teeth with a hard chewing surface formed by transverse, triangular, or ring-shaped ridges, common in herbivorous mammals such as elephants, manatees, and tapirs.

**Lophogastrida:** a still-extant and widespread order of nektic malacostracan crustaceans; 2016 research identified the earliest-known species, *Yunnanocopia grandis* and *Y. longicauda*, as part of the marine faunal radiation that followed the end-Permian extinction; China, middle Triassic.

**lophophorates:** a large group of aquatic animals that feed by means of a lophophore, including brachiopods, bryozoans, phoronids, and hyoliths; each is considered a phylum or a class, but their exact relationships are debatable.

**lophophore:** a coil-shaped, feathery feeding structure in lophophorates, varying greatly in shape and length; cilia on the lophophore sweep and pump food particles into the mouth of the animal.

**Loxonema:** a genus of gastropods in the order Murchisoniina; characterized by slender, high-spired shells with fine axial ornamentation lines; global distribution, Ordovician to Middle Jurassic.

**LUCA:** acronym for “last universal common ancestor,” an unidentified type of prokaryotic organism thought to have been living almost 4 billion years ago, only half a billion years after the formation of Earth; it was presumably simpler than its offspring, probably single-celled with no distinct nucleus; the earliest definitive organic fossil is dated at 3.7 billion years ago; see also **Archaea**.

**Lufengosaurus:** a genus of sauropodomorph dinosaurs in the family Massospondylidae. Bipedal and about 30 feet long and weighing almost 2 tons,

*Lufengosaurus* is notable for the preservation of collagen in some embryonic bones, by far the earliest-known example of soft-tissue preservation in a fossil. Since the proteins in collagen vary from species to species, “collagen fingerprinting” may be important in phylogenetic research. The bones from at least twenty individual embryos show that the embryos were growing faster than in other dinosaurs. China, Early Jurassic, 197–190 Ma.

***Lunataspis aurora***: a species of chelicerates discovered in Manitoba in 2008, the earliest-known xiphosuran; dated at 445 Ma and very similar to modern horseshoe crabs; Canada, Late Ordovician.

**Lycopodiophyta**: the lycophytes, the oldest division of vascular plants, known mainly for the large trees of the Devonian and Carboniferous but represented today by numerous families of smaller plants such as club mosses; characterized by primitive, narrow leaves known as microphylls, they reproduce by shedding spores; global distribution, late Silurian or Early Devonian to Recent.

***Lycoptera***: a genus of small freshwater teleost fish in the still-extant superorder Osteoglossomorpha; one of the earliest-known in the group, it includes species that are index fossils for the end of the Jurassic and the Cretaceous in China; Mongolia and China, Late Jurassic to Early Cretaceous.

***Lyginopteris***: a genus of early seed ferns in the order Lyginopteridales; like many other Paleozoic plant names, *Lyginopteris* was originally the name of a form genus (in this case for the stem) but is used now for the whole plant; small club-shaped glands occur on the surface of all parts of the plant; North America and Europe, Late Devonian to Late Carboniferous.

**Lyginopteridales**: the earliest pteridosperms, an order of climbing seed ferns in the extinct division Pteridospermatophyta; superficially similar in appearance to true ferns; Early Devonian to Carboniferous.

**Lysorophia**: an order of snake-like amphibians in the extinct class Lepspondyli; tetrapods but characterized by a slender, elongate body with very small limbs; possibly related to the Microsauria; North America and Europe, Pennsylvanian to middle Permian.

***Lystrosaurus***: a genus of dicynodont therapsids in the infraorder Dicynodontia. Surviving the end-Permian extinction, it became the most common large terrestrial animal of the Early Triassic. Mammal-like and about the size of a large pig, *Lystrosaurus* was herbivorous and semi-aquatic, with only two large (canine) teeth. (Its species ranged in size from 2 to 8 feet long.) *Lystrosaurus* probably used its robust forelimbs for digging and burrowing. Since its distribution encompassed Antarctica, Southern Africa, and India in the Early Triassic, it is one of the larger animals that provide information about the time of separation of Gondwana into its now widely removed parts. Late Permian to Early Triassic.

***Lythronax***: a monospecific genus of theropod dinosaurs, known from one fairly complete skeleton discovered in 2009; *L. argestes* is the oldest known true

tyrannosaurid and is ancestral to *T. rex*; it grew as large as 25 feet long and 5,500 pounds; southern Utah, Late Cretaceous, 80 Ma.

***Lytoceras***: a genus of ammonitid ammonoids, the type genus of the family Lytoceratidae; it was 3–5 inches in diameter and had a smooth shell and a complex suture; global distribution, Early Jurassic to Early Cretaceous.

**Lytoceratida**: a conservative order of ammonoids in the order Ammonitida; notable for having fewer but longer-lived species than other ammonoids, the early Lytoceratida evolved from phylloceratids and diversified into 12 families, the dominant one being the Lytoceratidae; global distribution, Late Triassic to Late Cretaceous.



# M

***Machairoceratops***: “saber-horned-face,” a monospecific genus of ornithischian dinosaurs in the subfamily Centrosaurinae; known from a partial skull described in 2016, it is estimated to be a medium-sized ceratopsian about 15 feet long; like its cousin *Nasutoceratops*, *M. cronusi* was marked by two long and curved eye-socket horns; Utah, United States; Late Cretaceous, 82–80 Ma.

**Machairodontinae**: “saber-tooth,” an extinct subfamily of cats with varying lengths of the canine teeth; the family is named for *Machairodus* and includes *Megantereon* and the later *Homotherium* and *Smilodon*; North America, Europe, Asia, and Africa; early Miocene to 10,000 years ago.

***Machairodus***: a genus of lion-sized cats in the subfamily Machairodontinae; global distribution, late Miocene to middle Pleistocene.

***Macoma***: a still-extant and very large genus of deep-burrowing clams in the order Veneroida and family Tellinidae; Pleistocene to Recent.

**Macraucheniiidae**: a family of perissodactyl ungulates in the order Litopterna, found only in South America; the Macraucheniiidae appeared in the Eocene and were the last surviving litopterns, disappearing about 12,000 years ago; research in 2014 on *Macrauchenia patachonica* seems to show that, although it looked like a camel, it was most closely related to perissodactyls such as the horse, rhinoceros, and tapir; South America, Eocene to Pleistocene.

**macrofossil**: a fossil large enough to be studied directly without a microscope.

**Macropodidae**: a still-extant family of marsupials in the order Diprotodontia; the Macropodidae include kangaroos and other extant genera as well as several extinct genera; Meganesia, late Oligocene to Recent.

**Macroscelididae**: a family of eutherian mammals in the order Macroscelida; although often called elephant shrews because of a very long snout and shrew-like shape, they are not closely related to either elephants or shrews; they are

insectivorous, ranging from mouse-size to rabbit-size, and their very long hindlimbs are adapted for jumping; widespread across Southern Africa, early Oligocene to Recent.

***Macrotaeniopteris***: a genus of low-growing plants with long, lanceolate leaves; global distribution, Early Triassic to Late Jurassic

**Madygen Formation**: a Triassic Konservat-Lagerstätte in Central Asia, dated between 230 and 225 Ma; its strata were laid down in forested floodplains with lakes, rivers, and swamps; it is known especially for its well-preserved insects and flora, as well as the unusual gliding reptile *Sharovipteryx* (see also ***Longisquama***); especially important because of the paucity elsewhere of Early Triassic insect fossils; Kyrgyzstan, Late Triassic.

**Maevarano Formation**: a Maastrichtian site in Madagascar where dozens of species of dinosaurs (including *Majungasaurus*, *Masiakasaurus*, and *Rapetosaurus*), reptiles, the large frog *Beelzebufo*, birds, and mammals have been found. Several bone beds in successive strata have been explored. Recent studies point to toxic algae as a possible cause of death of at least one group of different animals nestled together. Northwestern Madagascar, Late Cretaceous, 70–66 Ma.

***Maiacetus inuus***: a species of ancestral whales described in 2009; males grew to about 9 feet long, females 8 feet; a fetal skeleton found with several other sets of remains is the only known fetal specimen of an ancestral whale; *Maiacetus* evidently gave birth on land but spent most of its time in the water; notable for four flipper-like legs better for swimming than walking on land; Pakistan, middle Eocene.

***Maiasaura***: a genus of hadrosaurid ornithopod dinosaurs in the subfamily Saurolophinae; up to 30 feet long, it was a medium-sized hadrosaur, but it is notable especially for indications that hatchlings were altricial, requiring some parental care; see also **Egg Mountain**; North America, Late Cretaceous, 78–75 Ma.

***Maiopatagium furculiferum***: a species of early gliding mammals described in 2017, in the order Euharamyida and family Eleutherodontidae; about 9 inches long, it had skeletal adaptations for gliding as well as a skin membrane attached to forelimbs and hindlimbs; not related to the earlier glider *Volaticotherium*; China, Late Jurassic, 160 Ma.

***Majungasaurus***: a genus of large theropod dinosaurs in the family Abelisauridae; dated at 70–66 Ma and known from several skulls and considerable skeletal material, it is estimated to have been 20–23 feet long, weighing about a ton; it seems closely related to abelisaurids from India but not Africa or South America; first called *Majungatholus*; Madagascar, Late Cretaceous,

**Malacostraca**: the class of crustaceans that contains three subclasses: the Phyllocarida, Hoplocarida, and Eumalacostraca, the latter containing most of the familiar modern crustaceans; Cambrian to Recent.

***Mamenchisaurus***: a genus of large sauropod dinosaurs in the family Mamenchisauridae, discovered in 1952 by C.C. Young in the Sichuan province of China and known from several species found since then. The type species is *M. constructus*, notable for its very long neck, with large and elongated neck vertebrae; only *Sauroposeidon* is known to have a longer neck. Described in 1993, *M. sinocanadorum* grew up to 115 feet long, weighed between 50 and 75 tons, and had a neck up to 59 feet long. The length of the neck gave the family a long reach, but it is unclear whether they fed off high branches like a giraffe or kept their head close to the ground. Possible relatives are the slightly larger *Apatosaurus* and *Argentinosaurus*. China, Late Jurassic.

**Mammalodontidae**: a family of late Oligocene toothed mysticete whales; the two genera in the family are *Mammalodon* and *Janjucetus*, both about 10 feet long; possessing synapomorphies of both odontocetes and mysticetes, the Mammalodontidae seem to represent one of the transitional steps from toothed to baleen whales; see also **Aetiocetidae**; Australia and New Zealand, known only from the late Oligocene.

**Mammalia**: the class of mammals; the earliest stem-mammaliaforms appeared in the Late Triassic (see *Agilodocodon*, *Castorocauda*, *Hadrocodium*, *Kuehniotherium*, and *Morganucodonta*). They experienced a burst of evolutionary diversification early in the Middle Jurassic and then spread worldwide with relatively little diversification for 100 million years until the end of the Mesozoic. Then in the Paleocene began the rapid diversification leading to their present dominance in the world. The principal characteristics that differentiate them from other vertebrates are mammary glands, hair, three middle ear bones, a squamosal-dentary jaw joint, and a section of the brain called the neocortex.

**mammoth**: a general term used, sometimes interchangeably with mastodon, to refer to the extinct elephants of the Pleistocene, which are classified in the still-extant superfamily Elephantoidae and family Elephantidae. Some mammoths had upper and lower tusks as long as 7 feet and strikingly curved; they generally had more pointed skulls and more hair than modern elephants, and mammoth species ranged greatly in size. Found throughout North America, Africa, Europe, and Asia until recent times, the latest survived until about 7000 years ago.

***Mammuthus trogonotherii***: the steppe mammoth, one of several Pleistocene genera of mammoths in the family Elephantidae that were larger than modern elephants; also called *Mammuthus armeniacus*.

**Mammutoidea**: a suborder of proboscideans that includes the mastodons of the families Mammutidae and Stegodontidae but are not directly related to modern elephants; like the Elephantidae, they had only upper tusks; widespread in North America, Europe, Asia, and Africa in the Miocene; early Oligocene to Recent.

**Maniraptora**: the clade that includes the birds and the dinosaurs most closely related to them, principally the therizinosaurs, dromaeosaurs, and oviraptors; Late Jurassic to Recent.

**Mantophasmatidae:** a still-extant family of predatory insects in the order Notoptera, formerly considered a small order in its own right, called “Mantophasmatodea.” The family is now known only in Southwestern Africa but was probably once widespread. It contains only half a dozen species, one a recently discovered living African insect, and a similar one a few inches long, encased in amber, from the Eocene in Europe. These insects bear characteristics of the larger extant groups, the mantids and the phasmids. Europe and Africa, Eocene to Recent.

**manus:** plural manus, the distal part of the forelimb of vertebrates, corresponding to the human hand; it includes the wrist and hand or carpus and forefoot.

**Maotianshan Shales:** see **Chengjiang**.

**Mapusaurus roseae:** a genus of carcharodontosaurid dinosaurs discovered in Western Patagonia in the late 1990s; perhaps the largest carnivorous dinosaur, *Mapusaurus* was about 40 feet long and probably preyed on *Argentinosaurus*, one of the largest of all dinosaurs, possibly hunting in packs; Argentina, early Late Cretaceous.

**Marasuchus:** a genus of archosaurian dinosauriform reptiles; bipedal and less than 2 feet long, *Marasuchus* is one of several early genera close to the line of descent leading to the dinosaurs; it is known from two specimens dated about 235 Ma; Argentina, Late Triassic.

**marine transgression:** a long-term invasion of the sea over a large land area as a result of a warmer global climate and rising sea levels; such transgressions were widespread in the Early Ordovician, and even more in the Cretaceous, when they created large epicontinental seas like the Western Interior Seaway of North America.

**Marrella splendens:** a species of stem-group arthropods abundant in the Burgess Shale assemblage, the best-known of the marrellomorphs; only about an inch long, it superficially resembles trilobites but has significant gill and appendage differences; its appearance led Walcott to call it a “lace crab” because of several long spines around its body; Canada, middle Cambrian, 508 Ma.

**Marrellomorpha:** a subphylum of early arthropods considered to include three species of marrellids and several specimens called acercostracans; poorly known because of their lack of hard parts that could fossilize easily; North America, Europe, Asia, Africa, and Australia; early Cambrian to Devonian.

**Marsupialia:** “pouch animals,” mammals that bear young in a relatively undeveloped state, so that they must live for some time in an external pouch on the mother’s chest, where they survive on milk secreted through the skin. Metatherian mammals, the ancestors of marsupials, probably diverged from the placental mammals in the Middle Jurassic, but the oldest definitive marsupial appeared at only about 65 Ma, at the beginning of the Paleocene (see *Peradectes*). Marsupials originated in North America and migrated to South America, where they diversified greatly while it was still part of Gondwana. They reached Australia via Antarctica shortly before those

two continents separated in the early or middle Eocene, probably in a single dispersion event. Marsupials are extant in North and South America, Australia, and a few islands north of Australia.

***Marsupites***: a genus of large, purse-shaped articulate crinoids in the small order Uintacrinida; stemless, bowl-shaped, and with ten arms, *M. testudinarius* is the boundary marker for the beginning of the Campanian Stage of the Cretaceous; Europe, Late Cretaceous.

***Masiakasaurus***: a genus of small carnivorous dinosaurs; notable for being the only known theropod with long, conical, hooked front teeth that protrude from the front of its mouth; the teeth may have been used to stab small prey; coyote-sized, with a long tail; Madagascar, Late Cretaceous, 70–66 Ma.

**mass extinction**: see **extinction**.

***Massospondylus***: a genus of prosauropod dinosaurs of the Early Jurassic. Bipedal, 13 feet long, and weighing more than a ton, it had a sharp thumb claw on its small forelimbs. Researchers reported in 2012 that they had found a large nesting site of this dinosaur that may be 100 million years older than the previous oldest dinosaur nest site. The eggs are 2–3 inches long and were found in clutches of up to three dozen eggs in ten nests. The discovery indicates earlier complex social behavior in dinosaurs than previously thought. Southern Africa, 190 Ma.

**mastodon**: a term sometimes confused with **mammoth**, but referring more specifically to the slightly differentiated proboscideans of the extinct family Mammutidae and suborder Mammutoidea; North and Central America, late Miocene to late Pleistocene.

***Mastodonsaurus***: a genus of stereospondyl capitosaur temnospondyls; growing as long as 20 feet, *M. giganteus* is the largest known temnospondyl, with a large head, eyes on top and midway in the skull, and a short tail; Europe, Middle Triassic.

***Mastotermes electrodominicus***: a species of termite known from amber deposits of the late Oligocene; analysis of its DNA supports the view that termites and cockroaches have a common ancestor from which they evolved separately; Dominican Republic.

***Materpiscis***: see **Gogo Formation**.

**Matoniaceae**: a still-extant family of ferns in the order Gleicheniales; it appeared in the Permian and spread globally in the Jurassic and Cretaceous; the family disappeared from the Northern Hemisphere at the end of the Cretaceous and was thought to be a Lazarus taxon because of three surviving genera in Southeast Asia; but it is now known from Tertiary specimens from Antarctica, Argentina, Australia, and New Zealand; see also ***Weichselia***; Permian to Recent.

***Mathevia***: an enigmatic genus of small, worm-like animals possibly related to polyplacophorans; late Cambrian to Early Ordovician.

**Mawsonia:** a genus of large coelacanth fish in the family Mawsoniidae; the largest, *M. gigas*, was about 20 feet long and preyed on fish and large invertebrates; Africa and Brazil, Cretaceous, 110–100 Ma.

**Maxakalisaurus topai:** a species of titanosaurian sauropod dinosaurs discovered in Brazil and named in 2006; probably related to *Saltasaurus*, it is estimated to be at least 40 feet long and weigh 9 tons; notable for its osteoderms and vertical spine plates, it was herbivorous and had a long neck and tail, and a small head; Late Cretaceous, about 80 Ma.

**Mayomyzon pieckoensis:** a species of small, lamprey-like ostracoderms in the family Mayomyzontidae, known from the Pennsylvanian assemblage of the Mazon Creek site; United States, Late Carboniferous.

**Mazon Creek:** a Konservat-Lagerstätte in Northeast Illinois where several coal-mining sites, especially in the Francis Creek Shale, have produced very good fossils of about 500 species from the Late Carboniferous. The Mazon Creek deposits, laid down in a deltaic environment similar to the Grès à Voltzia, include terrestrial, freshwater, and marginally marine organisms from about 306 Ma, generally inside clay ironstone concretions. The most common fossils are insects, crustaceans, and other arthropods, as well as mollusks, jellyfish, and a variety of plants and trees. There are marine and freshwater bivalves but no corals or crinoids, and the only brachiopod is *Lingula*. Mazon Creek is known especially for the famous but enigmatic “Tully monster” (*Tullimonstrum*, *q.v.*). United States, Late Pennsylvanian.

**Mecochirus:** a genus of decapod crustaceans in the family Mecochiridae; *M. longimanatus*, the type species, is notable for the extreme length of its first pair of walking legs; several specimens in the Solnhofen deposits lie at the end of a short trackway, evidently a “death trail”; cosmopolitan, Jurassic to Cretaceous.

**Mecoptera:** a still-extant order of neopteran insects, commonly called scorpionflies; they may have been pollinators of gymnosperm plants before the appearance of the Hymenoptera in the early Mesozoic; global distribution, Early Carboniferous to Recent.

**Medullosaceae:** a family of seed ferns in the extinct order Medullosales; the largest known seed fern, growing more than 30 feet high, with large leaves and seeds; North America, Europe, Asia, and North Africa; Carboniferous to Permian.

**Megacerops:** a genus of perissodactyl mammals in the family Brontotheriidae; one of the larger brontotheres, the elephant-sized *Megacerops* stood about 8 feet high at the shoulder; it is also notable for a pair of blunt horns extending side-by-side from the nasal bone and the frontal bone; North America, late Eocene.

**megafauna:** term used for large terrestrial mammals — especially of the Pleistocene — weighing more than 100 pounds.

**Megaloceros:** a genus of large deer in the subfamily Cervinae; *M. giganteus*, called “Irish elk,” was almost 7 feet high at the shoulder and had a very wide (10 feet) and

heavy set of antlers; the five species of *Megaloceros* inhabited Europe and Asia from the Pliocene to the end of the Pleistocene.

***Megalocheilus atlas*:** an extinct species of cryptodiran tortoises in the still-extant family Testudinidae; weighing more than a ton, *M. atlas* is the largest known land tortoise; Asia, Miocene to Pleistocene.

***Megalodon*:** see *Carcharodon*.

***Megalograptus*:** a genus of large eurypterids in the family Megalograptidae; it was 4 feet long and had long, spiny claws and a scorpion-like tail but no stinger; North America, Early to Late Ordovician.

***Megalolamna paradoxodon*:** a proposed species of sharks in the family Otodontidae; known from 2-inch teeth found in Peru, California, North Carolina, and Japan; dated at 20 Ma, it seems to be a sister genus of the Paleocene-Eocene *Otodus*; cosmopolitan, known only from the Miocene.

**Megalonychidae:** a family of large, bear-like ground sloths in the order Pilosa and superorder Xenarthra; the type genus *Megalonyx*, including the huge *M. jeffersonii*, could maneuver bipedally, standing 10 feet tall and weighing more than a ton; North and South America, Oligocene to the end of the Pleistocene.

**Megalosauridae:** a family of tetanuran theropod dinosaurs; in addition to *Megalosaurus*, the family includes *Torvosaurus* and *Streptospondylus*; North America, Europe, and Asia; Triassic to Cretaceous.

***Megalosaurus bucklandii*:** a species of large theropod dinosaurs, 23 feet long and bipedal, with short but robust forelimbs; it was one of the first formally identified dinosaurs, described in the 1820s and named by Georges Cuvier for William Buckland, the early English paleontologist; England, Middle Jurassic.

**Meganesia:** a biogeographic name for the large land mass that comprised Australia, Tasmania, and New Guinea during Pleistocene ice ages when the sea level was low enough for land bridges joining them together; they have been separated for the last 10,000 years; also sometimes used for the region of the present lands.

***Meganeura monyi*:** a species of giant predaceous griffinflies in the order Meganisoptera; it had a wingspan of about 26 inches; Western Europe, Late Carboniferous to early Permian, 305–299 Ma.

***Meganeuropsis permiana*:** a species of giant griffinflies in the order Meganisoptera, with a wingspan of 28 inches and body length of about 17 inches; North America, early Permian.

**Meganisoptera:** an order of large-winged, predaceous insects, a Carboniferous offshoot of the Odonata, the class that includes the modern dragonflies; formerly called Protodonata; most were similar in size to modern dragonflies, but the order includes the largest known flying insects, such as *Meganeura* and *Meganeuropsis*,



which had wingspans up to 28 inches; global distribution, Early Carboniferous to late Permian.

***Megantereon***: a genus of early sabertooth cats in the subfamily Machairodontinae, probably ancestral to the later *Smilodon*; up to 330 pounds and bearing 3-inch canine teeth; North America, Africa, Europe, and Asia; early Pliocene (perhaps late Miocene) to middle Pleistocene.

**Megatheriidae**: the largest ground sloths, a large family of xenarthran mammals in the still-extant order Pilosa; members of the family ranged in size from 6 to 20 feet long and weighed up to 4.5 tons; South America, Oligocene to Pleistocene.

***Megatherium***: a genus of large mammals in the still-extant order Pilosa and extinct family Megatheriidae; it was the largest ground sloth, about 20 feet long and weighing more than 4 tons; it had three hooked claws on each foot and was primarily quadrupedal; it became extinct about 11,000 years ago, after the arrival of humans; South America, early Pliocene to late Pleistocene.

***Megazostrodon***: a genus of small early cynodont mammals in the family Megazostrodonidae; 4–5 inches long, a scansorial insectivore, it seems to represent one of the last transitional stages between the cynodonts and true mammals; Elliot Formation, South Africa, Late Triassic to Early Jurassic.

***Megistaspis***: a genus of ptychopariid trilobites in the family Asaphidae; Australia, Europe, Asia, and North America; Early to Middle Ordovician.

***Megistaspis acuticauda***: a large species of shovel-nosed burrowing ptychopariid trilobites; related to the smaller *Illiaenus* but more than a foot long and characterized by a distinct and pointed cephalon; cosmopolitan, Early Ordovician.

***Mei long***: “sleeping dragon,” a species of small troodontid dinosaurs in the Jehol biota; a basal troodontid, it is almost 3 feet long, with wing-like arms and long, clawed fingers; known from two well-preserved specimens, both found in a bird-like sleeping posture; neither has obvious feathers but may have had a feather-like coating; China, Early Cretaceous, 125 Ma.

***Melanopsis***: a genus of Miocene gastropod mollusks notable for its evolutionary stasis for 7 million years, followed by a period of rapid change for 2 million years as the environment changed from marine to freshwater; in this period the shell size increased and a distinctive shouldering pattern evolved; Europe and Asia, Miocene.

***Melanorosaurus***: a genus of early sauropodomorph dinosaurs in the family Melanorosauridae; quadrupedal and one of the larger prosauropods, it was about 26 feet long and weighed a little more than a ton; *Melanorosaurus* is dated about 210 Ma, close to its relative *Antetonitrus*; South Africa, Late Triassic.

***Melittosphex burmensis***: a species of bees in the family Melittosphacidae, preserved in amber; the earliest-known specimen of a bee, dated at 99–100 Ma; Burma, Early Cretaceous.



***Meniscotherium***: a genus of herbivorous protoungulate mammals in the family Phenacodontidae; ranging from 15 to 30 pounds, they had hooves and the selenodont teeth of ruminant herbivores; North America, Eocene.

***Menoceras***: a genus of perissodactyl mammals in the family Rhinocerotidae; about 5 feet long, it was smaller than its relative *Diceratherium* but had the same unusual pair of side by side nasal horns; North America as far south as Panama, late Oligocene to early Miocene.

**meraspis**: the intermediate growth phase of trilobites, during which the thorax and pygidium became distinct; see also **protaspis** and **holaspis**.

**Merostomata**: an obsolete term for a class of chelicerate arthropods that was considered to include the extinct order Eurypterida and the extant Xiphosura; the latter are now sometimes regarded as a class in their own right; Middle Ordovician to Recent.

***Merychippus***: a genus of three-toed Miocene horses in the family Equidae, the first known grazing horse; at 3 feet high it was the tallest horse of the time, and it gave rise to several other genera of grazers, such as *Hipparion* and *Protohippus*; North America, early to late Miocene.

**Merycoidodontidae**: a large family of artiodactyl ruminants in the still-extant suborder Tylopoda and extinct superfamily Merycoidodontoidea; previously called Oreodontidae; they were browsers with a selenodont dentition and claws instead of hooves; abundant in the Oligocene, they were pig-like in appearance but are generally considered camelids; known across North America from Oregon to Central America, late Eocene to Miocene.

***Mesacanthus***: a large genus of primitive acanthodian fish in the family Acanthodidae; ranging from a few inches to a foot in length, *Mesacanthus* is characterized by pectoral, anal, pelvic, and dorsal fin spines, and it is named for an unusual pair of pre-pelvic fins in the middle of the body; Scotland, Early to Middle Devonian.

***Mesocyon***: a species of dog-like mammals in the family Canidae and extinct subfamily Hesperocyoninae; see also ***Leptocyon***; weighing about 16 pounds, it is known only from sites in Oregon, California, Colorado, and Nebraska in Western North America; early Oligocene to early Miocene.

***Meshippus***: a genus of early Equidae in the extinct subfamily Anchitheriinae; slightly larger than *Hyracotherium* but still only about 2 feet high at the shoulder; a cousin, *Anchitherium*, migrated to Eurasia in the early Miocene, becoming extinct in the Pliocene; North America, late Eocene to early Oligocene.

***Mesolimulus***: a genus of xiphosurans in the family Limulidae; almost identical to the modern horseshoe crab, several specimens of *Mesolimulus* are known from the Solnhofen quarries, including a famous one that died at the end of a well-preserved 30-foot trackway; Europe, Late Jurassic 151–146 Ma.

**Mesonychidae:** a family of protoungulate mammals in the order Mesonychia, related to a variety of modern mammals, including whales, hippopotamuses, and dolphins. Although they were long thought to be direct ancestors of whales, their relationship is now thought to be more distant. Ranging from 3 to 13 feet in length and having four-clawed feet, the mesonychids encompassed a wide variety of herbivores and carnivores. They declined in the Eocene, with only one genus, *Mongolestes*, surviving into the Oligocene. Europe, Asia, and North America; early Paleocene to early Oligocene.

**Mesonyx:** a genus of carnivorous mammals in the family Mesonychidae; wolf-like in appearance and behavior although not directly related, *Mesonyx* grew to about 5 feet long, excluding its tail; North America and Asia, late Eocene.

**Mesophyticum:** term sometimes used for a paleobotanic division of time roughly corresponding to the Mesozoic Era and characterized by the plant life of the Mesozoic.

**Mesosauria:** a single-family order of small aquatic reptiles, also called Proganosauria. Their taxonomic position is controversial, some considering them basal “parareptiles,” others preferring to place them in the stem-reptile family Captorhinidae, and some even claiming similarities to synapsids. They are the earliest-known aquatic reptiles, possibly descended from terrestrial ancestors, and may be the earliest-known viviparous reptiles. About 3 feet long, they probably inhabited a saltwater basin where Southern Africa and South America were still joined in the early Permian.

**mesosuchians:** a large and paraphyletic grouping of archaic terrestrial or semi-aquatic reptiles, generally considered in the superorder Crocodylomorpha; characterized by elongated and flattened skulls, and in some genera very long tails; widespread in the Jurassic and Cretaceous.

**Mesothelae:** the primitive suborder of arachnids in the order Araneae, with only one extant representative, the Liphistiidae of East Asia; the Mesothelae are among the earliest spiders, known from North America and Europe from the Pennsylvanian to the Permian; see also *Palaeothele*.

**Mesozoic Marine Revolution:** Early in the Mesozoic Era, several marine predators developed new, durophagous shell-crushing abilities: first the placodont marine reptiles, then the ichthyosaurs, and in the Cretaceous the mosasaurs and ptychodontid sharks. Because of the increase in durophagy, the populations of ammonoids and other gastropods, crinoids, and brachiopods decreased rapidly, and the character of the benthos was changed greatly, with many sessile and slow-moving taxa becoming extinct. Some species developed new protections, such as lighter, streamlined bodies that could escape by swimming or jet propulsion. Bivalves survived better than brachiopods, mainly by burrowing and becoming infaunal; some, such as the Pectinidae, developed the ability to jump away from predators.

**Messel Shale Pit:** an Eocene Konservat-Lagerstätte near Frankfurt am Main. Representing a complete lakeside ecosystem in a subtropical forest, it has yielded a great variety of fossils, including especially mammals but also plants, insects and other arthropods, and invertebrates. The thirty-five mammal species include *Darwinius masillae*, possibly a very primitive primate, and the very unusual *Leptictidium*. See also *Palaeopython*. Germany, early Eocene, 49 Ma.

**Messinian Event:** (also known as Messinian Salinity Crisis) the drying up of the Mediterranean Sea at the end of the Messinian Age of the Miocene, from 5.96 to 5.33 Ma; the causes are unclear.

**Metacopina:** a suborder of ostracods in the order Podocopida; their carapaces have features that seem to be transitional between the other two podocopid suborders, the Platytopina and the Podocopina; global distribution, early Paleozoic to Early Jurassic.

**Metaplacenticerias:** a genus of ammonoids in the order Ammonitida and family Placenticeratidae; important as an index fossil for the late Campanian; Japan, California, and Antarctica; Late Cretaceous.

**Metasequoia:** a genus of deciduous redwoods with one species still living in China; originating in the Late Cretaceous, *Metasequoia* forests were found at high latitudes across the Northern Hemisphere until the Miocene.

**Metaspriggina:** a monospecific genus of very primitive chordates known from the Burgess Shale; it was so named because of a superficial similarity to the Ediacaran genus *Spriggina*, but the two are now considered unrelated; *M. walcotti* may be a craniate and possibly a primitive fish; Canada, middle Cambrian, 508 Ma.

**Metatheria:** an infraclass of therian mammals that includes all marsupials, extinct and living. The earliest-known metatherian fossils, such as *Sinodelphys szalayi*, have been found in Cretaceous sites in China. The first true marsupials are found in lower Paleocene strata in North America (see *Peradectes*). Migrating into South America by the end of the Cretaceous, marsupials then appeared in Europe and North Africa in the Eocene. They reached Australia in the early or middle Eocene, shortly before the island continent separated from Gondwana.

**metazoan:** an animal that has evolved beyond the one-celled stage, having a complex cell structure and nervous system; although long known to be widespread and diverse in early Cambrian deposits, only around 1950 were metazoans found in upper Precambrian strata in the Ediacara Hills of Australia.

**Metoposaurus:** a genus of large temnospondyl amphibians probably close to the ancestral stock of modern amphibians; up to 10 feet long, the salamander-like *Metoposaurus* probably occupied a crocodile-like niche, feeding mainly on fish; the genus includes *M. diagnosticus algarvensis* (discovered in Portugal in 2015) and three other members; Europe, Late Triassic, 230–200 Ma.

**Metriorhynchidae:** a family of marine crocodylomorphs in the clade Thalattosuchia; the type species is *Metriorhynchus* (“moderate snout”), about 10 feet long with a streamlined body, paddle-like forelimbs, and a tail fin; North and South America and Europe; Middle Jurassic to Early Cretaceous.

**Miacis:** a genus of arboreal carnivores in the extinct superfamily Miacoidea and family Miacidae; close to the ancestry of modern carnivores, weasel-sized *Miacis* descended from insectivores and had a larger brain than its cousins the creodonts; North America, Europe, and Asia; late Paleocene to late Eocene.

**Michelinia:** a genus of colonial favositid corals in the extinct order Tabulata; global distribution, Early Devonian to late Permian.

**Micraster:** an evolutionarily important genus of irregular atelostomate echinoids in the still-extant subclass Euechinoidea and order Spatangoida. Characterized by its heart shape and dense covering of small tubercles which supported a forest of short spines, *Micraster* lived in a burrow in marine sediment. Study of the gradually evolving changes in species of *Micraster* in 10 million years (almost 500 feet) of the chalk beds of the Late Cretaceous made it well-known in the nineteenth century as an example of evolution. North America, Europe, Africa, and Antarctica; Late Cretaceous to Paleocene.

**Microcystis:** a genus of freshwater cyanobacteria that can produce algal blooms with toxins that cause anoxia; global distribution, Permian to Recent.

**Microdictyon:** a genus of worm-like animals now known from several complete fossil specimens and considered a possible basal onychophoran, but it may be unrelated to any later taxa; see *M. sinicum*; Tommotian biota, global distribution, early Cambrian.

**Microdictyon sinicum:** a species of worm-like animals so far unrelated to later taxa; its discovery in 1989 is remarkable for solving the mystery of small, round phosphatic caps called *Microdictyon* that were one of the enigmatic elements of the small, shelly fauna; these caps covered the joints where the ten pairs of leg-like appendages joined the body of *M. sinicum*; China, Chengjiang biota, early Cambrian.

**Microdomatidae:** a family of marine gastropods in the superfamily Trochoidea; this family of high-spined sea snails includes the subfamilies Microdomatinae and Decorospirinae; North America, Asia, and Europe; Early Devonian to Early Triassic.

**microfossil:** a fossil whose typical form is microscopic in size; because so abundant and rapidly evolving, many microfossils are extremely useful in biostratigraphy; some of the more important groups are the diatoms, Foraminifera, Radiolaria, and other protists.

**micropaleontology:** the branch of paleontology dealing with fossils that require a microscope to see their form or their important characteristics.

**Microraptor:** a genus of small (less than 3 feet long) carnivorous feathered dinosaurs in the family Dromaeosauridae, known from several Aptian sites in Liaoning

Province. It had feathers on forelimbs and hindlimbs, which may have been used for short glides or flights. A 2012 study argues from comparisons of melanosomes with modern birds that the feathers were probably iridescent. Synonym: *Cryptovolans pauli*. China, Early Cretaceous, 125–113 Ma.

**Microsauria:** the most diverse and species-rich order of amphibians, in the subclass Lepospondyli; the microsaurians are all characterized by short tails and small legs but were otherwise very different in form and habit, some being primarily aquatic and others primarily terrestrial; North America and Europe; Late Carboniferous to late Permian.

**Microsyopidae:** a family of early primates in the extinct suborder Plesiadapiformes; the type genus is *Microsyops*; late Paleocene to middle Eocene.

**Microtheriomys brevihinus:** a small species of beaver, living about 28 Ma, that seems to be closely related to the modern beaver; discovered in the John Day Fossil Beds in Oregon in 2014, where several other beaver species have been found; North America, Oligocene.

**Microtragulus:** a genus of didelphoid marsupials in the extinct family Argyrolagidae; the omnivorous *Microtragulus* resembled a small kangaroo; South America, late Miocene to Pleistocene.

**Middle Awash:** an important site in Ethiopia for hominid and hominin fossils during the period between 5 and 2.5 Ma. A series of important fossils have been found here within a few surface miles of each other. The fossils, which have been found by different collectors over the last few decades and may or may not be directly related to each other, include several specimens each of the early *Ardipithecus ramidus* (about 4.4 Ma) and the later *Australopithecus anamensis* (about 4.2 Ma) and *Au. garhi* (2.5 Ma).

**Milleporidae:** a still-extant family of cnidarians in the class Hydrozoa and order Capitata, commonly called fire corals for their powerful sting, but not true corals; they form colonies of soft-bodied polyps but, like the stylasterines, differ from other Hydrozoa in having calcareous parts that fossilize; global distribution, Cretaceous to Recent.

**mimicry:** see **Batesian mimicry**.

**Miocene:** the fourth epoch of the Cenozoic, from 23 to 5.3 Ma. After the numerous extinctions of archaic mammals at the end of the Oligocene, the Miocene saw the almost global radiation of all modern mammals. If *Ardipithecus kadabba* is confirmed, it will mark the first appearance of hominins as coming at the end of the Miocene, between 5.8 and 5.2 Ma.

Although grasses appeared much earlier, in the late Paleocene, they did not spread rapidly until the end of the Oligocene. The early Miocene is characterized by an accelerated change from lush forests toward open grassland, so that by the end of the period open and wooded grassland communities were common worldwide. Ungulates in the Miocene evolved in response, developing specialized teeth for

grazing the tough grasses, as well as longer limbs to enable escape from predators in the open country. Although the northern continents saw considerable interchange of animals, South America and Australia continued to be isolated, developing many eccentric groups.

***Miocidaris***: a genus of pencil echinoids in the still-extant order Cidaroida and the type genus of the family Miocidaridae; one of the few cidaroids that survived the end-Permian extinction; North America, Europe, and Asia; late Permian to Early Jurassic.

***Mioplosus***: a genus of actinopterygian fish in the still-extant family Percidae; up to 20 inches long, they were predators; global distribution, early to late Eocene.

**Miosireninae**: one of several extinct subfamilies in the sirenian family Dugongidae; Europe, Africa, and North America; Oligocene to Miocene.

**Mississippian**: see **Carboniferous**.

**Mistaken Point**: an important Konservat-Lagerstätte in exposed surfaces of argillites on the Avalon Peninsula in Newfoundland, with a rich Ediacaran assemblage of several types of rangeomorph specimens, including *Fractofusus misrai*; some are similar to specimens found in Russia and Australia, while others are unknown except at Mistaken Point; Canada, Ediacaran, 575–560 Ma.

**mitosis**: the process of cell division by which cells in living organisms multiply. The process is almost identical in plants and animals, evidence that both are descended from a common ancestor. Genetic evidence indicates that this common ancestor may have been a one-celled organism that lived about 1.5 billion years ago.

**Mixodectidae**: a family of insectivorous mammals in the order Dermoptera; North America and Europe, Cretaceous to Paleocene.

***Mixosaurus***: “mixed lizard,” a genus of ichthyosaurs in the family Mixosauridae; a medium-sized ichthyosaur 3–6 feet long, the most common of the Triassic; probably transitional between earlier, eel-like forms and the porpoise-like ichthyosaurs of the Late Triassic; global distribution, Middle Triassic.

***Mixotoxodon***: a genus of notoungulates in the family Toxodontidae; the size of a rhinoceros and weighing about 4 tons, it was the largest notoungulate; South, Central, and North America; middle to late Pleistocene, the latest specimen dated at around 25,000 years ago.

**moa**: see **Dinornithidae**.

***Mobergella***: a problematic fossil in the “small, shelly fossil” group; a circular cap or shell, known especially from Scandinavia, early Cambrian.

***Modiolus***: a still-extant genus of medium-sized bivalve mollusks in the family Mytilidae and subclass Pteriomorphia; a burrowing mussel, attaching itself byssally to debris in sediment; global distribution, Early Devonian to Recent.

**modular evolution:** of organisms in which advanced anatomical components are combined with primitive components; the wukongopterid pterosaurs are a good example.

**Moeritheriidae:** a family of pig-like mammals in the order Proboscidea; although the moeritheres resemble tapirs and pygmy hippopotamuses, they are not related; they are probably not ancestors of elephants either, but a separate extinct branch of proboscideans; they were trunkless but bore long canines that can be considered small tusks; North Africa, late Eocene.

**mold:** an impression left by a dead organism in soft material that has solidified; an external mold is formed by sediment or volcanic material creating an impression of a dead organism; an internal mold is formed by material filling any void created by decay of the soft parts of an organism.

**molecular paleontology:** study of fossilized remains at the molecular level, focusing on genetic material such as DNA; investigators have identified possibly viable genetic material in insects preserved in amber as old as the middle Paleocene; molecular techniques have been important in research on such species as the *Quagga*, on hominins such as *Homo heidelbergensis* and the Denisovans, on dinosaurs such as *Diplodocus hallorum*, and even older organisms; some investigators advocate trying to recreate extinct organisms from this genetic material.

**Mollusca:** a large and very diverse phylum of marine and freshwater organisms. The most prominent extant classes are the Bivalvia, Gastropoda, Cephalopoda, Polyplacophora, Monoplacophora, Aplacophora, and Scaphopoda; two other classes are extinct and important in the fossil record: Rostroconchia and Helcionelloida. The main defining characters of mollusks are a muscular mantle, a rasping radula, and a definitive nervous system. Global distribution, Cambrian to Recent.

**Mongolestes:** a genus of protoungulate mammals in the family Mesonychidae; the last surviving mesonychid, *Mongolestes* was about 7 feet long and had larger teeth than other mesonychids; Mongolia, Eocene to early Oligocene.

**Monobathrida:** a large order of generally pelmatozoan monocyclic crinoids in the order Camerata; global distribution, Early Ordovician to late Permian.

**Monoclonius:** a contentious genus of ceratopsian dinosaurs usually classified in the subfamily Centrosaurinae; about 17 feet long and 6 feet high, it is characterized by one long horn on its beaked snout; known only from incomplete remains, some of which have been lost and some reclassified, *Monoclonius* is probably a *nomen dubium*.

**Monocyathida:** a class of archaeocyathans with only a single porous wall, usually solitary; Australia, Antarctica, North America, Asia, and Europe; middle Cambrian.

**monograptid fauna:** an important graptolite fauna, generally characterized by a single stipe, representing the graptoloids' tendency toward scandent growth and fewer stipes; see **Graptolithina**; early Silurian to Early Devonian.



***Monograptus***: a genus of graptoloids in the family Monograptidae; scandent, generally with a single straight stipe with hooked thecae; the first appearance of *M. uniformis* is considered the marker of the GSSP at the base of the Lochkovian Epoch (419.2 Ma), the beginning of the Early Devonian; global distribution, early Silurian to Early Devonian.

***Mononykus olecranus***: “single claw,” a unique species of theropod dinosaurs in the family Alvarezsauridae; 3 feet long and lightly built, with slender legs; very short but robust forelimbs, equipped with only one claw, which was 3 inches long; these may have been adaptations for hunting mound-living insects; known from only one partial specimen dated about 70 Ma; Nemegt Formation, Mongolia, Late Cretaceous.

**monophyletic group**: see **polyphyletic group**.

***Monophyllites***: a genus of ammonoids in the order Phyllocerata and family Ussuritidae; thin and evolute, 3–5 inches across; Asia, Europe, North America, and New Zealand; Middle to Late Triassic.

**monophodonty**: see **dentition**.

**Monoplacophora**: a primitive but still-extant group of mollusks with single, limpet-like shells. It is generally considered polyphyletic, but the fossil record is sparse and leaves many questions open; in some classifications the monoplacophorans are included in the Gastropoda despite considerable anatomical differences. They also have some features similar to segmented worms. The living monoplacophorans, such as *Neopilina*, are bottom-feeders in deep-ocean water. Cosmopolitan, early Cambrian to Recent.

**Monotremata**: “single-hole,” a still-extant order of egg-laying mammals; once widespread, the monotremes are now restricted to the platypus and echidna of Australia and New Guinea; characterized by reptilian, avian, and mammalian traits, including a cloaca through which the urinary, intestinal, and reproductive tracts all open to the outside, rather than with separate urogenital and intestinal openings; Late Triassic to Recent.

***Montanalestes***: a poorly known genus of small mammals closely related to later eutherians; known only from six teeth; United States, Early Cretaceous, 113–100 Ma.

**Montceau-les-Mines**: a Konservat-Lagerstätte in central France, noted for flattened and three-dimensional fossils of a tropical biota, including pteridosperms, insects, arachnids and other chelicerates, and tetrapods; France, Late Carboniferous.

***Monticulipora***: a genus of stenolaemate bryozoans in the order Trepostomata; massive colonies, sometimes encrusting brachiopods; North and South America and Europe, Late Ordovician.



**Montlivaltia:** a genus of large, solitary scleractinian corals in the family Montlivaltiidae; up to 4 inches across, cup-shaped to cylindrical; global distribution, Early Jurassic to Cretaceous.

**Morganucodon:** a genus of advanced cynodonts in the family Morganucodontidae, one of the earliest true mammals; about 4 inches long, it was omnivorous and had a double jaw joint; North America, Europe, and Asia; Late Triassic to Middle Jurassic.

**Morganucodonta:** an order of early mammaliaform cynodonts; generally considered true mammals, but their classification remains contentious; morganucodonts were shrew-sized and slender, with a relatively large head, and they probably had a good sense of smell; they had strong jaws that were able to crush insects with stiff exoskeletons; but their specialized, heterodont dentition indicates that they were also carnivorous; global distribution, Late Triassic to Late Jurassic.

**Moropus:** “slow foot,” a genus of clawed perissodactyl mammals in the superfamily Chalicotherioidea; found from Oregon to Florida through the Miocene, *Moropus* was more similar to horses than other chalicotheres; as its name indicates, it walked awkwardly because of its large forelimb claws; it stood about 8 feet high at the shoulder and weighed up to 600 pounds; United States, Miocene.

**Morotopithecus:** a genus of Miocene hominoids described in 2004 and dated at 20.6 Ma or earlier; known from dental, hip, and shoulder fragments, *Morotopithecus* may be transitional between the apes of the Miocene and more advanced hominoids; Uganda, early Miocene.

**Morrison Formation:** a large geologic formation in the Rocky Mountains of North America, stretching west from Kansas to central Utah and from New Mexico up to southern Alberta and Saskatchewan. The Morrison Basin fossils, most famous for many species of dinosaurs, comprise a complete community of terrestrial life in the Kimmeridgian and Tithonian Ages at the end of the Late Jurassic. Almost all locations are fluvial or lacustrine, with almost no marine strata. Important dinosaur specimens have been found at many outcrops of the formation, but the largest Konzentrat-Lagerstätten are Utah’s Dinosaur National Monument and Cleveland-Lloyd Dinosaur Quarry, Wyoming’s Como Bluff, and Colorado’s Dry Mesa Dinosaur Quarry.

**Mosasauroidea:** a family of large marine lizards in the order Squamata and extinct superfamily Mosasauridae. They probably evolved from the smaller, less specialized aigialosaurs in the Early Cretaceous and diversified worldwide to become the dominant marine predators, becoming extinct at the end of the period. First found in 1764 at Maastricht on the Meuse River, mosasaurs were air-breathing and ranged from 3 to 60 feet long. *Mosasaurus hoffmannii*, the type species and among the last of the mosasaurs, is dated between 70 and 66 Ma; its jaws were about 40 inches long and its body about 33 feet. Powerful swimmers, they have the body shape of a streamlined varanid, such as the modern monitor lizards. They preyed on fish of all sizes, sharks, ammonoids, turtles, and sea birds. They had double-hinged jaws, gulping down small prey whole; some species had two large teeth pointing back-

ward down the throat to prevent prey from escaping. Others, such as *Globidens* and *Prognathodon*, had blunt, rounded teeth adapted to crushing ammonoids and bivalves. They were covered with scales, and the presence of melanin in their skin indicates possible countershading like many modern fish (dark above and light below). Global distribution, Early to Late Cretaceous.

**Moschops:** a poorly known genus of dinocephalian therapsids in the family Tapinocephalidae; massively built, especially the skull, with long, stout teeth adapted for a herbivorous diet; known only from the Karoo Basin of South Africa, middle to late Permian.

**Mosinea:** a genus of arthropods in the family Euthycarcinidae; three post-abdominal exoskeletons are the only specimens of the famous *M. macnaughtoni*, one of the body fossils of early arthropods found along with their trackways in Cambrian strata in Wisconsin and Quebec; see also **Blackberry Hill**; North America, middle or late Cambrian.

**Moythomasia:** a basal genus of small palaeoniscid actinopterygian fish; only 4 inches long, *Moythomasia* had a downward-pointing tail with a row of bony nodes along its dorsal edge; like the much larger *Cheirolepis*, it had overlapping ganoid scales connected in a peg and socket design; Europe and Australia, Middle to Late Devonian.

**Mucrospirifer:** a well-known genus of brachiopods in the class Rhynchonellata and order Spiriferida. *Mucrospirifer* was 1–2 inches long, characterized by a long hinge line and a prominent fold and sulcus. Several species are index fossils for the Middle and Late Devonian. Asia, North and South America, and Europe; Early Devonian to Middle Mississippian.

**Müllerian mimicry:** see **Batesian mimicry**.

**Multituberculata:** a large and very successful order of protoeutherian mammals, classified separately from the Theria and the monotremes, but closer to the Theria; characterized by large incisors and two or three longitudinal rows of simple conical cusps; the order comprises many families, ranging from a few inches to 4 feet long; omnivorous but generally herbivorous, they include the earliest herbivorous mammals; global distribution but principally in the northern continents, Late Jurassic to early Oligocene.

**Murchisonia:** a very long-lived genus of prosobranch gastropods in the order Archaeogastropoda and extinct superfamily Murchisonioidea; characterized by an elongate, high-spired, and multi-whorled shell, generally with a slit band that runs in a spiral ridge from bottom to top; global distribution, Early Ordovician to Late Triassic.

**Muridae:** a family of small mammals including mice, rats, and gerbils; stem murids appeared in the early Eocene, probably sharing the ancestry of the Dipodidae, and true murids enter the fossil record in the early Miocene; the murids are the largest mammal family, diversifying from the middle Miocene to the Pliocene, and

since the Pleistocene thriving commensally with humans; global distribution, early Eocene to Recent.

**Mustelidae:** a large and still-extant family of caniform carnivorous mammals in the superfamily Musteloidea; the family includes the ancestors of modern weasels, martens, otters, badgers, minks, ferrets, wolverines, fishers, and stoats; like other Carnivora, the first mustelids probably descended from the Miacidae in the Eocene and quickly spread worldwide.

**Muttaborrasaurus:** a genus of ornithischian dinosaurs in the family Rhabdodontidae; omnivorous, up to 26 feet long and weighing 3 tons, it had significant forelimbs but was probably mainly bipedal; see also *Altirhinus*; Australia, Early Cretaceous, 112–100 Ma.

**Myalinidae:** a family of bivalve mollusks in the superfamily Ambonychioidea; marine and freshwater genera are important stratigraphically, especially in the Carboniferous; see also *Naiadites*; global distribution, Ordovician to Triassic.

**Myanmarpithecus:** a proposed genus of primates in the family Amphipithecidae, found in 2001 in the Pondaung Hills of Burma; Eocene.

**Mygalomorphae:** a still-extant infraorder of spiders that includes the funnel and trapdoor spiders; see also *Rosamygale*; cosmopolitan, Early Triassic to Recent.

**Mylagaulidae:** a family of sciuriform rodents which includes the horned rodent *Ceratogaulus*; possibly related to the Aplodontioidea, whose only extant member is *Aplodontia*, the mountain beaver; North America and Asia, late Oligocene to early Pliocene.

**Myllokunmingia:** a genus of basal chordates, generally considered the earliest-known vertebrate; about an inch long, it has a notochord and a skull and skeletal structures made of cartilage; China, early Cambrian, 530–525 Ma.

**Myلودon:** see *Paramylodon*.

**Myophorella:** a genus of marine bivalve mollusks in the order Trigoniida and extinct subfamily Myophorellinae; the irregularly shaped shell is covered with rows of tubercles; in some specimens the soft tissue has been mineralized and preserved; global distribution, Early Jurassic to Early Cretaceous.

**Myriapoda:** a subphylum of arthropods that includes centipedes, millipedes, arthropleurids, and other small groups; global distribution, Cambrian to Recent.

**Mysticeti:** the baleen whales, a suborder of generally toothless, filter-feeding Cetacea that appeared at the end of the Eocene or beginning of the Oligocene. The modern Mysticeti include fin, gray, right, and blue whales, the latter at 110 feet long being the largest animal known to have existed. They evolved from an archaeocete ancestor, probably separately from the odontocetes. Some early genera were partially toothed, and the evolution of fully edentulous baleen whales is well documented in the fossil record. The North Pacific family Aetiocetidae of the early

Oligocene was toothed but also had baleen structures in the jaw. The South Pacific family Mammalodontidae of the late Oligocene, including *Mammalodon* and *Janjucetus*, consists of early toothed mysticetes, some of them having a dentition similar to that of their terrestrial ancestors. The size of baleen whales stayed relatively constant through the Miocene but increased rapidly in the Pliocene for unknown reasons. Early Oligocene to Recent.

# N

***Nacholapithecus***: the most complete specimen of a Miocene ape, a genus of hominoids dated at 15 Ma and tentatively placed in the family Proconsulidae; Kenya, middle Miocene.

**Nacimiento Formation**: an early Paleocene heterogeneous non-marine formation in Western New Mexico, composed of sandstone, shale, and siltstone; laid down primarily in lacustrine and floodplain environments, it has produced many fossils from the time after the end-Cretaceous extinction, including champsosaurs, taenio-labidoids, and the early primate *Torrejonia*; United States, 65–61 Ma.

**Naegele's giant jaguar**: see *Panthera leo atrox*.

***Nahecaris***: a genus of malacostracan crustaceans in the subclass Phyllocarida; about 6 inches long, it has long antennae, a pointed tail, and several pairs of short legs; Germany and Morocco, Early Devonian.

***Naiadites***: a genus of non-marine bivalve mollusks in the family Myalinidae; along with *Carbonicola* and *Anthraconaia*, it is an index fossil in the British Coal Measures of the Carboniferous; cosmopolitan, Late Mississippian to Early Pennsylvanian.

**Nama Group**: rock formations in Namibia that have produced three-dimensional casts of Ediacaran and early Cambrian organisms.

***Nannippus***: “dwarf horse,” a genus of perissodactyl mammals in the family Equidae. It appeared in the late Miocene and co-existed with other North American horses until it became extinct in the late Pliocene. It was small and slender, the largest species as tall as a Shetland pony and resembling a gazelle. Differing from other horses, it had 3 toes on each foot. North America and Eurasia.

***Naraoia***: a genus of unusual trilobite-like arthropods in the order Nektaspida and family Naraoiidae; from 1 to 2 inches long, *Naraoia* had a soft exoskeleton and no thoracic segments, only the cephalon and a pygidium (or thoracopygidium) twice as

long as the cephalon; first discovered in the Burgess Shale, it was initially thought to be a crustacean and then was classified as a trilobite; North America, Asia, and Australia; early Cambrian to late Silurian.

**Nassellaria:** an order of marine protists in the subclass Radiolaria; their siliceous skeletons are circular and generally have spiky pseudopods; important stratigraphically where calcareous skeletons have dissolved; global distribution, Miocene to Recent.

***Nasutoceratops titusi:*** a species of mid-sized North American ceratopsian dinosaurs in the subfamily Centrosaurinae. Dated at 75 Ma and known only from a partial skeleton, *N. titusi* is considered a basal centrosaurine. It has a pair of curved, forward-facing horns, a large nose, and a skull 5–6 feet long. Kaiparowits Formation, Utah; Late Cretaceous.

**natural selection:** the basic process by which evolution occurs, combined with small genetic variations in individual organisms. Darwin, in his formulation of the process of natural selection, said that a species improves through the accumulation of many small inherited variations, each of which gives the individual possessing that variation an advantage in the competition, among all the members of the species, for the necessities of life. The offspring of these individuals will, over some period of time, outnumber disadvantaged individuals and at some point become a new species.

**Nautiloidea:** an important, still-extant subclass of externally shelled marine cephalopod mollusks that first appeared in the late Cambrian and flourished in the Ordovician. Nautiloids were the first large group of chambered cephalopods to develop; the chambers were separated by septa, through which a tube called a siphuncle passed to move water from one chamber to another. Most early nautiloids, such as *Orthoceras* and *Ellesmeroceras*, are orthoconic (straight-shelled), but curved and coiled shells also appeared early; the Tarphycerida of the Early Ordovician were the first of the coiled cephalopods, which became more numerous in the Devonian and Carboniferous. Orthoconic species declined in the Triassic and disappeared early in the Cretaceous.

The nautiloids are ancestral to the ammonoids, which appeared in the Early Devonian and also diversified rapidly. Nautiloids declined somewhat through the Paleozoic (probably through competition with their close relatives the Ammonoidea and Coleoidea), but they continued to diversify. Most became extinct at the end of the Permian, but the order Nautilida persisted, although in decreasing numbers after the Miocene; it is still represented by two genera, *Nautilus* and *Allonautilus*. For an early nautiloid, see *Plectronoceras*.

**Neandertal:** the name of the valley in northwestern Germany where the first Neanderthal skeleton was found in 1856.

**Neanderthal:** the common name of a group of hominins who lived in Europe, Africa, and Asia in the late Pleistocene from more than more than 300,000 years ago to about 30,000 years ago. They are now classified either as a separate species,

*Homo neanderthalensis*, or as a subspecies, *Homo sapiens neanderthalensis*. The Neanderthals were less dimorphic and somewhat shorter and heavier-set than modern humans, and were distinguished by a prominent brow ridge, a receding chin, and a slightly larger cranial capacity (1450 cc) than the modern average.

**Necrolestidae:** a monogeneric family of small pantothere metatherian mammals; the insectivorous *Necrolestes* seems to be unrelated to any modern animal; Argentina, early Miocene,

**Nectridea:** an order of aquatic amphibians in the extinct subclass Lepospondyli; generally similar to large newts, the largest grew to 3 feet long; the nectrideans are distinguished by large protrusions on either side of their flattened skull, which resembles a thick boomerang; North America, Europe, and Africa; Late Carboniferous to Permian.

**nektic:** referring to organisms that live in the water column, swimming actively in open water and able to move independently of water currents, as opposed to plankton, which drift with the current; see also **pelagic**, **planktic**, and **benthic**.

**nektobenthic:** swimming freely but just above the bottom.

**Nemagraptus:** a genus of early graptoloids in the family Nemagraptidae; generally characterized by multiramous S-shaped, reclined stipes; cosmopolitan, Middle to Late Ordovician.

**Nemagraptus gracilis:** a species of *Nemagraptus* whose first appearance marks the beginning of the Late Ordovician at 458.4 Ma; Sweden.

**Nematophyta:** a poorly known group of plants with characteristics of both vascular plants and algae; sometimes classified as a phylum containing the type genus *Nematothallus* and four other genera; North America and Europe, Silurian to Early Devonian.

**Nemegtosauridae:** a family of titanosaurian saurischian dinosaurs in the order Sauropodomorpha; classification disputed, possibly related to *Rapetosaurus* and *Saltasaurus*; Mongolia, Early to Late Cretaceous.

**Nemicolopterus crypticus:** a contentious species of small, toothless pterosaurs in the suborder Pterodactyloidea, possibly related to the Tapejaridae. It had curved toes, indicating that it was essentially a tree-dweller. Probably insectivorous, it lived in a forested area of Western China around 120 Ma, whereas most previously known pterosaurs have been found in coastal environments. It may be a hatchling or juvenile, but if it is an adult, it is one of the smallest known pterosaurs, since the holotype is the size of a sparrow. China, Early Cretaceous.

**Neocathartes:** see **Bathornithidae**.

**Neogene:** The second period of the Cenozoic Era, including the Miocene and Pliocene Epochs.

**Neognathae:** the larger of the two groups of living birds, dating back to about 100 Ma and including all living birds except the Palaeognathae (the flightless ratites and the tinamous); despite their name, they are believed to have appeared earlier than the Palaeognathae.

**Neoproterozoic:** the most recent era of the Precambrian Eon, from 1000 to 541 Ma.

**Neoptera:** a major taxonomic group of insects in the subclass **Pterygota**, *q.v.*; the Neoptera include almost all of the flying insects, specifically those that can flex their wings back over their abdomen.

**Neospirifer:** a genus of articulate brachiopods in the family Trigonotretidae; up to 2 inches across, characterized by robust valves and a prominent sulcus and fold; several genera are important index fossils; global distribution, Carboniferous to Permian.

**Neosuchia:** a large and very diverse clade of crocodylomorphs that includes the extant crocodiles and their relatives as far back as the Early Jurassic.

**neotype:** a type specimen selected as a replacement holotype when the original has been lost or destroyed.

**Neovison macrondon:** the sea mink, one of several formerly terrestrial mammals that have evolved into a saltwater habitat; formerly called *Lutreola* and *Mustela vison*. It bore a pelt that was 30 inches long when processed, much larger and bulkier than that of the terrestrial species. *Neovison* lived in coastal waters off northeastern North America and was thus not truly marine. Since its remains date back only about 5,000 years, it was probably a recently differentiated species. However, it is poorly known because of being hunted to extinction in the mid-nineteenth century before it could be studied thoroughly.

**Nerinea:** a high-spired genus of marine snails in the extinct family Nerineidae; global distribution, Jurassic and Cretaceous.

**Nesophontes:** the only genus in the extinct soricomorph family Nesophontidae; commonly called West Indies shrews, these small insectivorous mammals may have survived until the early twentieth century; possibly related to the still-extant Solenodontidae of Cuba and Haiti; known only from the Caribbean, late Pleistocene to Holocene.

**Neurankylus:** a genus of baenid turtles widespread in Western North America in the Cretaceous; possibly related to the moderate-sized *Compsemys* of the Paleocene; freshwater, with only 9 vertebrae but an extra pair of ribs; North America and Asia, Late Cretaceous to Paleocene.

**New Zealand avifauna:** see *Harpagornis*.

**Ngandong fauna:** the fossil remains of several hominins found between 1931 and 1933 at Ngandong, Java, commonly referred to as the "Solo man" fossils; the site is



about 100 km from Trinil, the site of the "Java man" find; because of a cranial capacity range of 1035–1255 cc, Solo man may represent a transitional stage between *Homo erectus* and *H. sapiens*; late Pleistocene, between 140,000 and 500,000 years ago.

**Nimravidae:** a family of carnivorous mammals; not true cats like *Smilodon* or the earlier machairodonts, but still classified in the order Feliformia; among their non-felid traits are non-retractable claws and several skeletal differences; North America, Europe, and Asia; middle to late Miocene.

**Nimravides:** a genus of machairodont felids; 6 feet long and about 220 pounds, it is a sabertooth cat and not classified in the Nimravidae, which are not true cats; North America, middle to late Miocene.

**Nimravus:** a genus of small saber-toothed mammals in the family Nimravidae; cat-like but not a true felid, *Nimravus* was 4 feet long and probably weighed less than 70 pounds; Western North America, early to middle Oligocene.

**Niobrara Sea:** see **Western Interior Seaway**.

**Nipponites:** a genus of heteromorph ammonoids in the suborder Ancyloceratina and family **Nostoceratidae**, *q.v.* Famous for a very unusual shell form, *Nipponites* resembles a tangle of knots. The tubular shell reaches lengths of almost 2 feet if extended and might reach a diameter of 10 inches if coiled planispirally in the normal ammonoid manner. But it coils on itself on different axes, creating a globular shape only 3–4 inches in diameter. Japan, Asia, North America, and possibly Madagascar; Late Cretaceous.

**Nodosauridae:** a large family of ornithischian dinosaurs in the suborder Ankylosauria. Herbivorous, squat, and quadrupedal, they grew as long as 20 feet. Nodosaurids were heavily armored, generally with large shoulder spikes, but without a tail club. North America, Europe, Asia, and Antarctica; Late Jurassic to Late Cretaceous.

**Noeggerathiales:** an unusual order of fern-like vascular plants in the division Tracheophyta and extinct class Progymnospermopsida; they have some similarities to modern conifers and araucarians, but they may have reproduced by spores; there was a notable 2012 discovery of a specimen in a large (20 square km) forest buried in lower-Permian volcanic ash in China, but because of gaps in their fossil record, they are still poorly defined and may be related to the Sphenopsida or Pteropsida; North America, Europe, and Asia; Late Devonian to Late Triassic.

**Noguerornis:** one of the oldest known enantiornithine birds, a poorly known specimen from the beginning of the Cretaceous; much smaller than *Archaeopteryx* but more capable of flight; El Montsec, Spain, Early Cretaceous, 130–125 Ma.

**nomen dubium:** a name of unknown or doubtful application, often referring to a lost type specimen.

**Nostoceratidae:** a diverse family of heteromorph ammonoids in the suborder Ancyloceratina and superfamily Turrilitoidea; most genera coil in unusual directions, sometimes partly planispirally; *Nipponites* resembles a randomly coiling knot, while the tubular *Bostrychoceras* and the type genus *Nostoceras* create a helical spire shape; global distribution, Late Cretaceous.

**Nostolepis:** a genus of acanthodian fish in the order Climatiformes and family Climatidae; a “spiny shark,” known principally from scales but thought to be as long as 4 inches; North America, Europe, Asia, and New Zealand; late Silurian to Middle Devonian.

**Notharctus:** a genus of adapiform primates of North America; related to *Smilodectes* and possibly the Amphipithecidae, the lemur-like *Notharctus* is a well-known example of the evolutionary trend in primates toward greater brain size, reduction of muzzle size, and the capability for stereoscopic vision — cephalic hallmarks of advanced primates and of humans; early to middle Eocene.

**Notharctus tenebrosus:** a species of *Notharctus* found first in Wyoming in 1870, dated at 50 Ma; evidently adapted to a fine-branch niche in its arboreal habitat, having long fingers, an opposable thumb, and nails instead of claws; North America, middle Eocene.

**Nothosauroidae:** an order of seal-like aquatic sauropterygian reptiles with two suborders, Nothosauria and Pachypleurosauria. From 8 to 13 feet long, the nothosaurs evolved from the much smaller pachypleurosaurs, which were 8 inches to 3 feet long. The nothosaurs were related but probably not directly ancestral to the marine plesiosaurs that replaced them at the end of the Triassic (see **Pistosauria**). North America, Europe, Asia, and Africa; Early to Late Triassic.

**Nothrotheriidae:** an extinct family of ground sloths related to the larger Megatheriidae; they migrated to North America at the beginning of the Pleistocene as part of the Great American Biotic Interchange; South and North America, late Miocene to 11,000 years ago.

**Nothrotheriops shastensis:** the Shasta ground sloth, a species of giant sloth in the family Nothrotheriidae; *N. shastensis* appeared at the beginning of the Pleistocene and became extinct about 11,000 years ago; known from Mexico to Oregon and especially abundant in the La Brea Tar Pits; Western North America, Pleistocene.

**Notiomastodontinae:** a subfamily of proboscideans in the extinct suborder Euelephantoidea and family Gomphotheriidae; South America, late Pleistocene.

**Notioprogonia:** a probably paraphyletic suborder of primitive mammals in the extinct order Notoungulata, with a more primitive dentition than that of any other notoungulate; 3–5 feet long, some genera resembled rabbits in appearance; two families are currently recognized, the Henricosborniidae and the Notostylopidae; South America; Paleocene to Eocene.

**notochord:** a stiff, flexible dorsal rod, the main identifying character of chordates; the notochord is the developmental and evolutionary precursor of the vertebrate backbone.

**Notocupoides:** a genus of coleopteran insects in the family Ommatidae; 4–5 inches long, it is known only from the Madygen Formation; Kyrgyzstan, Late Triassic, 230–225 Ma.

**Notoryctidae:** a still-extant family of marsupial moles in the order Notoryctemorphia; they have no external ears, and their eyes are vestigial lenses under the skin; poorly understood but possibly related to the fragmentary Miocene mole *Yalkaparidon coheni*, found in Queensland in 1985; Australia, Miocene? to Recent.

**Notosuchus:** a genus of crocodylomorph reptiles in the order Notosuchia; about 3 feet long and 80 pounds, *Notosuchus* preyed on small animals; poorly known and restricted to the Coniacian and Santonian Ages, 90–84 Ma; South America, Late Cretaceous.

**Notoungulata:** a large order of hoofed mammals in the superorder Meridiungulata; some genera, such as *Mixotoxodon* and *Toxodon*, were quite large, but others filled the same ecological niches as rabbits and hyraxes; basically South American, but some genera (see **Mixotoxodon**) are found as far north as the Southern United States; Paleocene to 11,000 years ago.

**Nucleolitidae:** a family of generally atelostomate echinoids in the superorder Microstomata and order Cassiduloida; the most primitive genus is *Pronucleolites*; North and South America, Europe, Africa, and Asia; Middle Jurassic to middle Pleistocene.

**Nummulitidae:** a family of large foraminiferans in the order Rotaliida. Lenticular and from half an inch to 4 inches in diameter, nummulites are named for their coin shape. Characterized by narrow, helical coils of septa, they are found principally in shallow-water deposits of the Paleogene, but they still exist in some tropical areas. They appear in the limestone used for the Egyptian pyramids and were probably used as jewelry and coins in Egypt. Cosmopolitan, Early Cretaceous to Recent.

**Nuna:** see **Rodinia**.

**Nyasasaurus:** a genus of early dinosauriform reptiles that may be the earliest dinosaurs; the type species, *N. parringtoni*, is dated at 243 Ma, much earlier than any other of the oldest dinosaurs known (see **Eoraptor**, **Herrerasaurus**, and **Staurikosaurus**); described in 2013, it has not yet been definitively classified, but research in 2017 supports its identification as a dinosaur; Tanzania, Early Triassic.

**Nyctitheriidae:** a family of soricomorph mammals; scansorial insectivores, the family is generally considered eulipotyphlan (related to shrews, hedgehogs, and moles) but claimed by some as euarchontan (closer to tree shrews and primates); North America, Europe, Africa, and Asia; Late Cretaceous to early Miocene.

***Nyctosaurus***: a genus of pterodactyloid pterosaurs, notable for a large crest supported by two antler-like spars 1–2 feet long; smaller than its relative *Pteranodon*, its body was only a foot long, but *Nyctosaurus* had a wingspan of up to 7 feet; known only from Kansas and probably short-lived; United States, Late Cretaceous, 86–84 Ma.

**Nymphaeales**: see *Pluricarpellatia*.

# O

**Obolellata:** one of the three extinct classes of brachiopods in the subphylum Rhynchonelliformea; a small class formerly labeled inarticulate but now considered primitively articulate; early to middle Cambrian.

**Obolellida:** “small coin,” an order of rhynchonelliform brachiopods in the class Obolellata, characterized by impunctate biconvex shells. Among the earliest brachiopods, they were a short-lived but widespread order that began to exhibit some articulation in the later genera. They are considered part of the Tommotian biota, the early Cambrian wave of evolution of invertebrate animals that included the archaeocyathans, trilobites, and echinoderms. Cosmopolitan, early to middle Cambrian.

**Obovothyris:** a genus of terebratulid brachiopods in the family Zeilleriidae; it had a long loop and a biconvex, punctate shell; Europe, Middle Jurassic.

**Ocepeia:** a genus of small, primitive mammals placed tentatively in the clade Paenungulata; known from several skull fragments, it was a cat-sized herbivore; Morocco, middle Paleocene.

**Octocorallia:** a subclass of anthozoan cnidarians including the soft corals and sea pens; generally colonial polyps without a calcareous or aragonitic skeleton; cosmopolitan, Cambrian to Recent.

**Odobenidae:** see **Otarioidea**.

**Odonata:** an order of pterygote carnivorous insects that includes the dragonflies (Anisoptera) and damselflies (Zygoptera); possibly related to the giant *Meganisoptera* of the Carboniferous and Permian; traditionally grouped with mayflies and several extinct groups in the paraphyletic classification Palaeoptera; the dragonflies and most damselflies cannot fold their wings back over their abdomen; global distribution, Triassic to Recent.

**Odontoceti:** a suborder of toothed whales, such as the modern orcas, sperm whales, beaked whales, dolphins, and porpoises; the early odontocetes appeared in

the late Eocene, the Agorophiidae being the most primitive; the Oligocene superfamily Squalodontoidea may be ancestral to most modern odontocetes; global distribution, late Eocene to Recent.

***Odontochelys semitestacea*:** “half-shelled turtle with teeth,” a genus of stem-turtles in the family Odontochelyidae; the oldest known turtle, dated about 220 Ma, just after the time when the first dinosaurs appeared; about 16 inches long, with a plastron covering its belly but only the knobby rudiments of a carapace on its back; found in marine deposits but probably partly terrestrial; Guizhou Province, China, Late Triassic.

**Odontognathae:** an obsolete term for a group of primitive toothed birds of the Cretaceous, similar to modern birds in having a pygostyle; current classifications have reorganized the group in the large clade Ornithurae; North and South America, Cretaceous.

***Odontogriphus omalus*:** a species of soft-bodied bilaterian mollusks in the family Odontogriphidae. The oldest mollusk known, prominent in the Burgess Shale, it continues to figure in current debates about the origins of mollusks, brachiopods, and annelids. *Odontogriphus* has an ovoid, shell-less body up to eight inches long, with simple gill-like structures surrounding the bottom of the foot on the underside. Its stomach, intestines, outer membrane, mouth, and radula are also visible in the specimens. Canada, middle Cambrian, 508 Ma.

**Odontopleurida:** an early order of trilobites related to the order Lichida; spinose, especially the pygidium, which is smaller than the cephalon; global distribution, middle Cambrian to Late Devonian.

**Oepikellidae:** a family of sexually dimorphic ostracods in the extinct superfamily Oepikelloidea; generally characterized by biconvex shells without a sulcus; global distribution, Ordovician to Devonian.

***Ogygiocarella*:** a small genus of asaphid trilobites in the family Asaphidae; famous as an early “flatfish” discovery, it was described in 1698 by Edward Lhywd; slightly more than an inch in length, it is isopygous, flattened, and oval in shape; Wales and South America, Middle Ordovician.

**Öhningen site:** a locality on the German border with Switzerland that has produced many fossils from the Miocene, including the 3-foot-long salamander *Andrias scheuchzeri*, turtles, and many well-preserved flowers and insects; also spelled Oeningen; Germany, late Miocene.

**Oldhaminidina:** a suborder of strophomenid articulate brachiopods characterized by a lobed brachial valve and convex pedicle valve; cosmopolitan, late Paleozoic.

***Olenellus*:** a stratigraphically important genus of trilobites in the order Redlichiida and the only currently recognized genus in the subfamily Olenellinae; generally characterized by a very large, semicircular cephalon, elongated thorax, and very small pygidium; North America, in the Olenellus zone of the early Cambrian.

***Olenoides***: a genus of trilobites in the order Corynexochida and family Dorypygidae; up to 4 inches long, characterized by small eyes, a raised glabella extending to the front of the cephalon, and many slender pygidial spines; more than 100 well-preserved specimens have been found in the Burgess Shale, including several with soft-tissue preservation; North America and Asia, middle to late Cambrian.

***Olenus***: a genus of trilobites in the order Ptychopariida and family Olenidae; characterized by 12–15 thoracic segments and pleurae with sharp recurved tips; an important index fossil, *Olenus* was widespread in the late Cambrian; the name comes from Olenus, a character in Greco-Roman mythology who was transformed into a stone pillar; global distribution, late Cambrian.

**Oligocene**: the third epoch of the Cenozoic, from 34 to 23 Ma. New modern mammals were relatively rare, a fact reflected in the name, “time of few recent groups.” Among new animal orders were the first barnacles, pigs, rats, and deer. The world climate continued to cool, causing some extinctions and fragmentation of marine populations. Early in the epoch, Antarctica began to be covered with ice, and the Grande Coupure in Eurasia caused several extinctions and large-scale rearrangement of biozones. Several large mammals became extinct, such as the brontotheres and embrithopods, but ungulates in general grew larger.

**Oligopygoida**: a small order of irregular echinoids with a well-developed lantern; closely related and possibly ancestral to the Clypeasteroidea of the late Paleocene; Caribbean and Mexico, Eocene to Paleocene.

***Olorotitan***: a genus of lambeosaurine dinosaurs in the family Hadrosauridae, known only from an almost complete specimen found in the Amur region of Russia; it was about 26 feet long and had an unusual fan-shaped crest; Eastern Russia, Late Cretaceous, 72–66 Ma.

**Omomyidae**: an important early family of tarsier-like primates in the suborder Haplorrhini and the infraorder Tarsiiformes; the earliest-known crown primates and probably ancestral to modern tarsiers; North America, Europe, and Asia; early Eocene to early Miocene.

***Oncorhynchus rastrosus***: the largest known species of fish in the family Salmonidae; known from two specimens from Central Oregon, they were probably anadromous like the modern salmon; notable especially for the two 1-inch fangs protruding to the side like warhog tusks; they grew to about 9 feet long and weighed about 1000 pounds; United States, Miocene to Pleistocene.

**ontogeny**: the growth and development of individual organisms.

***Onychodus***: “claw tooth,” a genus of basal sarcopterygian fish in the family Onychodontidae; poorly known but up to 12 feet long, *Onychodus* is characterized by a pair of retractable tooth whorls at the anterior end of the jaw; possibly related to *Psarolepis*; Canada, Europe, and Australia, Middle to Late Devonian.

***Onychonycteris finneyi*:** the earliest-known primitive bat, in the family Onychonycteridae; notable in having claws on all ten fingers but probably not able to echolocate, so taken as evidence that bats could fly efficiently before some developed echolocation; North America, late Eocene, 52 Ma.

**Onychophora:** the “velvet worms,” a still-extant phylum of small, caterpillar-like, predatory animals. The modern onychophorans live generally in moist terrestrial habitats. Their fossil record is sparse, but discoveries of the 1990s show that they were an important and diverse group of marine invertebrates in the Cambrian. Paleozoic onychophorans are traditionally placed in their own class, the Xenusia; they were entirely marine and had a terminal mouth, as opposed to the ventral mouth of modern onychophorans. From the Burgess Shale assemblage, the famous *Hallucigenia* is considered an onychophoran, and *Aysheaia* is also thought to be related. The Carboniferous genus *Helenodora* is considered basal to modern onychophorans. See also *Peripatus*. Global distribution, Cambrian to Recent.

***Onychopterella*:** “claw wing,” a genus of middle-sized chelicerate arthropods in the family Eurypteridae; its last walking legs are long, and its swimming legs end in a small claw; known mainly from the Silurian of North America, smaller specimens (about 6 inches long) have been found in the Gondwanan Soom Shale of South Africa; Late Ordovician to Silurian.

**oogonia:** see **charophyte**.

***Opabinia*:** a stem-arthropod genus of soft-bodied animals found only in the Burgess Shale; *O. regalis*, the only known species, had a segmented body with lobes on the sides, a fan-shaped tail, and a long and slender proboscis; more unusual are its five eyes and a backward-facing mouth below the head; it is tentatively placed in the order Radiodonta; see also *Jianfengia*; Canada, middle Cambrian, 508 Ma.

***Opallionectes*:** a species of Cretaceous plesiosaurs identified in 2006; known only from Central Australia, where it was found in company with the smaller plesiosaur *Umoonasaurus*; *Opallionectes* was 16 to 18 feet long and is notable for its large number of needle-like teeth adapted to trapping small fish and squid; Early Cretaceous, about 115 Ma.

**operculum:** a structure in many animals, usually calcitic, whose function is usually to seal an aperture by opening and closing; a prominent feature in gastropods, ammonoids, and other cephalopods.

***Ophiacodon*:** “snake tooth,” a genus of primitive synapsid reptiles in the family Ophiacodontidae, possibly the ancestor of all later synapsids. About 10 feet long, it was much larger than earlier ophiacodontids and one of the largest early synapsids, with a large snout containing more than 160 needle-like teeth. *Ophiacodon* was partly aquatic and similar to crocodiles in some ways although only distantly related, and so an example of convergent evolution. North America and Europe, Late Pennsylvanian to early Permian.



***Ophiderpeton***: an unusual genus of snakelike lepospondyl amphibians in the order Aistopoda; 2–3 feet long and very slender, it was mostly terrestrial and probably fossorial; it had 200 vertebrae in its spine and no limbs; North America and Europe, Early Carboniferous to early Permian.

**Ophiocystioidea**: a class of stemless echinoderms in the still-extant subphylum Echinozoa; similar to modern sea urchins and characterized by a flattened, dome-shaped test; global distribution, Early Ordovician to Late Cretaceous.

***Ophiopinna***: a genus of brittle stars, ophiuroids in the family Ophiuridae; about an inch across, hundreds of specimens are preserved at La Voulte-sur-Rhône, some with paddle-shaped spines, possibly an adaptation for swimming; France, Middle Jurassic.

**Ophiurida**: the brittle stars, a still-extant order of asterozoan echinoderms in the class Ophiuroidea; characterized by a sharply defined circular central disc with five (sometimes more) slender arms that can move horizontally for locomotion; global distribution, Devonian to Recent.

**Ophiuroidea**: a class of echinoderms in the still-extant subphylum Asterozoa, encompassing the brittle stars (Ophiurida) and basket stars (Euryalida); as in the sea stars (Asteroidea), the central body extends into five or more arms, but the ophiuroid body is sharply distinguished from the slender, very flexible arms, which are as much as 20 times longer than the diameter of the body; since the ophiuroids, like sea stars, disintegrate rapidly after death, complete skeletons are rare; global distribution, Ordovician to Recent.

**Opiliones**: a still-extant order of arachnids characterized principally by very long legs; although similar to spiders, they are not closely related; known as harvestmen, they originated in the Devonian, the oldest known being *Eophalangium sheari* (Early Devonian, from the Rhynie Chert); global distribution, Devonian to Recent.

***Opipeuterella***: a genus of nektic proetid trilobites in the family Telephinidae; it is remarkable for very large eyes that extend below the plane of the body, indicating that it was free-swimming; the thorax is slender and the pygidium ends in a spine; cosmopolitan, Early to Middle Ordovician.

**Opisthothelae**: a suborder of arachnids in the spider order Araneae, comprising almost all true spiders; see also **Mesothelae**; global distribution, Carboniferous to Recent.

**opossum**: see **Didelphidae**.

**Orbiculoidea**: a large and long-lived genus of inarticulate brachiopods in the order Lingulida; phosphatic and generally only 1 to 2 inches in diameter, with a functional pedicle; global distribution, Early Ordovician to Cretaceous.

**Ordovician**: the second period of the Paleozoic Era, from 485 to 444 Ma, divided into Early, Middle, and Late Epochs. It was a time of high sea levels and marine transgressions until the severe glaciation at the end of the period. During the

Ordovician, the southern continent Gondwana coalesced and drifted south, and Laurentia, Baltica, and other land masses became separated from each other.

Between 485 and 460 Ma, about 50 million years after the great radiation of life of the early Cambrian, marine life again experienced great changes. In a rapid and extensive diversification of organisms in the Early and Middle Ordovician, the numbers of biological orders and families more than doubled, especially in brachiopods, bivalves, corals, crinoids, bryozoans, and gastropods. This development is referred to as the Great Ordovician Biodiversification Event (GOBE). In the Middle Ordovician, localized faunas became established in different parts of the world, and these faunas remained relatively stable until the great Permian extinction ended the Paleozoic Era.

The first vertebrates with bone appeared at the beginning of the Ordovician, including the first agnathans, the jawless fish; and the first primitive jawed fish are known from the middle of the period. In fact, all major groups of fish originated during the Ordovician. Although vertebrates still appeared only in marine environments, there was greater overall ecological complexity than in the Cambrian. There was great diversity of marine invertebrates, although relatively few new invertebrate body plans appeared. The first definitive terrestrial plants appeared, and, despite a lack of complete fossil specimens, there is some evidence of aquatic arthropods venturing into terrestrial environments.

**Ordovician extinction:** the first of the five great extinctions, at the end of the Ordovician Period, about 444 Ma. More than one hundred families of invertebrates and as many as 60 percent of marine genera became extinct, making it second only to the end-Permian extinction in the number of extinct genera. As in the other mass extinctions of the Paleozoic, this one seems to have occurred in several pulses. But at the end of the Ordovician, more than in the Devonian or Permian, these pulses were strongly associated with several major glacial events.

**oreodonts:** see **Merycoidodontidae**.

**Oreopithecus:** “mountain ape,” a genus of Miocene hominoids; it weighed between 60 and 80 pounds and had characteristics of hominids and of dryopithecines; also possibly related to the parapithecines of the Oligocene; known only from European and African sites of the late Miocene.

**Ornithella:** a genus of articulate brachiopods in the order Terebratulida and family Zeilleriidae; pentagonal in outline and notable for its long loop; North America, Europe, and Asia; Middle Jurassic.

**Ornithischia:** the “bird-hipped” dinosaurs, one of the two large orders. Ornithischians are characterized by a four-pronged arrangement of pelvic bones similar to that of birds, which are generally considered descendants of coelurosaurian theropods. Another typical ornithischian trait is the predentary, a horn-covered beak-like structure at the front of the lower jaw bone that probably made it easier to crop vegetation.

Although birds have traditionally been considered saurischians, some classifications place them in the Ornithischia, and a proposed new classification of dinosaurs in 2017 separates the theropods into a group of their own. Almost all ornithischians are herbivorous, the principal groups being the ankylosaurs, ceratopsians, ornithopods, hadrosaurs, and stegosaurs; one group known to be omnivorous is the heterodontosaurids. Global distribution, Late Triassic to Late Cretaceous.

***Ornithocheirus simus***: “bird hand,” a species of pterodactyloid pterosaurs known only from fragmentary English specimens of the 1860s; medium-sized, with a wingspan of about 8 feet, and with a distinctive crest at the tip of its beak; since the 1970s, several other species once assigned to *Ornithocheirus* have been reassigned or questioned; *O. simus* seems similar to Brazilian pterosaurs like *Anhanguera*, but relationships are still unclear; England, Cretaceous, 110 Ma.

***Ornitholestes***: “bird thief,” a monospecific genus of bipedal theropod dinosaurs; known only from an almost-complete skeleton found at Como Bluff, Wyoming, in 1900; lightly built and about 7 feet long, *Ornitholestes hermanni* had long forelimbs and long, clawed fingers, preying mainly on small mammals and lizards; United States, Late Jurassic.

***Ornithomimus***: a genus of small, bird-like dinosaurs in the family Ornithomimidae and order Saurischia; a fast runner, superficially similar to ostriches, *Ornithomimus* was 12 feet long, weighed less than 400 pounds, and was probably covered with feathers; synonym: *Dromiceiomimus*; Western North America, Late Cretaceous, 77–66 Ma.

**Ornithopoda**: a suborder of medium to large herbivorous dinosaurs in the order Ornithischia. They include virtually all of the bipedal ornithischians (except the Pachycephalosauridae). The early ornithopods were small (3–10 feet long), and later ornithopods became semi-quadrupedal, the largest (such as the Iguanodontidae and Hadrosauridae) weighing as much as 25 tons. The ornithopods generally had three digits, especially the later genera. Global distribution but rare in the Southern Hemisphere, Early Jurassic to Late Cretaceous.

***Ornithorhynchus anatinus***: the duck-billed platypus, one of the few living monotremes; semi-aquatic and egg-laying but a mammal, the modern platypus dates back to 100,000 years ago, closely related to monotremes of the Cretaceous; found only in Eastern Australia, the adult is 1–2 feet long and toothless, but it possesses a poisonous spur on the hind foot; see also *Steropodon*.

**Ornithoscelida**: a term referring to different groupings of dinosaurs; first proposed by T.H. Huxley in 1869 in his argument for seeing birds as descendants of dinosaurs, the term has been revived in a 2017 proposal for a large-scale revision of dinosaur classification; in this proposal the Ornithoscelida includes the Ornithischia and the Theropoda as sister groups, the Theropoda including the probable ancestors of birds.

**Ornithurae:** a proposed term for all modern birds and their immediate ancestors, back to the common ancestor of *Ichthyornis* and *Hesperornis*; the basic modern trait is a short, fused pygostyle tail, as opposed to the longer, straight tails of primitive birds.

***Orrorin tugenensis*:** a controversial species of hominins found in the late 1990s in Kenya; it seems to be in the line of descent from chimpanzee to advanced hominins, possibly to humans, but is known only from fragments; between 6.1 and 5.7 Ma, 1.5 million years earlier than similar hominins.

**Orsten Konservat-Lagerstätten:** upper Cambrian deposits in Sweden, part of the Alum Shale Formation. The Orsten beds have yielded important fossils since the late twentieth century, especially of arthropod larvae and rare animals such as pentastomes and tardigrades. These fossils are typically phosphatized and preserved inside calcareous nodules, so that when the nodules are dissolved, often a three-dimensional shell is left that preserves body structures in fine detail. Some of the Orsten fossils have no counterparts in the fossil record — the recently discovered pentastomes are almost the only extinct pentastomes of which there is any record, and yet these fossil species are very similar to modern members of the phylum.

**Orthoidea:** a superfamily of articulate brachiopods in the order Orthida and sub-order Orthidina; characterized by impunctate shells, an open delthyrium, and a functional pedicle; global distribution, early Cambrian to the end of the Permian.

**Orthida:** an order of brachiopods in the class Rhynchonellata; the Orthida, which include the earliest-known articulate families, arose early in the Cambrian and diversified rapidly into the Ordovician; global distribution, early Cambrian to middle Permian.

***Orthoceras*:** “straight horn,” a genus, now considered monospecific, of nautiloid cephalopods in the order Orthocerida. The type species *O. regulare* was orthoconic: cone-shaped, thin, and about 6 inches long. The genus was long considered much larger, extending from the late Cambrian to the Triassic, but most species have been reassigned. Orthocerids form Ordovician key beds in North America, Europe, and Africa. Similar to but not related to *Baculites*, *q.v.* Global distribution, Early Ordovician to Early Devonian.

**orthocones:** cephalopods whose shell is an elongated, straight, tapering cone.

**orthogenesis:** an obsolete biological hypothesis that organisms have an innate tendency to evolve in a certain way that is determined by an internal driving force, rather than by external processes such as natural selection; advanced in the early twentieth century, it was soon universally refuted and abandoned; see also *Gryphaea*.

**Orthopsidae:** a family of Mesozoic euarchinoids in the order Orthopsida, characterized by a camarodont lantern; global distribution, Jurassic and Cretaceous.

**Orthoptera:** an order of neopteran flying insects that includes the suborders Ensifera, the crickets and katydids, and Caelifera, the grasshoppers. Adapted for

saltation, orthopterans are chewing insects with two pairs of wings; most genera have stridulatory organs on their wings, used to produce sound when rubbed with the hindlegs. The earliest known are the Ensifera from the Late Carboniferous. Global distribution, Late Carboniferous to Recent.

***Oryctodromeus*:** “digging runner,” a genus of hypsilophodont ornithischian dinosaurs in the family Thescelosauridae, one of the earlier thescelosaurids; herbivorous and basically bipedal but with forelimbs that seem to be adapted to digging, it is the only confirmed burrowing dinosaur; one site contains the remains of an adult and two juveniles in a burrow almost 7 feet long; North America, Late Cretaceous, Cenomanian, 99–97 Ma.

***Osmunda*:** a still-extant genus of large ferns in the order Osmundales; characterized by erect rhizomes and naked sporangia; it evolved in Gondwana, in the Triassic or possibly late Permian, and spread worldwide; *O. claytoniana* is an example of evolutionary stasis, having remained almost unchanged 180 million years after its appearance in the Triassic.

**ossicle:** a small bony structure; see **dermal ossicles**.

**ossicone:** a horn-like protuberance consisting of a bony core permanently covered with skin; they are found on modern giraffes and okapis and their ancestors, such as *Sivatherium*, and also on other mammals, such as *Uintatherium*.

**Osteichthyes:** the bony fishes, the latest major group of fish, appearing in the late Silurian. The osteichthyans are generally considered a superclass and divided into two main groups, the ray-fins (actinopterygians) and lobe-fins (sarcopterygians). The earliest-known osteichthyan is the Early Devonian *Guiyu oneiros*, dated around 419 Ma, and the group developed slowly in the Devonian during the dominance of the acanthodians and placoderms. (See also *Psarolepis*.) But by the Carboniferous the osteichthyans and the chondrichthyans had supplanted the earlier groups, and they now account for more than half of all vertebrate groups.

**osteoderm:** a thin bony plate that forms part of the protective skin covering of many animals, extant and extinct, especially reptilians and amphibians, but found also in many xenarthran mammals.

**Osteoglossomorpha:** a still-extant superorder of teleost bony fish, among the most primitive teleosts. The group includes some of the largest of all living (*Arapaima*) and extinct (*Xiphactinus*) fish. One of the earliest-known genera is *Lycoptera*, especially important in Mesozoic biostratigraphy in China. The osteoglossids are named “bony tongue” because many of them employ a specialized biting technique that involves the tongue and the roof of the mouth. Global distribution but now primarily in the Southern Hemisphere, Jurassic to Recent.

***Osteolepis*:** “bony scale,” a genus of primitive sarcopterygian fish in the subclass Rhipidistia and family Osteolepidae, related to the stem-tetrapods that began to colonize the land in the Devonian; 8 inches long, it is characterized by large square scales covered with cosmine, with small nerve canals running through the dermal

covering; see also **Eusthenopteron** and **Tetrapoda**; Europe, Asia, and Antarctica; Late Devonian.

**osteolith:** a completely mineralized fossil bone.

**Osteostraci:** an order of small to medium-size, fish-like jawless marine vertebrates characterized by a large, bony headshield and a rounded mouth on the underside of the head; the osteostracans were among the most advanced agnathans; global distribution, middle Silurian to Late Devonian.

**Ostlingoceras:** a genus of heteromorph ammonitid ammonoids in the family Turrititidae; its tightly coiled helical shell resembles a long, thin gastropod; cosmopolitan, early Late Cretaceous, 100–94 Ma.

**Ostracoda:** a large and very old subclass of small crustacean arthropods, many species of which have remained relatively unchanged since the Silurian; they have two valves and superficially resemble bivalve mollusks, but most are microscopic, with some freshwater species as large as 30 mm; both freshwater and marine, ostracods are the most common arthropods in the fossil record; global distribution, Cambrian to Recent.

**ostracoderms:** “shell skin,” an informal term for several groups of armored jawless fish of the early Paleozoic, usually with a bony headshield; they were gradually replaced by placoderms and other jawed fish in the Devonian; global distribution, late Cambrian (but first recorded in Early Ordovician) to Devonian.

**Ostrea:** the common oyster, a large and still-extant genus of sessile bivalves in the order Ostreoida; global distribution, Permian to Recent.

**Otarioidea:** a superfamily of pinnipeds that includes the Odobenidae (walruses and sea lions) and the Otariidae (fur seals); extinct members are *Enaliarctos* and the Desmatophocidae; see also **Phocidae**; cosmopolitan, middle Miocene to Recent.

**Otavipithecus:** an obscure genus of Miocene apes, the earliest hominoid found in subequatorial Africa; Namibia, 13 Ma.

**Otodus:** an early genus of large sharks in the still-extant order Lamniformes and family Otodontidae; known from teeth and vertebrae, it is estimated to have been about 30 feet long and a macro-predator; see also *Megalolamna*; global distribution, Paleocene to Eocene or Miocene.

**Ottoia:** a genus of predatory burrowing worms in the family Ottoiidae, considered a stem-group priapulid; 3–4 inches long, it used its muscular toothed proboscis to prey on hyoliths and trilobites; known definitively only from the Burgess Shale; Canada, middle Cambrian, 508 Ma.

**Ovalocephalus:** a genus of phacopid trilobites in the family Pliomeridae; the body is oval, with a strongly pentagonal glabella, small eyes, 12–20 deeply furrowed thoracic segments, and a small pygidium; Italy, Spain, and China; Early Ordovician, about 475 Ma.

**Oviraptor:** a genus of theropod saurischian dinosaurs in the family Oviraptoridae; generally ostrich-size but with a shorter neck and a long tail. Its name is misleading. A spectacular find in the Gobi Desert in 1993 of an oviraptor fossilized above a nest of 15 to 22 oviraptor eggs provided direct evidence that oviraptors brooded their eggs and exhibited other bird-like behaviors. Although the interpretation is disputed and the nest has been disturbed by vertisol movement, this raptor was probably brooding rather than preying on the eggs. China, Late Cretaceous, 76–72 Ma.

**Oxyaenidae:** a family of relatively small carnivorous mammals formerly placed in the polyphyletic order Creodonta but now separated in the proposed superorder Laurasiatheria; characterized by a broad head and large jaw, with teeth designed for crushing; plantigrade, walking flat-footed; North America, Europe, and Asia; Paleocene to Eocene.

**Oxynoticeras:** a genus of ammonoids in the order Ammonitida, characterized by a smooth, laterally compressed shell with a sharp keel; *O. oxynotum* is an index fossil in the Early Jurassic; North America, Europe, and Africa; Early to Middle Jurassic.

**Ozarkodina:** a genus of conodonts in the order Ozarkodinida that contains important index fossils for the late Silurian, including *O. crista*, *O. bohemia*, and *O. snajdri*; the extinction of the genus is one of the indices marking the GSSP at the end of the Frasnian Age of the Late Devonian; see also *Ancyrodella rotundiloba*; global distribution.

**Ozarkodinida:** an order of conodonts in the unranked clade Prioniodontida; global distribution, Ordovician to Middle Jurassic.

**Ozawainellidae:** a family of foraminiferans in the order Fusulinida and superfamily Fusulinoidea; North America, Asia, and Europe; Carboniferous to late Permian.

# P

**Pachycephalosauria:** “thick head,” a suborder of relatively small ornithischian dinosaurs; bipedal and generally herbivorous, they are characterized by a very thick skull roof; they include the genera *Stegoceras*, *Troodon*, *Pachycephalosaurius*, and possibly *Dracorex*; North America and Asia, Late Cretaceous.

***Pachycrocuta brevirostris*:** the giant hyena of the late Pleistocene, the largest known at 240 pounds; it preyed on the giant elk and woolly rhinoceros, and the *Homo erectus* bones of the Longgushan Cave site in China (300,000–600,000 years ago), evidently gnawed by a predator, may bear the tooth marks of the giant hyena; China, Pliocene to middle Pleistocene.

***Pachydyptes*:** a monospecific genus of very large penguins (family Spheniscidae); *P. ponderosus* was a flightless bird with large flippers adapted to swimming, about 5 feet long; New Zealand, late Eocene.

**Pachypleuroosauria:** a suborder of sauropterygian reptiles in the order Nothosauroidae; generally less than 3 feet long, slender, and lightly built, but *Keichousaurus* and some other genera grew up to 9 feet long; Europe and Asia, Middle to Late Triassic.

***Pachyrhinosaurus*:** “thick nose,” a genus of ceratopsian dinosaurs in the subfamily Centrosaurinae. From 20 to 26 feet long and weighing up to 4 tons, it is notable for thick and ornamented bosses on the head and nose, and it also had several horns on a large neck-frill. Several specimens have been found in Northern Alaska and date from a time when climatic conditions were somewhat warmer than at present, but still colder in winter than previously thought possible for dinosaurs. Alaska and Alberta, Late Cretaceous, 74–69 Ma.

**paddlefish:** see *Polyodon*.

***Pagetia*:** a genus of very small agnostid trilobites in the family Eodiscidae; less than half an inch long, it had eyes, only two thoracic segments, and an annulated



pygidium with very prominent rings; well-known from the Burgess Shale but found worldwide, middle to late Cambrian.

**Painted Hills:** an area in the John Day Basin of Central Oregon that preserves a great variety of fossils of the Eocene and Oligocene in multi-colored layers of volcanic ash that accumulated in the large lakes of the area; the weathering of the volcanic deposits produced paleosols of different types and colors.

***Pakasuchus*:** an unusual monospecific genus of small crocodylomorphs with mammal-like dentition and other characteristics different from most crocodiles; considered a notosuchian, *P. kapilimai* was the size of an elongated house cat; Tanzania, Early Cretaceous, 105 Ma.

***Pakicetus*:** a genus of archaeocete whales in the family Protocetidae. Probably the most basal whale, the quadrupedal *Pakicetus* was about the size of a dog and lived primarily on land, probably semi-aquatic. Characterized by whale-like ear bones, *Pakicetus* is known from several skull specimens and skeletal fragments. Pakistan, early Eocene.

**Palaeacanthaspidae:** the most widespread family of primitive placoderms in the order Acanthothoraci; armored with plates and thick spines; North America, Europe, and Asia; Early Devonian.

**Palaeochinoidea:** a superfamily of regular echinoids in the subclass Perischoechinoidea; characterized by thick, polygonal, tessellate ambulacral plates that bevel over each other to form a rigid test; rare but widespread in North America and Europe, Silurian to early Permian.

***Palaeudyptes*:** a genus of large early penguins (family Spheniscidae); between 4 and 5 feet long, it was slightly larger than the modern emperor penguin; New Zealand, South America, Antarctica, and Australia; middle or late Eocene to late Oligocene.

***Palaeobatrachus*:** a genus of anurans in the extinct family Palaeobatrachidae; 3–4 inches long, it was an early and long-lived genus of frogs; Europe, Early Cretaceous to Miocene or possibly Pleistocene.

***Palaeocastor*:** an early land beaver that excavated vertical helical burrows up to 10 feet deep; see also **Agate Fossil Beds**; North America and Asia, Oligocene.

**Palaeocharaceae:** a group of charophytic algae descended from the Middle Devonian Eochara, both characterized by sinistrally spiralled gyrogonites; global distribution, Early Cretaceous.

***Palaeocharinus*:** an early genus of trigonotarbid arachnids; only a tenth of an inch long but equipped with fangs, it preyed on insects; Scotland, Early Devonian, 408 Ma.

***Palaeocircus*:** a genus of predatory birds in the still-extant family Accipitridae; France, late Eocene to Oligocene.

**Palaeocopida:** an order of straight-hinged ostracods, including at least the suborder Beyrichicopina; the assignment of other groups continues to be debated; global distribution, Ordovician to Cretaceous.

**Palaeodictyoptera:** a possibly paraphyletic order of medium-sized to large insects, the largest of five orders in the superorder Palaeodictyopteroidea. They are characterized by two pairs of dragonfly-like wings, sucking mouth parts, and a pair of winglets (paranotal lobes) on the prothorax. Several species had wingspans of up to 22 inches; among the largest known are *Moravia grandis*, *Lithomantis carbonarius*, and *Mazothairos*. See also *Dunbaria*. Cosmopolitan, Late Carboniferous to late Permian.

**Palaeodictyopteroidea:** a superorder of beaked insects in the subclass Pterygota; formerly Palaeodictyoptera. The first herbivorous insects and indeed the first terrestrial herbivores, they comprised 50 percent of the known Paleozoic species of insects. Some species were second in size only to the largest Protodonata. Their extinction at the end of the Permian left many niches to be filled by the insects of the Triassic. Global distribution, Middle Carboniferous to end-Permian.

**Palaeodonta:** a discarded term for a polyphyletic grouping of some primitive artiodactyl mammals such as the oreodonts, all of which are now classified in either the suborder Tylopoda or the suborder Suina.

**Palaeognathae:** the smaller of the two groups of living birds; they first appeared around 70 Ma and spread worldwide but survive only in the flightless ratites and the tinamous; almost all extant flying birds are classified as Neognathae.

**Palaeoisopus:** a genus of pycnogonid arthropods, possibly related to the modern pycnogonid sea spiders; known only from the Hunsrück Slate; Germany, Early Devonian.

**Palaeomastodontidae:** a family of elephantoid proboscideans currently assigned to the Afrotheria; probably ancestral to modern elephants, they had tusks and weighed more than 2 tons; Kenya, late Eocene to early Oligocene.

**Palaeomerycidae:** a family of artiodactyl ungulates in the still-extant infraorder Pecora and superfamily Cervoidea, close to the ancestry of modern deer and giraffes; global distribution except Australia, Eocene to Miocene.

**Palaeonisciformes:** a paraphyletic group of primitive actinopterygian fish in the subclass Chondrostei; important especially because they have features that became common in most later actinopterygians; also basic to understanding the structure of the sarcopterygians and their descendants the terrestrial vertebrates; global distribution, late Silurian to Late Cretaceous.

**Palaeoniscum:** a genus of freshwater actinopterygian fish in the extinct family Palaeoniscidae; about a foot long, it had a blunt snout and heterocercal tail fin, and was notable for its replaceable teeth; also called *Palaeoniscus*, *Palaeothrissum*, and *Geomichthys*; Europe and Asia, late Permian.

**Palaeopantopoda:** an order of sea spiders, marine arthropods in the class Pycnogonida, not arachnids but closer to them than to other arthropods; Europe, Devonian to Jurassic.

**Palaeophonus:** one of the oldest known arachnids, a genus of scorpions; between 3 and 4 inches long, it had gills and is thought to have lived in water and on land, preying on small animals and fish; North America and Europe, Silurian to Carboniferous.

**Palaeoptera:** a term traditionally applied to all groups of flying insects that cannot fold their wings back over their abdomen; the classification of the palaeopterans is unsettled, but the group is probably paraphyletic; most palaeopterans are extinct, the only surviving orders being the Odonata and the Ephemeroptera.

**Palaeopython fischeri:** a species of Eocene snakes as long as 7 feet; notable for a three-trophic-level fossil found at the Messel Shale Pit; inside the snake's stomach is a lizard (*Geiseltaliellus maarius*), inside which is an unidentified insect; Germany, 48 Ma.

**Palaeoryctidae:** a family of non-placental eutherian mammals tentatively placed in the order Cimolesta; part of the placental evolutionary radiation late in the Cretaceous, they were shrew-like and mainly insectivorous, but their dentition resembles that of later carnivores; North America, Asia, and Africa, Late Cretaceous to Paleocene.

**Palaeosaniwa:** a monospecific genus of carnivorous lizards in the family Varanidae; about 10 feet long, *P. canadensis* resembled modern monitors, and its dentition is essentially like that of a Komodo dragon; Western North America, Late Cretaceous, 75–70 Ma.

**Palaeosmilia:** a horn coral, a genus of solitary rugose corals traditionally placed in the extinct order Stauriida and family Palaeosmilidae but considered a doubtful genus by some; characterized by radially arranged septa; type species *P. murchisoni*; Europe, North Africa, Asia, and North America; Early Carboniferous to Permian.

**Palaeospondylus:** a genus of enigmatic primitive fish-like vertebrates, tentatively placed in the class Pteraspodomorphi; it is known only from the area of Caithness, Scotland, where hundreds of specimens have been found; it was jawless, eel-like, and 2–3 inches long, but whether its skeleton is calcified or cartilaginous is unclear; Middle Devonian.

**Palaeotarbus:** a monospecific genus of the arachnid group Trigonotarvida; *P. jerami*, originally called *Eotarbus*, was among the first terrestrial animals; England, late Silurian.

**Palaeothele montceauensis:** a species of mesothele spiders in the order Araneae; originally named *Eothele*, it is the earliest-known mesothele, known from two specimens from Montceau-les-Mines; France, Late Carboniferous.

**Palaeotheriidae:** a family of herbivorous perissodactyl hippomorphs, close to the ancestry of the Equidae; the type genus *Palaeotherium* resembled a small rhinoceros and was possibly in the line of descent to horses; Europe and Asia, Eocene through Oligocene.

**paleobiochemistry:** the study of chemical processes and their evolution in the fossil record.

**paleobioclimatology:** the study of the changes in climate in the geological past and of the effects of these changes on animal and plant life.

**paleobiocoenosis:** an assemblage of fossils of an interrelated community of organisms that lived together.

**paleobiogeography:** the study of the effects on organisms of the dynamic interaction of geologic processes (such as plate tectonics) with biological developments and climatic and environmental changes.

**paleobiology:** the branch of paleontology concerned with the biology of extinct organisms and their relationship to modern organisms.

**paleobotany:** the study of plant fossils and their interrelationships with other organisms in the geological past; also called paleophytology.

**Paleocene:** the first epoch in the Cenozoic Era, from 66 to 56 Ma. The GSSP marking the beginning of the era is the worldwide occurrence of an iridium layer associated with a large asteroid impact. The end-Cretaceous extinction affected plant life less severely than animal life, so that in the Paleocene conifers and cycads continued to dominate in the higher latitudes. Angiosperms spread, especially in the Southern Hemisphere; the first grasses appeared toward the end of the period. The first modern sand dollars, clypeasteroid echinoids, appeared in the sea, and ants diversified rapidly on land. Large flightless birds appeared, and mammals diversified rapidly, filling the many ecological niches left vacant at the end of the Cretaceous. Most modern fish groups were present and continued with relatively little change through the Cenozoic.

**paleoclimatology:** the study of past climatic conditions throughout geologic time, and of the causes of worldwide and local climatic variation; it involves especially sedimentology, palynology, glaciology, limnology, pedology, phytogeography, and the study of certain marine organisms such as coral.

**paleodepth:** the water depth at which a geologic stratum was deposited.

**paleoecology:** the study of the relationships between fossil organisms and their environment.

**Paleogene:** the first period of the Cenozoic Era, including the Paleocene, Eocene, and Oligocene Epochs.

**paleogeography:** the study of the changes in the distribution of the earth's land masses caused by tectonic plate shifting in the geological past.

In the billions of years of earth's existence, sections of the crust have moved constantly in the shifting of tectonic plates, sometimes called continental drift. Throughout Paleozoic time, the most constant large land mass was the southern section, called Gondwana; it was located generally in the lower part of the Southern Hemisphere and included what is now South America, Africa, Antarctica, Australia, Madagascar, and India. The Northern Hemisphere long contained only smaller fragments of land — what is now North America, Greenland, Europe, and Northern Asia.

But around 400 Ma, in a great mountain-building event called the Variscan orogeny, the northern fragments began to coalesce into a land mass called Laurasia and drift southward. By the end of the Carboniferous, around 300 Ma, all of the large land masses were locked together in the most recent global supercontinent, Pangaea, which extended in the Permian from the South Pole almost to the North Pole. Then, during the Late Triassic and Early Jurassic, the two sections began to drift apart, separating the organisms on the Laurasian segment from Gondwana. The three main sections of Laurasia — North America, Europe, and Asia — continued to drift apart from each other in the Cretaceous, isolating the dinosaurs and other land animals on each segment.

Since the beginning of the Cretaceous, although sporadic and fluctuating, the movement of the continents has generally been away from each other. Late in the Cretaceous, Africa and India broke off from Gondwana, with India moving northward; Antarctica separated from Australia at the end of the Eocene, and from South America in the early Oligocene, isolating their animals and plants. All of the present continents existed in the Paleocene, but as they moved, some have changed in size, notably North America and Asia, which have grown by accretion; nevertheless, the total global land mass today is comparable to that of the Triassic.

**paleoichnology:** the study of trace fossils showing evidence of the actions of organisms in the geological past, such as fossilized footprints, tracks, and burrows; increasingly important in research on fossil ecosystems, providing evidence on the activities and interactions of organisms in the past.

**paleomorphology:** the study of the structure and form of extinct plants and animals.

**paleontology:** the study of ancient life in the form of fossils, especially the evolution of new species and their distribution in space and time.

**paleopalynology:** the stratigraphic study of fossilized pollen, spores, particulate organic matter, and other wind-borne palynomorphs; important in the study of plant evolution and in the correlation of geological strata; also significant in studying climate change.

***Paleoparadoxia:*** a genus of large to medium-sized herbivorous mammals in the extinct order Desmostylia. A large marine relative of elephants that appeared in the Miocene and became extinct about 11,000 years ago, *Paleoparadoxia* had very large forelimbs, and its eyes were near the top of the head. Notable for the backward

angle of the teeth, it probably ate seaweed and sea grasses. It is now thought to have been almost fully marine like the modern sirenians. Northern Pacific coastal regions from Japan to Alaska and as far south as Baja California.

**paleopedology:** the study of paleosols, fossil soils of the geological past, either as part of a sequence of sedimentary strata or as a persistent soil surface that is no longer actively forming.

**Paleophytic:** term sometimes used for a paleobotanic division of time in the early Paleozoic Era, a time of transition from algae to gymnosperms; it was a period when peridophytes were abundant, from the late Cambrian up to the time of the appearance of gymnosperms in the Late Devonian.

**paleosol:** a fossil soil horizon in the geologic past, typically altered in place by biological, chemical, and physical processes; paleosols vary according not only to their geological structure but also to the community of plants and animals that occupied them.

***Paleothyris*:** a genus of primitive anapsid reptiles of the late Paleozoic, tentatively placed in the Romeriida; similar to *Hylonomus*, which was also found in Nova Scotia a few million years earlier; *Paleothyris* was about a foot long and probably ate insects and other small animals; Nova Scotia, Canada, middle Pennsylvanian, 312–304 Ma.

**palmate:** of a leaf divided into separate lobes or leaflets spreading from the base like fingers of a hand.

**palynofacies:** an assemblage of palynomorphs and other organic matter in a sedimentary stratum.

**palynomorphs:** organic microfossils from 5 to 500 microns in size, consisting of pollen, spores, sporopollenin, silica, chitin, or pseudochitin.

**palynostratigraphy:** the application of palynologic techniques to the study of geological strata; wind-borne palynomorphs, spread over great distances, are especially useful in correlating marine and non-marine sediments.

***Pampaphoneus biccai*:** “plains killer,” a species of dog-sized carnivorous dinocephalians in the family Anteosauridae, known from one specimen, a skull identified in 2012 in Brazil; middle Permian.

**Pampatheriidae:** ancestral armadillos, a family of large armored xenarthran mammals in the still-extant order Cingulata. Originating in South America in the Eocene, some weighed more than 400 pounds. When the Panama land bridge formed in the Pliocene, some genera emigrated to North America. All the larger ones, along with their relatives the glyptodonts, became extinct in the Quaternary extinctions. Eocene to Pleistocene.

**Pandanaceae:** a group of tropical plants in the order Pandanales; although called screw-pines, they are mostly palm-like and of medium height, and some genera are

lianescent; tropical areas from Oceania and Australia across the Indian Ocean to West Africa, Cretaceous to Recent.

**Panderichthyidae:** a small family of Devonian fish characterized by two pairs of lobed fins and an unusual pattern of skull bones; probably ancestral to all tetrapods; Latvia and North America, Late Devonian.

**Panderodus:** an early genus of conodonts in the family Panderodontidae; its elements are generally simple and horn-shaped, with fine striations, some of which are caused by radial lamellae; Ordovician to Silurian.

**Pangaea:** a term for the supercontinent created by the convergence of almost all land masses between the Late Carboniferous and Early Jurassic. See **paleogeography**.

**Pannotia:** “all southern,” the most common name for a short-lived (roughly 650–560 Ma) Neoproterozoic supercontinent completely within the Southern Hemisphere, with the African craton centered on the South Pole.

**Panphagia:** a monospecific genus of early sauropodomorph dinosaurs in the family Guaibasauridae; found in a middle Carnian layer of the Ischigualasto Formation, *P. protos* is one of the earliest dinosaurs; named “eating all” because its dentition suggests an omnivorous diet, it may represent a transitional stage between the carnivorous theropods and the herbivorous sauropods; Argentina, Late Triassic, 231 Ma.

**Panthalassa:** the Panthalassic Ocean, surrounding the supercontinent Pangaea from the Permian to the Jurassic Period.

**Panthera leo atrox:** a species of large, lion-like carnivores in the family Felidae, also called Naegele’s giant jaguar; short-legged and heavy-bodied, 25 percent larger than the modern African lion, it grew up to 4 feet at the shoulder and nine feet long head to tail; related to the Eurasian cave lion; North America, late Pleistocene to 11,000 years ago.

**Pantodonta:** an order or suborder of generally herbivorous eutherian mammals, generally considered cimolestids; early forms weighed about 20 pounds, and some later species, such as *Coryphodon*, weighed more than 1,000 pounds; global distribution except Australia, Paleocene to Eocene.

**Pantolestidae:** a family of semi-aquatic, non-placental eutherian mammals in the order Cimolesta and suborder Pantolesta; among the largest protoeutherians, some grew to 3 feet from nose to tail, the later species resembling otters; North America and Europe, Late Cretaceous to Oligocene.

**pantotheres:** a polyphyletic group of mouse- and rat-sized mammals, some of which may be close to the line of descent of primitive marsupial and placental mammals, including the Dryolestidae, Amphitheriida, Necrolestidae, and others.



***Pan troglodytes***: the larger of the modern chimpanzees, which split off from their Bonobo cousins about 1 Ma; the chimpanzees branched off the human line of descent about 6 Ma.

***Papio angusticeps***: the earliest-known baboon, identified from a skull fragment found in the cave at Malapa, South Africa, where *Australopithecus sediba* was found; this fossil, 2 million years old, differs very little from the modern baboon; the fossil record of baboons is sparse, but they seem to have appeared very recently; Pleistocene.

***Pappochelys***: a genus of small diapsid reptiles that seems to be intermediate between earlier diapsids like *Eunotosaurus* and primitive turtles like *Odontochelys*. Its body is 6 inches long and its tail another 6 inches. *Pappochelys* is characterized by two pairs of temporal fenestrae and by flattened ribs and gastralia that are beginning to fuse together, a step in the process that led to the carapace and plastron of later turtles. Europe, Middle Triassic, 240 Ma.

***Pappotherium***: a monospecific genus of small early eutherian mammals, known only from a jawbone with two teeth found in Texas; possibly in the metatherian order Deltatheroidea; United States, Early Cretaceous, 113–109 Ma.

***Paraceratherium***: a genus of very large hyracodont perissodactyl mammals in the extinct subfamily Indricotheriinae; resembling a large, hornless rhinoceros, it was one of the largest land mammals ever, 18 feet high at the shoulder, 26 feet long, and weighing 25–30 tons; also called *Indricotherium* and *Baluchitherium*; Asia, early Oligocene to early Miocene.

**Paracrinoidea**: “near crinoid,” a small class of blastozoan echinoderms in the subphylum Crinozoa; they superficially resemble stalked crinoids in having a stem, thecae, and arms; North America and Europe, Early Ordovician to early Silurian.

***Paradoxides***: a genus of large early trilobites in the order Redlichiida, the largest species over 3 feet in length; also characterized by a very long thorax and two spines longer than its body, extending backward from the cephalon; index fossil for the Avalonian beds of the middle Cambrian; North America, Europe, and North Africa; early to late Cambrian.

***Parahagla***: see *Habrohagla*.

***Parakidograptus acuminatus***: a species of pterobranch graptolites in the order Graptoloidea; its first appearance marks the beginning of the Silurian at 443.8 Ma; Great Britain.

***Paralititan strömeri***: a species of titanosaurian dinosaurs, an extremely massive sauropod found in 1999 at the Bahariya oasis in Egypt, near where Ernst Strömer had made important finds in the early twentieth century. A six-foot humerus and other upper-body bones make it clear that it was one of the largest dinosaurs. Estimated to be 85 feet long and weighing 65 tons, it may be almost as large in mass



as another titanosaurian, *Argentinosaurus*. Egypt, Late Cretaceous, 94 Ma, not long after Africa and South America separated.

**Paramyidae:** a family of the earliest-known rodents, in the suborder Sciuromorpha; scansorial and squirrel-sized, they may have lived in trees and competed with early primates; probably the basal stock of the order Rodentia; North America, Europe, and Asia, late Paleocene to late Eocene.

**Paramylodon:** a genus of giant ground sloths in the order Pilosa and the extinct family Mylodontidae; about 10 feet long and weighing more than a ton, it is also notable for the dermal ossicles embedded in its thick skin; formerly called *Myloodon*, it is known from widespread North American deposits from Canada to Central America; late Pliocene to late Pleistocene.

**Paranthropus:** a genus of hominins similar to and possibly descended from gracile australopithecines; known from several skull and other fragments dated between 2.3 and 1.2 Ma; East Africa.

**Paranyctoides:** a genus of Late Cretaceous eutherian mammals; the earliest-known erinaceomorph, the scansorial *Paranyctoides* has some characteristics of true insectivores; North America and Uzbekistan, 89–66 Ma.

**Paranyroca:** a genus of anseriform birds in the extinct family Paranyrociidae or family Anatidae; known from two specimens found in North Dakota; United States, middle Miocene.

**Paraparchitoidea:** a superfamily of robust ostracods in the extinct order Kloedenellocoquina; global distribution, Devonian to late Permian.

**paraphyletic group:** see **polyphyletic group**.

**Parapithecidae:** a family of primitive anthropoid primates in the superfamily Parapithecioidea, known especially from the middle Oligocene Fayum deposits of Egypt. The parapithecines are difficult to classify but may be the most primitive advanced primates known. One member of the family, *Apidium*, may be ancestral to *Oreopithecus*, but its affinities are still unclear. Africa and Asia, Eocene to Oligocene.

**Parapuzosia:** a genus of very large ammonoids in the order Ammonitida and family Desmoceratidae; the largest known ammonoids, with fossil shells almost 7 feet across; global distribution, Late Carboniferous.

**Parasaurolophus:** a genus of very large duck-billed herbivorous dinosaurs in the family Hadrosauridae, characterized especially by the long, distinctive crest from the nose to behind its head. Several theories try to explain the function of this unusual crest, such as to generate trombone-like sounds, to support a decorative flap of skin, or to provide a sign of sex recognition. These hadrosaurs are known from a few specimens of three species; the type species, *P. walkeri*, was about 31 feet long and weighed almost 3 tons. North America, 76 Ma.

***Paraschwagerina***: a genus of fusulinid foraminiferans that are index fossils for the early Permian; they occupied a deep marine environment, far offshore; North America, Europe, and Asia; early to middle Permian.

***Paraselkirkia***: a genus of predatory priapulid worms in the family Selkirkiidae; similar but larger (6 inches) than the Burgess Shale *Selkirkia*, *q.v.*; known only from the Chengjiang biota, China, early Cambrian.

**Parasemionotidae**: a family of small, bony actinopterygian fish in the subclass Neopterygii and extinct order Amiiiformes; global distribution, Early to Middle Triassic.

**Parasuchia**: see **Phytosauria**.

**paratheres**: see **Xenarthra**.

**Parathuramminoidea**: a superfamily of foraminiferans in the suborder Fusulinina; characterized by a test with a globular or tubular chamber; global distribution, Ordovician to Permian.

**paratype**: a specimen of a type species other than the holotype; several paratypes may be used in identifying the species.

**Parazoa**: a subkingdom of eukaryotic multicellular animals whose only known living members are the sponges and the placozoan *Trichoplax*; parazoans early evolved into a line separate from all other animals, splitting off from the Eumetazoa in the early Neoproterozoic, about 940 Ma; although they have differentiated cells, they have no organs or tissues.

**Pareiasauridae**: a family of bulky, armored herbivorous reptiles in the suborder Procolophonomorpha; formerly included in the paraphyletic order Captorhinida; as long as 10 feet and as heavy as 1,300 pounds, some species are notable for a great number of scutes covering the body and for heavy cephalic ridges and knobs; Africa, Europe, and Asia; middle to late Permian.

**Paris Canyon**: a site in Idaho being developed in 2017, dated at only 1.3 million years after the end-Permian extinction; its fossil assemblage may indicate a more rapid recovery of marine life after the extinction than previously thought; United States, Early Triassic.

***Parkinsonia***: a genus of ammonoids in the order Ammonitida and superfamily Perisphinctoidea, with a laterally compressed and strongly ribbed shell; index fossil for the Bajocian age; North America, Europe, and Asia; Middle Jurassic.

***Parksosaurus***: a genus of hypsilophodont ornithomimid dinosaurs in the family Thescelosauridae; it resembles *Thescelosaurus*, another ornithomimid also from the Maastrichtian; about 8 feet long and bipedal, it was a slender, fast, herbivorous animal; Alberta, Late Cretaceous, 70 Ma.

***Parvancorina***: “small anchor,” a genus of enigmatic Ediacaran animals with some arthropod-like characters; known from circular molds, less than an inch wide, and

characterized by a central ridge with a raised semicircular arc at one end of the ridge; similar in shape to trilobites but probably unrelated; found in marine sediments in Russia and Australia, and also on the underside of some Australian paleosols; 560–555 Ma.

***Patagonykus***: a monospecific genus of theropod dinosaurs in the family Alvarezsauridae; known from a partial skeleton, *P. puertai* was about 7 feet long; Argentina, Late Cretaceous, 94–87 Ma.

***Patagotitan mayorum***: a species of large titanosaurian sauropod dinosaurs described in 2017; known from partial skeletons of seven individuals, it is estimated to have been 120 feet long and weighing 69 tons, but these estimates may be revised downward; Argentina, Early Cretaceous, 102 Ma.

***Patellina* (foraminiferan)**: a still-extant genus of dish-shaped spirillinid foraminiferans in the family Patellinidae; global distribution, Late Jurassic to Recent.

***Patellidae* (gastropod)**: a still-extant family of gastropods in the order Eogastropoda; imperforate limpets, specialized for clinging to rocks under their cap-shaped shell; global distribution, Permian to Recent.

***Paterinida***: an order of early inarticulate brachiopods in the subphylum Linguliformea and class Paterinata; characterized by biconvex, rounded, generally phosphatic shells; global distribution, early Cambrian to Middle Ordovician.

***Patriomanis***: a monospecific genus of pangolins in the suborder Eupholidota and family Patriomanidae; *P. americana*, well-known from several partial specimens found between 1970 and 2016, is the only known North American pangolin, although modern pangolins are widespread in Asia and Africa; see also ***Eomanis***; late Eocene to Oligocene.

**peak zone**: a stratigraphic zone in which a specific organism occurs in its greatest abundance, or which is dominated by an exceptional abundance of one or more types of organisms.

***Pecopteris***: a common form genus of fossil foliage especially from the marattialean fern *Psaronius*, but also from a seed fern and several filiclean ferns; especially prominent in the Carboniferous and Permian; global distribution, Devonian to Miocene.

***Pectinidae***: the scallops, a family of bivalves in the superfamily Pectinoidea. The Pectinidae are characterized by a single adductor muscle and a basically triangular shell, which is usually ridged and from 1 to 5 inches wide. They are benthic, but most genera differ from other bivalves by swimming freely. Although the Pectinidae were the most diverse Mesozoic bivalves, they became almost extinct at the end of the Cretaceous but then again radiated rapidly in the Cenozoic. Global distribution, Triassic to Recent.

***Pederpes finneyi***: a species of stem-tetrapod amphibians in the family Whatcheeriidae; an important specimen for its occurrence in the period of time

called Romer's Gap; about 3 feet long and with a large, somewhat triangular head, this tetrapod has several features indicating greater terrestriality than any earlier animal; Scotland, Early Carboniferous, about 348 Ma.

**Pedetidae:** a still-extant family of African rodents in the order Sciuromorpha; the modern springhares differ only slightly from the earliest Pedetidae, which arose in the Miocene.

**pedicle:** the stalk that is present in most brachiopods, attaching the pedicle valve to a hard substrate, usually below the animal.

**Peking Man:** see *Homo erectus pekinensis*.

**pelagic:** living in open water, typically in the water column of the ocean, neither near shore nor at the bottom; pelagic animals include birds as well as free-swimming or floating organisms; see also **nektic**, **planktic**, and **benthic**.

**Pelagornis:** a widespread genus of large sea birds of the Neogene; one of the Miocene species, *P. sandersi*, had probably the widest wingspan known in a bird, as much as 24 feet (see also *Argentavis magnificens*); *Pelagornis* is notable for the bony spikes in its mouth which it used to grasp its prey, live or dead fish; global distribution.

**pelmatozoan:** "stem animal," a term formerly referring to the paraphyletic subphylum of echinoderms called Pelmatozoa, which were attached to the sea substrate by a stem; the term is still used informally to refer to organisms with this habit; global distribution, early Cambrian to Recent.

**Peltephilus:** a genus of fossorial horned armadillos, South American xenarthran mammals in the still-extant order Cingulata and family Chlamyphoridae. It was characterized by large claws and bony scutes on its head and bands of scutes across its back; it also bore at least one pair of small horns on the top of its snout, forward of the eyes. The function of the horns is unclear, although they offered at least some defense for the eyes. These horns represent an example of convergent evolution in two unrelated animals since the size and placement of the horns is similar to that of *Ceratogaulus*, the horned rodent of the Neogene of North America and the only other known fossorial horned mammal. Argentina, Chile, and Bolivia; Oligocene to middle Miocene.

**Peltobatrachus:** "shielded frog," a genus of armored temnospondyl amphibians in the family Peltobatrachidae; about 2 feet long, it was armored with a series of narrow plates covering its entire body; Africa, late Permian.

**pelecosaurs:** "bowl lizard," now an informal term for a paraphyletic stem group of synapsids that were the dominant animals of the Carboniferous and Permian. Among the earliest amniotes, pelecosaurs arose in the Pennsylvanian and are considered ancestral to therapsids and eventually to mammals. Their bowl-shaped pelvic structure gave them greater agility and speed on land than earlier reptiles like *Hylonomus*. They are most noticeable for the high and partly vascularized sails

stretched on elongated neural spines down the back of several genera; in species like *Dimetrodon* and *Edaphosaurus*, these formed a spectacular sail of several square feet. Another important character of some pelycosaur was one or two pairs of longer, grasping teeth at the front of the snout, the precursors of the canine teeth that have been one of the hallmarks of the synapsid-mammal lineage ever since. North America and possibly Europe, Early Pennsylvanian to late Permian.

***Pengana***: a genus of predatory birds in the still-extant family Accipitridae; Australia, early Miocene.

**Pennatulacea**: the sea pens, an order of soft-bodied, generally feather-shaped anthozoan cnidarians in the subclass Octocorallia; colonies of dimorphic polyps, most of them attached to the substrate by a stalk, but some capable of movement; global distribution, Cambrian to Recent.

**Pennsylvanian**: see **Carboniferous**.

***Pentacrinites***: a genus of articulate stemmed crinoids in the order Isocrinida, characterized by a small cup and five long, repeatedly branching arms at the end of a stem as long as 3 feet; the stem is pentagonal in cross-section; thought to have grown on driftwood and thus be semi-planktic; global distribution, Middle Triassic to Eocene.

**Pentamerida**: an order of biconvex articulate brachiopods in the class Rhynchonellata, characterized by impunctate, somewhat pentagonal shells and a short hinge line; global distribution, middle Cambrian to Late Devonian.

**Pentastomida**: the “tongue worms,” a small and controversial phylum of parasites on terrestrial animals and on some fish. Characterized by internal plates separating the body cavity pentamerally when seen in cross-section. Many biologists have considered them to be an offshoot of the branchiurans, a group of crustaceans. Since 1994, however, discoveries of several pentastomes in upper Cambrian strata in Canada and the Orsten Lagerstätten of Sweden (see also *Heymonsicambria* and *Linguatula*) have shown that the pentastomes have persisted almost unchanged until the present, convincing many authorities that they should be accorded phylum status. Global distribution, late Cambrian to Recent.

***Pentecopterus decorahensis***: the earliest-known species of eurypterids, sea scorpions, discovered in the early twenty-first century near Decorah, Iowa; as long as 6 feet, they were armed with a dozen clawed arms and had a three-foot tail used in swimming; unlike some larger Paleozoic sea scorpions, they were efficient predators; North America, Middle to Late Ordovician, 460 Ma.

**Pentoxylales**: an order of gymnosperms that were small shrubs or trees. Their affinities are unclear, but they are related to ginkgos and may be in the line of descent to angiosperms. A stem genus *Pentoxylon* and a seed-bearing cone genus *Camoconites* have been described for the genus *Taeniopteris*. The Pentoxylales were an important part of the Gondwana flora in the Jurassic. Known only from India and New Zealand, Jurassic and possibly Early Cretaceous.

***Pentremites***: a genus of blastoid echinoderms in the order Spiraculata and family Pentremitidae; attached to the substrate by a slender stalk, from 4 to 12 inches long; North America, Early Carboniferous.

**peppered moth**: see *Biston betularia*.

***Peradectes***: a genus of early marsupials in the family Peradectidae; the type species, *P. minor*, was only 8 inches long from head to tail; thought to be a scansorial omnivore, it appeared just after the end-Cretaceous extinction; North and South America, early Paleocene.

**periodic extinction**: the theory that major extinctions have occurred since the Permian at regular intervals of about 26 million years.

***Peripatus***: a still-extant genus of velvet worms (phylum Onychophora) in the family Peripatidae; similar to *Aysheaia* of the middle Cambrian but Paleozoic collection failure leaves the possible relationship unclear; Central and South America, Myanmar, Australia, and New Zealand; Late Cretaceous to Recent.

**Periptychidae**: an early family of tapir-like protoungulate placental mammals; characterized by vertical, wrinkling ridges on their molars, and ranging in size from 30 to 200 pounds, some periptychids were omnivorous and others were herbivorous; North America and possibly Eastern Asia, Late Cretaceous through Paleocene.

**perissodactyls**: ungulates having an odd number of toes, especially herbivorous terrestrial mammals having a large central digit on each foot, such as the horse, tapir, and rhinoceros; the earliest perissodactyls appeared in the late Paleocene (see **Artiodactyla** and *Hyracotherium*).

***Perittodus apscanditus***: “hidden odd tooth,” one of several new stem-tetrapods discovered by Jennifer Clack in 2016; its dentition is complex and different from other tetrapods; see also **Tetrapoda**; England, Late Devonian.

***Permarachne novokshonovi***: a species of proto-spiders in the order Uraraneida and family Permarachnidae; known only from a Russian specimen (a molt) described in 2005; see also *Attercopus*; Ural Mountains, Permian, 280 Ma.

**Permian**: the final period of the Paleozoic Era, from 299 to 251 Ma. Although it was a relatively hot and dry time, sea levels sank, evidently because of ocean floor changes accompanying the formation of the supercontinent Pangaea. Pelycosaur-grade synapsid reptiles survived from the Late Carboniferous into the Permian, followed by pareiasaurian reptiles and the first therapsids, which diversified rapidly toward the end of the period. Cycads and conifers became widespread as the drying climate gradually ended the coal swamps of the Carboniferous; the *Glossopteris* flora dominated Gondwana plant life. The period ended with the most severe mass extinction in Earth's history, setting the stage for the dinosaurs of the Mesozoic.

**Permian extinction**: the most severe of the five great extinctions, marking the end of the Paleozoic Era at 252.2 Ma. Like the four other mass extinctions, the Permian event may have occurred in several phases. Two smaller extinction pulses occurred

at 259.8 and 254.1 Ma, marking the end of the Capitanian and Wuchiapingian Stages respectively; both may have contributed to the more extensive extinction at 252.2 Ma, referred to as the end-Permian extinction.

At least 90 percent of marine species became extinct, while the terrestrial extinctions were less severe but still estimated to be 75 percent of species, especially the large herbivores. Most lineages of insects were not severely affected except for the pterygote superorder Palaeodictyopteroidea, which became extinct at about 252 Ma. Among the marine groups that did not survive were the trilobites, rugose corals, and eurypterids, and among those that survived in only one or two orders were the brachiopods, crinoids, and nautiloids. After the Permian extinction, mollusks came to rival arthropods for dominance in marine environments, and modern corals and bryozoans replaced the Paleozoic types.

Several factors have been suggested as causes, but volcanic eruptions (see **Siberian Traps**) are increasingly stressed as the primary cause, especially because of high levels of carbon dioxide emitted into the atmosphere. There was clearly global environmental degradation, including low levels of oxygen in the oceans, evident in widespread sediments. Other possible causes are global cooling and the disappearance of many nearshore environments as the continents coalesced into Pangaea.

**Peronopsis:** a genus of trilobites in the order Agnostida and family Peronopsidae; isopygous, similar to *Itagnostus*; global distribution, middle to late Cambrian.

**Perudyptes:** a genus of large penguins in the family Spheniscidae; flightless and adapted for diving like all penguins, *Perudyptes* was about the size of the modern emperor penguin and is one of the earliest definitive penguins known, dated at 42 Ma; Peru, middle Eocene.

**pes:** plural **pedes**, the distal part of the hindlimb of bipedal vertebrates, corresponding to the human foot.

**Petalichthyida:** an order of flattened placoderms, characterized by cranial and trunk shields, and a partly ossified skeleton; probably benthic; Australia, Asia, Europe, and North America; Devonian to Carboniferous.

**petalodont dentition:** teeth that are specially hardened, flat-crowned, and embedded in the palate, an adaptation for grazing on tough organisms like crinoids, sponges, and other encrusting animals.

**Petalodontidae:** a family of primitive skate-like holocephalic fish in the subclass Chondrichthyes and order Petalodontiformes; their classification is obscure because they are known primarily from their petalodont teeth; *Belantsea* and *Janassa* are the best-known genera; North America and Europe, Carboniferous to Permian.

**Petrolacosaurus kansensis:** the earliest-known diapsid, a species of North American reptiles in the order Araeoscelida; about 16 inches long and insectivorous; Kansas, Late Pennsylvanian, 302 Ma.

**Peytoia:** see **Anomalocarididae**.



***Pezophaps solitaria***: the Rodrigues solitaire, a species of birds in the order Columbiformes and extinct subfamily Raphinae; *Pezophaps* (“pedestrian pigeon”) is a monospecific genus but is closely related to *Didus solitarius*, the dodo. *Pezophaps*, the size of a swan and flightless, was endemic to the island of Rodrigues, in the Indian Ocean east of Madagascar. It was discovered in 1691 and was hunted to extinction within a century.

***Pezosiren portelli***: “walking sirenian,” the earliest-known fully quadrupedal sirenian, placed in the family Prorastomidae with the fully aquatic *Prorastomus*. Probably amphibious and similar in habit to the modern hippopotamus, it represents an important transitional stage between fully terrestrial mammals with four legs and fully aquatic mammals with flippers. Jamaica, early Eocene.

**phaceloid**: of colonial corals, having tubular corallites with separate walls, joined together at the base.

**Phacopida**: “lens-face,” a large and diverse order of trilobites with three suborders: Phacopina (with schizochroal eyes), Cheirurina (holochroal eyes), and Calymenina (holochroal eyes); global distribution, late Cambrian to the end of the Devonian.

***Phacops rana***: a famous species of trilobites in the order Phacopida, notable for its very large eyes and the warty surface of the glabella; North America and Africa, Middle Devonian.

**Phalangiotarbida**: an order of early arachnids, considered a sister group of the Opiliones but possibly related also to the Acari; Europe and North America, Devonian to Permian.

***Phanerorhynchus***: a genus of chondrosteian fish in the family Phanerorhynchidae; characterized by large body scales, unjointed fin rays, and vertical jaw suspension; Europe, Late Carboniferous.

**Phanerozoic**: “visible life,” the geologic eon from the beginning of the Cambrian to the present.

***Phareodus***: a genus of freshwater osteoglossomorph fish in the family Osteoglossidae; 6–7 inches long, it was known in two species, *P. encaustus* and *P. testis*; North America, Europe, Asia, and Australia; Cretaceous to Eocene.

**Phascolarctidae**: “pouch bears,” a still-extant family of marsupial mammals in the order Diprotodontia; it includes only one extant species, the modern koala (*Phascolarctos cinereus*), but about eight extinct genera are known, including *P. stirtoni*, which became extinct in the late Pleistocene; arboreal herbivores weighing as much as 50 pounds, the family originated in the late Oligocene and is closely related to the Vombatidae; Australia, Oligocene to Recent.

***Phascolonus***: a genus of herbivorous Australian marsupials in the order Diprotodontia and family Vombatidae; one of several extinct genera of large



wombats, *Phascolonus* weighed about 450 pounds; it is known from the middle Pliocene to the middle or late Pleistocene.

**Phenacodontidae:** an early family of herbivorous mammals, possibly ancestral to later mammals; their size increased from 15 to 120 pounds from the Paleocene to the Eocene; the type genus *Phenacodus*, resembling *Hyracotherium* but slightly stockier, was one of the earliest and most primitive of the ungulates; North America and Europe, Paleocene and Eocene.

**Phillipsastreidae:** a family of generally colonial rugose corals in the order Stauriida and suborder Columnariina; its corallites did not have separate walls, but had radially arranged and sometimes curving septa, resulting in a star-shaped pattern; global distribution, Early to Middle Devonian.

**Phillipsia:** a genus of small trilobites in the order Proetida and superfamily Bathyroidea; isopygous, with a large cephalon and a large pygidium; although not numerous, it was one of the last trilobites; North America, Europe, and Asia; Carboniferous to late Permian.

**Phiomysidae:** a small family of rodents in the suborder Hystricomorpha; Africa, late Eocene to middle Miocene.

**Phoberomys:** a genus of giant rodents in the suborder Hystricomorpha and family Dinomyidae. About the size of a buffalo, almost 10 feet long and weighing up to 1500 pounds, it was one of the largest rodents known. (See also *Josephoartigasia*.) It had small forelimbs and teeth typical of herbivores, and was notable for a long tail which it could use to balance on two feet to look over the vegetation of the swamplands where it lived. Northern South America, known only from the late Miocene.

**Phocidae:** the true seals, a family of pinnipeds in the superfamily Phocoidea; probably descended from *Enaliarctos* and possibly related to the ursids; earless and overall more specialized for aquatic life than their relatives, the Odobenidae and Otariidae; global distribution, middle Miocene to Recent.

**Pholadomya:** "hole clam," a still-extant genus of inarticulate marine bivalves in the superorder Anomalodesmata and order Pholadomyoidea, widespread in the Mesozoic; deep-burrowing, up to 5 inches long; the shell gapes open at the posterior end so that the siphon can be partially withdrawn; Late Triassic to Recent.

**Pholidophorus:** a genus of small, primitive teleost fish in the order Pholidophoriformes; one of the earliest teleosts, it had ganoid scales and its skeleton was partly bone and partly cartilage; South America, Europe, and Africa; Middle Triassic to Late Jurassic.

**Pholidota:** the pangolins, an order of mammals once distributed globally and dating back to the Paleocene; now extant only in Africa and Southeast Asia.

**Phoronida:** a still-extant but very small phylum of lophophorates related to brachiopods and bryozoans. They are tube-dwelling vermiforms that filter-feed by means of the cilia on a crown of tentacles. From 1 to 20 inches long, they have no

hard parts, and there are no undisputed fossil specimens except as trace fossils in the form of the chitinous tubes that they construct as burrows. Living phoronids burrow into both soft and hard substrates. Global distribution, Early Devonian to Recent.

**Phorusrhacidae:** a family of large, flightless carnivorous birds in the order Cariamiformes. Characterized by a large head and neck, with short wings used only for balance, they averaged about 5 feet high. The phorusrhacids lived on the South American continent while it was an island in the early Cenozoic. Probably seizing and killing their prey by battering it on the ground, they were the principal carnivores of the continent until it joined North America in the late Pliocene, when saber-toothed cats, jaguars, and wild dogs migrated southward. The largest of the phorusrhacids, *Kelenken*, found in Patagonia in 2004, grew as high as 10 feet and weighed as much as 500 pounds. South America, early Paleocene to late Pliocene.

***Phorusrhacos longissimus*:** a genus of carnivorous birds in the family Phorusrhacidae; notable for a long skull and long jaw with a hooked beak; South America, Miocene.

**phyletic gradualism:** a model of evolution that stresses steady, gradual evolutionary change (see **anagenesis**) as the basic mode of speciation; this gradual evolutionary change is considered to occur throughout the history of the lineage.

**Phyllocarida:** a still-extant subclass of crustaceans in the class Malacostraca, characterized by a folded bivalved carapace that covers almost the entire body; it includes three orders; the extinct Hymenostroaca and Archaeostraca, and the extant Leptostraca, a small but long-lived group that appeared in the Cambrian; most other crustaceans are classified in the Eumalacostraca; global distribution.

***Phylloceras*:** a genus of nektic ammonoids in the order Phylloceratida; the smooth shell, 4–10 inches long, is laterally flattened with no ornamentation; global distribution, Late Triassic to the end of the Cretaceous.

**Phylloceratida:** a conservative Mesozoic order (or suborder) of ammonoids; generally smooth or weakly ornamented, they are marked by a complex phylloid suture; the phylloceratids are probably ancestral to the highly diverse Jurassic and Cretaceous ammonoids and themselves persisted almost unchanged from the Early Triassic to the Late Cretaceous; global distribution.

***Phyllograptus*:** a colonial graptolite of the Ordovician in the order Graptoloidea and family Phyllograptidae; distinguished by the oval, leaf-like shape of the colony, which was 1–2 inches long; several species are index fossils for the Early Ordovician; global distribution, Early to Late Ordovician.

**phylloid:** leaf-like, in the shape of a leaf.

**Phyllolepidida:** “leaf scale,” an order of small, flattened placoderms, possibly related to the arthrodires; the phyllolepidids were freshwater predators with whole-plate armor, a wide mouth, and probably only vestigial eyes; several genera in three families are known globally from the Early and Middle Devonian, but *Phyllolepis* was

the only genus to survive into the Famennian, the final stage of the Devonian; Early to Late Devonian.

***Phyllothea***: a widespread genus of jointgrasses in the order Equisetales; global distribution, Late Carboniferous to late Permian.

**phylogeny**: the evolutionary history of a biological organism and its relationship to other organisms.

***Physalis***: see **Solanaceae**.

**phytolith**: “plant stone,” a microscopic siliceous structure persisting in plant tissue after the decay of the plant; a common element in the fossil record, phytoliths may identify changes in paleoenvironments, and they may also reveal information about the diet of herbivorous animals; see also **grasses**.

**Phytosauria**: an order of semi-aquatic archosaurian reptiles, about 6 feet long, heavily armored, and with an elongated snout; formerly called Parasuchia. An example of convergent evolution, the phytosaurs closely resembled the unrelated crocodiles, but their ancestry is obscure. They were widespread in the northern continents but unknown in Southern Africa, South America, Australia, and Antarctica. Middle to Late Triassic, possibly Early Jurassic.

***Pierolapithecus catalaunicus***: an ape fossil discovered in 2004 near Barcelona that had the upright posture of human beings, an ape-like body, and fingers like those of chimpanzees; dated at 13 Ma, it is unique and a possible step in the evolution of ape to human; only one specimen has been found; Spain, Miocene.

***Pikaia***: an enigmatic genus of small primitive chordates known from the Burgess Shale. It was first considered a polychaete worm or stem-arthropod but was later identified as perhaps the oldest ancestor of chordates; it is now generally assigned to the subphylum Cephalochordata. Laterally compressed and ribbon-shaped, the soft-bodied *P. gracilens* was only about 2 inches long. Canada, middle Cambrian, 508 Ma.

***Pilina***: a genus of monoplacophorans in the family Tryblidiidae; United States and Europe, Ordovician to Silurian.

**“Piltdown Man”**: a sophisticated hoax perpetrated in 1912 by Charles Dawson, who claimed to have discovered a missing link between apes and humans; the fraud was discovered forty years later when advanced dating techniques showed that the specimen was actually only 50,000 years old; subsequent examination revealed that it was a deliberate combination of a human cranium with the jaw of an ape, probably an orangutan.

***Pinacosaurus***: a genus of ornithischian dinosaurs in the family Ankylosauridae; herbivorous, 16–20 feet long with a spiked tail club, it lived between 80 and 75 Ma; Mongolia, Late Cretaceous.

**Pinopsida:** a still-extant class of cone-bearing gymnosperm trees, the most successful group of gymnosperms still living; the earliest conifers of the Middle Carboniferous and early Permian had sub-compact cones but may have been the first plants whose seeds could remain dormant for a considerable time before germination; see also **Araucaria** and **Lebachia**; global distribution, Middle Carboniferous to Recent.

**Pisco Formation:** an important Konzentrat-Lagerstätte on the southern coast of Peru; known for the only definitive specimen of the large whale *Livyatan* as well as the aquatic sloth *Thalassocnus* and other well-preserved specimens of whales, penguins, marine crocodiles, and sharks; South America, middle Miocene to middle Pliocene.

**Pistosauria:** an order of marine reptiles in the superorder Sauropterygia; about 10 feet long and characterized by an elongated neck and skull, they were probably transitional between nothosaurs and the larger plesiosaurs; North America, Europe, and Asia; Early Triassic to Late Cretaceous.

**Pithecanthropus:** an obsolete term, once applied to several hominins that are now classified as *Homo erectus*.

**Pityaceae:** a family of plants of the Carboniferous long thought to belong to the Cordaitales but now assigned to the Pteridospermophyta; global distribution, Early Carboniferous.

**Placenticerias:** a genus of large ammonitid ammonoids in the family Placenticeratidae and superfamily Hoplitoidea; relatively smooth-shelled, they ranged from 1 to 3 feet across; global distribution, Late Cretaceous.

**Placerias:** a genus of dicynodont therapsids in the family Stahleckeriidae; it was among the largest herbivores of the Triassic and one of the last surviving dicynodonts; from 6 to 11 feet long and weighing up to 4,400 pounds, *Placerias* was beaked with two strong upper tusks; its lifestyle was similar to that of a hippopotamus, spending much of its time in the water; Southwestern United States, Late Triassic.

**Placodermi:** “plated skin,” the earliest class of gnathostome vertebrates, primitive jawed fish of the middle Paleozoic; from a few inches to 30 feet long, they had heavy bony armor covering their head, neck, and sometimes thorax; they were the first fish with pelvic fins, the first evolutionary step toward hindlimbs in the tetrapods, and some of the first fish to colonize freshwater environments were placoderms (see **Phyllolepidia**); global distribution, middle Silurian to the end of the Devonian.

**Placodontia:** an order of diapsid marine reptiles in the order Sauropterygia. The placodonts ranged from 3 to 10 feet long and used their flattened teeth to prey primarily on mollusks. The early type genus *Placodus* resembled modern marine iguanas in body structure, but the later genera developed turtle-like body armor as a defense against the growing numbers of nothosaurs and plesiosaurs toward the end

of the Triassic; placodonts are not, however, related to turtles. Europe, Asia, and Africa; Early to Late Triassic.

**Plagiaulacidae:** a family of small basal multituberculate mammals in the suborder Plagiaulacida; North America, Europe, and Asia; Late Jurassic to Early Cretaceous.

**Plagiosauroidae:** “flat lizard,” an enigmatic superfamily of early labyrinthodont amphibians in the order Temnospondyli; about 3 feet long, they were characterized by completely cylindrical vertebrae and a very short, wide skull (about 6 inches long and 9 inches wide in *Gerrothorax*); South Africa, South America, and Asia; Early to Late Triassic.

**planktic:** referring to organisms that do not swim actively, independent of the water current; they may swim weakly but generally drift with the current.

**Planocephalosaurus:** an early genus of rhychocephalian diapsid reptiles in the family Sphenodontidae; only about 8 inches long, it was similar in most other respects to the modern tuatara; North America and Europe; Late Triassic, 210–200 Ma.

**plastron:** the hard ventral covering of turtles.

**Plateosaurus:** “broad lizard,” a genus of basal prosauropod dinosaurs; from 15 to 34 feet long and weighing up to 9,000 pounds, it was among the largest of its time; it appeared at the end of the Triassic and survived into the Early Jurassic; Central and Northern Europe.

**Platybelodon:** “flat tusk,” the most common shovel-tusked gomphothere, a genus of large proboscideans in the family Amebelodontidae; *Platybelodon* was similar to *Amebelodon*, another shovel-tusker; Africa, Europe, Asia, and North America; Miocene.

**Platyceratidae:** a family of cap-shaped gastropods in the order Euomphalina, often with irregular growth. Snail-like, they are notable for a symbiotic relationship since they are found only clinging to crinoids, usually on the calyx. Sometimes found near the anus, they may have been coprophagous, but their place of attachment is marked by a scar in some specimens and even a small hole in others, so that they may have been parasitic. Global distribution, Ordovician to Jurassic, and possibly later.

**platypus:** see *Ornithorhynchus*.

**Platyrrhini:** an infraorder of anthropoid primates that comprises the New-World monkeys. They are characterized by nostrils that face sideways and by prehensile tails. The Platyrrhini diverged from the Catarrhini in the late Eocene or early Oligocene, but they have remained primarily alike, an example of parallel evolution. South America, Eocene to Recent.

**Platysomidae:** a family of palaeonisciform fish in the suborder Platysomoidei; deep-bodied and vertically flattened, with ganoid scales; global distribution, Carboniferous to Triassic.

***Plectronoceras:*** “spur horn,” a genus of primitive chambered cephalopods in the subclass Nautiloidea and order Ellesmerocerida; the earliest-known nautiloid, it is known from only a few specimens and was evidently short-lived; its tapering conical shell was 1 inch high, with several septa and a siphuncle; its body plan was not yet well-adapted to swimming as the orthoconic shells of later nautiloids; North America, late Cambrian.

**Pleistocene:** the next-to-last epoch of the Cenozoic Era, variously considered to have begun between 2.6 and 1.8 Ma and lasting to 11,700 years before 2000 A.D.

**Plesiadapiformes:** a paraphyletic suborder of the oldest primates, appearing in the Cretaceous, diversifying rapidly in the late Paleocene, and then disappearing at the end of the Eocene; the suborder is generally considered to include the families Paromomyidae, Plesiadapidae, Microsyopidae, and Campodeidae; North America, Europe, Asia, and Africa.

***Plesiadapis:*** the type genus of the family Plesiadapidae, it is significant in being the only primate until *Homo sapiens* to inhabit both the Old and the New World; North America and Europe, late Paleocene to early Eocene.

**Plesiocidaroida:** an order of regular echinoids in the subclass Euechinoidea, poorly known but one of the groups of euechinoids diversifying in the Late Triassic after almost all echinoids became extinct at the end of the Permian; Italy and North Africa, Late Triassic, 240–220 Ma.

**plesiomorphy:** a character shared by an organism with primitive ancestors.

**Plesiosauridae:** the earlier of the two families of large marine reptiles in the order Plesiosauria (see **Elasmosauridae**); global distribution, Triassic to Late Cretaceous.

**Plesiosauria:** “near lizard,” an order of mainly marine reptiles in the superorder Sauropterygia; plesiosaurs grew to more than 40 feet long and had longer necks than tails; they used their four strong flippers to become especially efficient swimmers; appearing near the end of the Triassic, the plesiosaurs are related to the nothosaurs but directly descended from the pistosaurs; they flourished worldwide in the Jurassic and persisted to the end of the Cretaceous.

**Pleuracanthodii:** see **Xenacanthida**.

**pleural lobes:** the lateral segments of a trilobite’s body, on both sides of the thorax.

***Pleurodictyum:*** a genus of dome-shaped colonial tabulate corals in the family Favositidae; characterized by slender polygonal corallites; *P. problematicum* is usually found with the tubes of the worm *Hicetes* at the base of the colony, evidently

built on the tubes and possibly commensal with the worm; global distribution, late Silurian to Carboniferous.

**Pleurodira:** “side neck,” the smaller of the two still-extant suborders of turtles in the order Testudines; pleurodires are different anatomically from the cryptodires in several ways because of the lateral flexure of the head, withdrawing it to the side, in front of one of the forelimbs; Australia, Africa, and South America; Jurassic to Recent.

**Pleuromeiaceae:** a family of small trees 3–4 feet high, lycophytes that may be related to the Lepidodendrales and possibly ancestral to the modern Isoetaceae; *incertae sedis*, however, because of a scarcity of fossil specimens; global distribution, Carboniferous to Early Triassic.

**pleuronectiform:** having both eyes on one side of head, characteristic of many flat fish and bottom feeders.

**Pleurotomaria:** a large extinct genus of Paleozoic sea snails, gastropod mollusks in the still-extant superfamily Pleurotomarioidea; related to the modern abalone but characterized by a coniform or trochiform shell; global distribution, Early Jurassic to Early Cretaceous.

**Pliobates cataloniae:** a proposed species of hominoid in the family Pliobatidae, described in 2015 as being close to the divergence between lesser and great apes; dated at 11.6 Ma, this gibbon-like tree-dweller weighed about 10 pounds and has several skeletal similarities to hominids; Spain, middle Miocene.

**Pliocene:** the fifth and last epoch of the Cenozoic period, from 5.3 to about 2.6 Ma. Early hominins had appeared at the end of the Miocene, and many variants are found in Pliocene strata throughout Africa and Asia. The period saw the beginning of the decline of the large mammals of the Miocene, a decline which culminated in the Quaternary extinctions. The Panama land bridge joined the Americas about 3 Ma, resulting in great changes in the animal populations of the two continents (see Great American Biotic Interchange).

**Pliohippus:** a North American horse descended from Merychippus and ancestral to *Equus*; middle to late Pliocene.

**Pliohyracidae:** the largest family of early hyraxes in the order Hyracoidea; partly arboreal but several genera cow-sized; Africa, Eocene to Pliocene.

**Pliomera:** a well-known genus of phacopid trilobites in the family Pliomeridae. It is distinguished by a pentagonal glabella; small, raised eyes; up to two dozen thoracic segments; and a small pygidium. Argentina, Norway, Iran, Russia, and China; Early Ordovician, 479–472 Ma.

**Pliomeridae:** a family of Ordovician phacopid trilobites in the suborder Cheirurina; several subfamilies are monophyletic but others are uncertain; global distribution, Early to Late Ordovician.



***Pliopithecus***: a genus of early hominoid primates in the superfamily Pliopithecoidea; *Pliopithecus* appeared in Asia in the early Miocene and spread into Europe before disappearing about 10 Ma; although gibbon-like, it is not considered a direct ancestor of the gibbons; see ***Propliopithecus***.

**Pliosauroidae**: a suborder of marine sauropterygian reptiles in the order Plesiosauria, characterized by a relatively short neck and a massive skull; a 33-foot-long specimen found in the early twenty-first century is the first entire intact skeleton of a pliosaur; it was recovered at Spitsbergen, 800 miles from the North Pole; Europe, Africa, and Australia; Early Jurassic to Late Cretaceous.

***Plotosaurus***: “swimmer lizard,” a genus of mosasaurs in the order Squamata; strong swimmers, it was similar to ichthyosaurs but more closely related to turtles; known only from a complete skull and skeletal fragments found in Central California, it is estimated to have grown to as much as 40 feet long; synonym: *Kolposaurus*; United States, Late Cretaceous, 70–66 Ma.

***Pluricarpellatia***: a genus of flowering aquatic plants in the still-extant order Nymphaeales; found in the Crato Formation of Brazil and dated about 112 Ma, it is a basal angiosperm; with flowers, seeds, large leaves, and branching rhizomes, it resembles modern water lilies; Brazil, Early Cretaceous.

**Poaceae**: the large family of grasses, in the order Poales; see **grasses**; Late Cretaceous to Recent.

***Podokesaurus***: “swift-footed lizard,” a genus of very small saurischian dinosaurs in the superfamily Coelophysoidea; characterized by tiny forelimbs and long, delicate tail and neck, *Podokesaurus* was about 3 feet long; it is known only from two partial specimens, and identification as a genus separate from *Coelophysis* is debatable, but it is among the earliest dinosaurs found in Eastern North America; Early Jurassic.

***Poebrotherium***: “grass-eater,” a genus of even-toed ungulates in the family Camelidae; at 3 feet high, *Poebrotherium* was about the size of a goat, larger than its ancestor *Protylopus*; North America, late Eocene to early Oligocene.

***Pogonodon***: a genus of carnivorous feliform mammals in the family Nimravidae; weighing 50–80 pounds, with 2-inch canines, *Pogonodon* probably hunted from ambush; it was widespread in North America in the Oligocene and may have survived in Eurasia into the Miocene.

***Pojetaia***: a genus of small, primitive bivalve mollusks in the order Fordillida and family Fordillidae; suboval, less than one-tenth of an inch long; global distribution, early middle Cambrian.

***Polacanthus***: “many spines,” a contentious genus of ankylosaurian dinosaurs tentatively placed in the family Nodosauridae; poorly known from body fragments, it was quadrupedal, well-armored with dorsal spines, and estimated to be about 16



feet long; two *nomina dubia* associated with it are *Hylaeosaurus* and *Horshamosaurus*; England, Early Cretaceous, 130–125.

**polychaetes:** see **annelids** and **scolecodonts**.

**Polydolopidae:** a family of small South American marsupials in the order Paucituberculata, similar to the modern shrew opossums; South America and Antarctica, middle Paleocene to middle Eocene or possibly Oligocene (see also *Antarctodolops*).

**Polygnathidae:** a family of conodonts in the suborder Ozarkodinina; the family includes several genera that are important as index fossils; global distribution, Silurian to Late Triassic.

***Polygnathus costatus partitus*:** a species of ozarkodinid conodonts in the family Polygnathidae; the index fossil whose first appearance marks the beginning of the Middle Devonian at 393.3 Ma; global distribution.

***Polyodon spathula*:** the American paddlefish, a still-extant species of cartilaginous acipenseriform fish in the family Polyodontidae; averaging about 5 feet long, it is characterized especially by its paddle-shaped, elongated rostrum; the species is known from the Late Cretaceous and the middle Eocene Green River formation; North America, Cretaceous to Recent.

**polyphyletic group:** a group of organisms that do not derive from a single common ancestor in the group, so that the name of the group is used only informally. A monophyletic group is a clade consisting of an ancestor and all of its descendants, as opposed to a paraphyletic group, which consists of a common ancestor and some but not all of its descendants. Paraphyletic groupings are still useful; for instance, dinosaurs and birds are paraphyletic but obviously greatly different from each other.

**polyphyodonty:** see **dentition**.

**Polyplacophora:** the chitons, a still-extant class of marine mollusks known from the Cambrian but with a sparse fossil record; synonym: Amphineura. They are characterized by an oval, flattened body covered with a dorsal shell of 7 or 8 calcareous, slightly overlapping plates. See also *Wiwaxia*. Global distribution, Cambrian to Recent.

**polyprotodont:** an informal term used for a diverse grouping of primitive marsupials that arose in the Cretaceous and was succeeded by the diprotodonts.

***Pondaungia*:** a species of small, primitive haplorrhine primates in the family Amphipithecidae; synonym: *Amphipithecus*; probably frugivorous, similar in some ways to the adapiform primates of North America; Burma, early Eocene.

**Porifera:** the phylum of sponges. Whether the phylum is monophyletic is in dispute, but it is generally considered to date from the late Precambrian, with definitive specimens appearing in the early Cambrian. It contains several classes: Hexactinellida, Calcarea, Sclerospongiae (polyphyletic), and Demospongiae. The

Archaeocyatha, Heteractinida, Stromatoporoidea, and Receptaculitidae are also considered sponges in some classifications.

**Porocharaceae:** a family of charophytic algae in the order Charales, probably ancestral to the post-Paleozoic family Raskyellaceae and others; cosmopolitan, Carboniferous to Cretaceous.

**Poroxylaceae:** a monogeneric family of pteridospermous plants formerly assigned to the Cordaitales but now considered progymnosperms or seed ferns; global distribution, Carboniferous.

**Posidonia Shale:** see **Holzmaden**.

**Postosuchus:** “crocodile from Post,” a genus of large archosauromorph reptiles in the family Rauisuchidae. Most specimens come from the Post Quarry in West Texas, but others have been found across the Southern United States. Up to 15 feet long and 4 feet high, *Postosuchus* is variously estimated to have weighed between 600 and 1500 pounds and was one of the dominant predators of the Triassic in Southwestern North America. Its forelimbs were somewhat shorter than the hindlimbs but were robust enough to enable it to walk either bipedally or quadrupedally. North America, Late Triassic, 222–201 Ma.

**Precambrian Eon:** the long period of geologic time preceding the Paleozoic Era, up to 541 Ma. There are signs of organic life as far back as 4 billion years, and fossils of bacteria as old as 3.5 billion years. The first structurally complex eukaryotes appeared about 1.5 billion years ago, but the first multicellular animals came much later, around 700 Ma. The last part of the Precambrian, the Ediacaran Period (630–541 Ma), is marked by rapidly diversifying marine animals.

**preservational environment:** a depositional environment that fosters the preservation of fossils, especially in relation to the degree of acidity in the soil or marine strata, since high acidity tends to dissolve bone and other organic remains.

**Priapulida:** a still-extant phylum of burrowing marine worms; characterized by a tubular shape, spines around the mouth, and an extensible, spiny feeding proboscis; some species are tolerant of anoxia and hydrogen sulfide; stem-group priapulids are known from Cambrian strata, with the earliest crown-group specimens appearing only in the Late Pennsylvanian; see also *Ottoia*; global distribution, Late Carboniferous to Recent.

**Pricyclopyge:** a genus of small deep-ocean trilobites in the order Asaphida and family Cyclopygidae; characterized by a broad glabella and very large eyes, it may have swum upside down; Europe and Asia, Early to Late Ordovician.

**Primelephas:** a genus of primitive elephants with four tusks in the subfamily Elephantinae; one of the first elephants, probably ancestral to the Mammutioidea and to modern elephants; similar to the gomphotheres; Africa, Miocene to Pliocene.

**Primitiopsis:** a genus of dimorphic ostracods in the order Paleocopida; it probably lived in the deep subtidal zone; cosmopolitan, Late Devonian and Silurian.

**primitive features:** characteristics of an organism that are relatively close to those of its ancestors, as opposed to advanced features.

**Prioniodontida:** a clade of conodonts with composite teeth, including the suborders Ozarkodinina, Prioniodinina, and others; global distribution, Early Ordovician to Triassic.

**Prionocylus:** a genus of ammonoids in the order Ammonitida and family Collignoniceratidae; ranging in size between 2 and 4 inches, several species are index fossils for the Turonian Stage of the Late Cretaceous; global distribution, 94–90 Ma.

**Prionosuchus:** a genus of very large temnospondyls in the family Archegosauridae; the largest amphibian at an estimated 30 feet long, it is known from two partial specimens; Brazil, middle Permian.

**Priscacara:** a genus of freshwater actinopterygian fish in the still-extant family Cichlidae; of medium size, it is characterized by a flattened oval body and spiny dorsal, anal, and ventral fins; North America, early to late Eocene.

**Priscansermarinus:** “ancient sea goose,” a monospecific genus of crustacean arthropods similar to the modern gooseneck barnacle and classified in its order, Pedunculata; *P. barnetti* is known only from the Burgess Shale and is considered the oldest known barnacle; Canada, middle Cambrian, 508 Ma.

**Pristerodon:** a genus of dicynodont therapsids, type species *P. mackayi*; about 2 feet long but only a few inches high, the herbivorous *Pristerodon* seems to be one of the first animals able to hear airborne sounds, as opposed to vibrations in the ground; Southern Africa and India, late Permian.

**Proailurus:** a genus of cat-like carnivores, close to the ancestry of the Felidae, probably ancestral to *Pseudaelurus*; about the size of a lynx but with slender limbs and a long tail; partially arboreal; Europe and Asia, late Oligocene to Miocene.

**Proanura:** an order of amphibians ancestral to the modern order Anura, the frogs; a very sparse fossil record leaves their phylogeny questionable; the only recognized Mesozoic proanuran is *Triadobatrachus*, a Triassic amphibian from Madagascar; authorities disagree as to whether the Temnospondyli, the Lepospondyli, or some other Paleozoic group may be the ancestors of the Anura, which appeared in the Jurassic.

**Probactrosaurus:** a genus of Cenomanian ornithischian dinosaurs, one of the smallest and earliest hadrosaurs; about 18 feet long and weighing up to a ton, it was principally quadrupedal, with long and slender forelimbs; similar in several ways to *Iguanodon*, the ancestor of the hadrosaurs, but with a thumb spike and weaker forelimbs; China, Late Cretaceous, 96–88 Ma.

**Probainognathus:** “advanced jaw,” a monospecific genus of small cynodont therapsids; carnivorous and the size of a very small dog, *P. jenseni* is one of the earliest therapsids to have a squamosal-dentary jaw joint similar to the typical mammalian

structure; it may be related to the Chiniquodontidae; Argentina and Brazil, Late Triassic, 235–220 Ma.

***Probathyopsis***: a basal uinthere, a small genus of early dinoceratan ungulates, closely related to the Asian *Prodinoceras*; North America, late Paleocene to early Eocene.

***Probesodon***: a genus of early cynodonts in the family Chiniquodontidae; dog-sized, one of the larger chiniquodontids; South America, Middle to Late Triassic.

**Proboscidea**: an order of mammals that originated in Africa in the early Eocene and had achieved nearly global distribution by the middle Miocene. The earliest proboscideans, such as *Moeritherium*, were trunkless, but Oligocene species such as *Paleomastodon* had a rudimentary trunk and short tusks. The order includes the two surviving species of elephants as well as the extinct mammoths, gomphotheres, deinotheres, and possibly the desmostylians.

**Procaviidae**: the modern family of hyraxes, known principally from Africa, where some of their ancestors in the Pliohyracidae had evolved into sirenians and elephants; Africa, Europe, and Asia; Miocene to Recent.

***Proceratops***: see **Ceratopsia**.

**Procolophonia**: a suborder of small herbivorous reptiles related to the Pareiasauria; formerly included in the paraphyletic order Captorhinida; the colophonids were about a foot long with large eyes and were probably fossorial; they survived the end-Permian extinction and diversified in the Triassic; South Africa, Antarctica, and Brazil; late Permian to Late Triassic.

***Proconsul***: a genus of arboreal hominoid primates in the family Proconsulidae; about the size of a modern baboon, *Proconsul* was sexually dimorphic and bore characteristics of both monkeys and apes; the four named species differ mainly in body size, the specimens ranging from 10 to 150 pounds; possibly ancestral to *Propliopithecus* and later primates, including humans; Kenya and Uganda, early Miocene, 23–25 Ma.

***Procoptodon***: a genus of short-faced kangaroos in the family Macropodidae and extinct subfamily Sthenurinae; the genus includes the smallest of the Sthenurinae, *P. gilli*, while *P. goliath* was about the same size as *Sthenurus*, weighing more than 500 pounds; they probably moved more slowly than modern kangaroos; Australia, Pliocene to late Pleistocene.

***Procynosuchus***: “before dog-crocodile,” a genus of basal cynodont therapsids in the family Procynosuchidae; the size of a cat, it was quadrupedal and was probably semi-aquatic; it was notable for a very primitive dentition and a long tail; Europe and Africa, Late Permian.

***Prodinoceras***: a genus of basal uinthere ungulates in the order Dinocerata; they were about 10 feet long and very similar to *Probathyopsis* of North America; Mongolia, late Paleocene.

***Prodryas persephone***: a species of lepidopterans in the family Nymphalidae, a butterfly known from a single, unusually well-preserved specimen found in the Florissant Fossil Beds; about an inch wide, the specimen shows the wing venation and even the original color patterns; United States, late Eocene.

**Productida**: a large order of late Paleozoic articulate brachiopods; a very diverse order containing a wide range of shapes, generally characterized by concave-convex shells and by spines on the surface; global distribution, Ordovician to Triassic.

**Proetida**: an order of generally small trilobites, very similar to the Ptychopariida; characterized by a narrow rostral plate and a high, sometimes pitted, glabella, most were less than an inch long; the only order of trilobites to survive the Devonian extinction, the Proetida diversified and persisted through the Carboniferous and Permian, but they disappeared from the fossil record shortly before the end-Permian extinction; global distribution, Early Ordovician to Permian.

***Proganochelys***: a genus of stem-turtles in the order Testudines; dated at 210 Ma, it is the oldest turtle found with a complete shell, carapace and plastron; it was different in several ways from modern turtles; about 3 feet long, it had a spiked tail ending in a club and was probably mainly terrestrial; Europe and Asia, Late Triassic.

**Proganosauria**: see **Mesosauria**.

***Prognathodon***: a genus of squamatan reptiles in the family Mosasauridae. Several species of these large mosasaurs, ranging from 20 to more than 40 feet long, were widespread at the end of the Cretaceous, preying on fish, ammonoids, other shellfish, and turtles. Skulls and teeth from phosphate deposits near Khouribga, Morocco, are well-known as commercial specimens. Two almost-complete specimens from Canada show fins and stomach contents, including a 5-foot-long fish. *Prognathodon* is similar to *Globidens* in its shape and in a robust skull, and its teeth also are specialized for crushing shellfish, although sharper-pointed than the blunt teeth of *Globidens*. North America, Eurasia, Africa, and New Zealand; 71–66 Ma.

**progymnosperms**: woody, spore-bearing plants intermediate between ferns and gymnosperms; global distribution, Middle Devonian to Mississippian.

**Prokennalestes**: a poorly known genus of basal eutherian mammals, considered a possible ancestor of *Kennalestes*; known only from an individual ear bone; China, Early Cretaceous, 120 Ma.

**Prolacertiformes**: see **Protosauria**.

**Prolecanitida**: one of the longer-lived and most speciose orders of ammonoids, with more than 1200 species; discoidal or thinly lenticular, they are notable for the increasing complexity of their suture from the Devonian to the Permian; global distribution, Late Devonian to Late Triassic.

***Promicroceras***: a small genus of ammonoids in the order Ammonitida and family Eoderoceratidae; characterized by strong ribbing and small spines; one of the

common fossils of the Sinemurian stratum on the Dorset coast, between 199 and 192 Ma; England, Early Jurassic.

***Promissum pulchrum***: a species of conodonts in the suborder Prioniodinina; one of the few known fossil imprints of the animal and the largest known at 16 inches long; Soom Shale, South Africa; Late Ordovician.

**pronghorn**: see **Antilocapridae**.

***Pronucleolites***: see **Nucleolitidae**.

***Proplaeotherium***: a genus of very small perissodactyl mammals at first classified in Palaeotheriidae but in 2004 placed in Equidae; it was found in the Messel Shale Pit in 1849 and later across Europe and in China; a forest browser on leaves and berries (found with its stomach contents), it stood 1–2 feet high at the shoulder and weighed only about 22 pounds; hoofless, it had nail-like hooflets at the ends of the toes, four on the manus and three on the pedes; Europe and Asia, Eocene.

***Proplebeia dominicana***: a species of stingless bee found in amber deposits in the Dominican Republic; its successfully reconstituted and copied DNA, 40 million years old, is the oldest yet recovered for study; Caribbean, late Eocene.

***Propliopithecus***: a genus of early anthropoid primates in the family Pliopithecidae, possibly ancestral to the early hominins; only 1.5 feet long and with stereoscopic vision, it was more advanced than the earliest primates; it was probably ancestral to *Pliopithecus*, and was closely related to the early Oligocene *Aegyptopithecus*; North Africa, middle to late Oligocene.

**Prorastomidae**: a family of primitive sirenians, possibly ancestral to the modern dugongs and manatees; known only from two Jamaican specimens, the partly terrestrial *Pezosiren* of the early Eocene and the fully aquatic *Prorastomus* of the middle Eocene.

***Prorichthofenia***: an unusual genus of reef-forming strophomenid brachiopods in the order Productida and family Richthofeniidae; characterized by their conical, horn-shaped pedicle valve, with the upper valve acting as a lid covering the cone; North America and Europe, middle to late Permian.

***Prorubidgea***: a synonym of *Aelurognathus*.

***Prosaurolophus***: a genus of duck-billed dinosaurs in the subfamily Saurolophinae; medium-sized hadrosaurids, they were about 30 feet long and had a prominent crest above the eyes; North America, Late Cretaceous, 76–73 Ma.

**prosauropods**: the first sauropod dinosaurs, which were among the first dinosaurs to evolve from the theropods at the end of the Middle Triassic. Prosauropods developed and spread rapidly, the large *Plateosaurus* and others surviving the Triassic extinction, followed by *Anchisaurus* in the Early Jurassic and then by the sauropods themselves, which eventually achieved global distribution and some of which were

among the largest of all dinosaurs. See also *Nyasasaurus* and *Herrerasaurus*. Triassic to Cretaceous.

**Prosimii:** see **Strepsirrhini**.

**Protarchaeopteryx:** a species of coelurian theropod dinosaurs in the infraorder Oviraptorosauria; probably flightless although it had long, bird-like legs and true feathers on body, wings, and tail; more than 3 feet long, it was larger and more primitive than *Archaeopteryx* but lived 10 million years later; one of several feathered dinosaurs in the Jehol biota; China, Early Cretaceous, 125 Ma.

**protaspis:** the hatching ontogenetic phase of trilobites; see also **holaspis** and **meraspis**.

**Proteroctopus:** a monospecific genus of cephalopods tentatively placed in the family Palaeoctopodidae; if *P. ribeti* is an octopus, it is the oldest known; known only from one specimen found at La Voulte-sur-Rhône; France, Middle Jurassic.

**Proterosuchidae:** a family of reptiles, probably paraphyletic but considered basal archosaurs. When most large therapsids became extinct at the end of the Permian, the proterosuchids became the largest carnivores and flourished at the beginning of the Triassic; they were replaced by phytosaurs and crocodylians in the Middle Triassic. Global distribution except North America, late Permian to Middle Triassic.

**Proterosuchus:** one of the earliest archosaurs, in overall appearance similar to modern crocodiles except for its distinctive hooked premaxilla; up to 7 feet long with long jaws, it was one of the largest land reptiles of its time; first found in the Karoo Basin of South Africa and now known also from China; Early Triassic, 252–250 Ma.

**Proterotheriidae:** a diverse family of horse-like South American ungulates in the order Litopterna; the proterotheres arose in the Paleocene and flourished in the Eocene before declining in the Miocene; most genera became extinct in the Pliocene at about the time that true horses arrived in South America; one genus, however, survived in Argentina and Uruguay into the Pleistocene.

**Protichnites:** see *Diplichnites*.

**protists:** an informal group of unrelated simple, eukaryotic organisms that are not animals, plants, or fungi; they are microscopic and chiefly aquatic.

**Protoavis:** a contentious specimen with a bird-like skull and other bird-like features. Dated at 225 Ma, it has been proposed as an early avian evolutionary branch from the time of the earliest dinosaurs, but since it is known from only an assortment of fragments, its reconstruction is questionable. The tentative reconstruction indicates an animal 1–2 feet long. Although it is unclear whether it had a true wishbone, *Protoavis* seems unlikely to be ancestral to modern birds. Post Quarry, Texas, Middle to Late Triassic.



**Protoceratidae:** a long-lived family of herbivorous artiodactyl ungulates; the males were notable for a pair of rostral horns near the nose as well as a pair of horns at the back of the head; they had relatively long limbs and resembled deer and elk, growing up to 6 feet long; North America, middle Eocene to early Pliocene.

**Protoceratopsidae:** a family of ornithischian dinosaurs in the suborder Ceratopsia; herbivorous, with the characteristic ceratopsian neck frill and large skull, but only up to 9 feet long; known only from Asia, Late Cretaceous, 100–70 Ma.

**Protocetus:** a genus of archaeocete cetaceans in the family Protocetidae, one of the earliest oceangoing whales, fully aquatic and bearing only vestigial limbs that probably could not have supported its weight on land. Like the deep-ocean *Rodhocetus*, *Protocetus* had unfused sacral vertebrae, so that it could use its tail efficiently for propulsion in the water. In addition, it had the advanced character of vestigial hindlimbs unattached to the backbone. Egypt, middle Eocene.

**protoconodonts:** an obscure group of small animals that may be either the earliest conodonts or a stem group of Chaetognatha; they seem at least quite different from the euconodonts; cosmopolitan, late Precambrian to Early Ordovician.

**Protodonata:** see **Meganisoptera**.

**Protoeumalacostraca:** an obscure group of early crustaceans that are thought to be the stem group of the subclass Eumalacostraca, which includes most of the living crustaceans; the eumalacostracans appeared in the Devonian, but their predecessors remain in doubt.

**Protopteridales:** an order of fern-like plants in the class Polypodiatae; eusporangiate, producing sporangia at the edges of their leaves, and herbaceous or woody; now considered to be related to the Rhyniales; cosmopolitan, Devonian.

**Protorosauria:** an order of archosauromorph reptiles that flourished in the Triassic; synonym: Prolacertiformes. They are generally characterized by very long necks and short bodies (see *Tanystropheus*). Some families, such as the Tanystropheidae, are 15–20 feet long, while the Drepanosauridae are only 1–2 feet long. The Protorosauridae of the late Permian, which were about 7 feet long, are the earliest-known archosauromorphs. South America, Europe, and Asia; late Permian to Late Triassic.

**Protosalvinia:** a genus of early land plants; similar to some phaeophytes (brown algae) but generally considered one of the earliest bryophytes, probably a liverwort; known from several Late Devonian specimens found in North and South America.

**Protosirenidae:** a monogeneric family of aquatic mammals in the order Sirenia; like their descendants the manatees, the protosirenians inhabited temperate to tropical waters; *Protosiren* had hindlimbs, which have disappeared in the modern species; the type species of the genus is *Protosiren fraasi*; North America, Europe, and Asia; Eocene.



**Protosuchia:** a group of small to medium-sized archosaurian reptiles in the super-order Crocodylomorpha; about 3 feet long, they were slender and terrestrial; global distribution, Late Triassic to Early Cretaceous.

**Protosuchus:** a genus of basal crocodylomorphs that appeared near the boundary of the Triassic and Jurassic; primarily terrestrial, *Protosuchus* was 3 feet long and moderately armored, and its hindlimbs were somewhat longer than its forelimbs; North America and Africa, Early Jurassic.

**Prototaxites:** an enigmatic genus of large, mid-Paleozoic tree-like structures; estimated to be as much as 3 feet in diameter and 26 feet high, they were named “early yew” because of the long, intertwined tubes that formed the trunk, resembling the proto-vascular structure of other early plants such as the Calamitales or Nematophyta; now considered probably fungal or algal; North America, Europe, and Saudi Arabia; Late Silurian to Late Devonian, 420–370 Ma.

**Prototheria:** an obsolescent term for a subclass of mammals that includes the order Monotremata; Late Triassic to Recent.

**Protungulatum:** a genus of early ungulate mammals, considered a non-placental eutherian; rat-sized, *Protungulatum* had a distinctive foot structure and crushing molars designed for eating plants; probably related to the arctocyonids; North America, Late Cretaceous to Paleocene.

**Protura:** “primitive tail,” an enigmatic still-extant order of very small soil-dwelling insect-like animals tentatively placed in the phylum Hexapoda; less than 2 mm long and eyeless, they have no antennae or pigmentation; they are characterized by six legs, a cylindrical body, and a conical head; their fossil record is very sparse, but they are thought to be primitive hexapods, going back perhaps to the Early Devonian.

**Protylopus:** a genus of even-toed ungulates in the family Camelidae; one of the earliest camelids, it was about the size of a rabbit; North America, middle Eocene.

**proximal:** referring to a body part of a bilaterian animal that is closer to the center of the body than a distal part; in plants, referring to an area near the point of attachment.

**Psammodontidae:** a family of holocephalic fish; characterized by bradyodont dentition consisting of rectangular toothplates in two rows meeting at the midline; North America and Europe, late Devonian to late Permian.

**Psammosteidae:** a family of heterostracan fish of the Devonian; with a round and flattened body, they ranged in size from the early genus *Drepanaspis* (about 1 foot long) to some at the end of the Devonian that were 6 feet long; they were the only heterostracans that survived the Frasnian extinction, but were finally extinguished in the Hangenberg Event at the end of the Famennian Stage; global distribution, Early to Late Devonian.

**Psarolepis:** an enigmatic early genus of lobe-finned fish; it exhibits a combination of osteichthyan and non-osteichthyan gnathostome characters; perhaps a basal oste-

ichthyan, close to the common ancestry of sarcopterygians and actinopterygians; China, dated as early as 418 Ma, at the beginning of the Devonian.

***Psaronius***: a genus of tree ferns in the still-extant order Marattiales; the name originally referred to only the stem. Growing more than 30 feet high, *Psaronius* has trunk specimens as large as 3 feet in diameter at the base. It is notable for the structure of its trunk, which consisted of many thin roots intertwined with stems, somewhat similar to the manner of *Tempskya*. The leaves grew in a crown at the top of the trunk and are known mainly as the form genus *Pecopteris*, with the leaves of some species classified as the form genus *Sphenopteris*. Global distribution, Late Carboniferous to late Permian.

***Pseudaelurus***: a genus of Miocene mammals in the family Felidae, the first felid to appear in North America; early species were the size of a domestic cat, while later ones reached the size of a cougar; North America, Europe, and Asia, early to late Miocene.

**Pseudoborniales**: an early order of sphenopsid plants in the class Equisetopsida, growing to 60–75 feet; cosmopolitan, known only from the Late Devonian.

***Pseudocidaris***: a genus of sea urchins, Mesozoic euechinoids in the family Hemicidaridae; *P. mammosa* is famous for its bulbous, club-shaped spines; Europe, Africa, and Asia; Middle Jurassic to Early Cretaceous.

**Pseudosuchia**: a clade now considered to include living crocodylians as well as the reptiles that arose in the Early Triassic and dominated the terrestrial carnivorous niches of the Late Triassic, including the rauisuchians; all except the Sphenosuchia and Crocodyliformes were extinguished in the Triassic extinction; cosmopolitan, Triassic to Recent.

***Psigraptus jacksoni***: a species of anisograptid graptolites, notable for specimens of three-dimensional pyritized remains of zooids; the specimens show, however, no tentacles or other morphological details; Australia and Korea, Early Ordovician.

***Psiloceras spela* group**: a group of smooth ammonitid ammonoids in the family Psiloceratidae; its first appearance marks the beginning of the Early Jurassic at 201.3 Ma; Austria.

**Psiloceratidae**: a family of ammonoids in the order Ammonitida, probably descended from the Ussuritidae; psiloceratids generally have a smooth surface or blunt ribbing; cosmopolitan, Early Jurassic.

***Psilophyton***: a genus of fern-like tracheophytic plants in the class Trimerophytopsida and family Psilophytaceae; among the first vascular plants, they grew from underground rhizomes, with naked branches and a spore-producing structure at the tips of branches; *P. forbesii* is the largest known at about 2 feet, but most were 1 foot high; North America, Europe, and Asia; Late Silurian to Late Carboniferous.

***Psittacosaurus***: a speciose genus of Asian ceratopsian ornithischian dinosaurs in the family Psittacosauridae. It includes more species than any other dinosaur genus

and is also one of the most completely known dinosaur genera because known from several complete skeletons and hundreds of individual specimens. It is the most common dinosaur in the Jehol biota. *Psittacosaurus* was bipedal, generally 6–7 feet long, and characterized by a large, parrot-like beak. Early in the Cretaceous, probably around 130 Ma, the psittacosaurids split off from the neoceratopsian branch which led to the familiar horned and frilled ceratopsians of the Late Cretaceous. See also *Liaoceratops*. China, Mongolia, and Siberia; Early Cretaceous, 123–100 Ma.

***Pteranodon*:** “toothless wing,” a genus of large pterosaurs in the suborder Pterodactyloidea; they were toothless and had a large beak and a large cranial crest, and the largest species had a wingspan up to 23 feet; they are especially well-known, with more well-preserved specimens known than any other pterosaur; North America and Europe, Late Cretaceous, 86–84 Ma.

***Pteraspis*:** “wing shield,” a genus of small, jawless fishlike vertebrates in the subclass Heterostraci and order Pteraspidiformes. They were finless except for small wing-like protrusions at the sides of the shield over the gills, which may have aided in swimming. They are also characterized by a striking medial dorsal spine extending backward from the wide shield that protected the forward half of the body; the rest of the 7-inch-long body was covered by small scales. North America and Europe, Early Devonian.

***Pterichthyodes*:** a genus of freshwater antiarch placoderms in the family Asterolepidae; distinguished by jointed wing-like appendages extending outward on both sides of the head; it had a heterocercal tail fin and eyes on top of the head-shield; up to a foot long, it had heavy anterior armor and scales on the posterior, differing from its cousin *Bothriolepis*, which was posteriorly naked, with no scales; it may have used its pectoral appendages to pull itself along the bottom; known only from Scotland, Middle Devonian.

**Pteridospermatophyta:** the seed ferns, a large extinct group of gymnosperms similar to tree ferns except that they bore seeds and pollen-bearing structures on the fronds. Currently four orders are recognized: Callistophytales, Lyginopteridales, Medullosales, and Peltaspermales. Some similar plants survived to the Eocene, but the relationship is unclear. The seed ferns have also been called Cycadofilicales and sometimes Pteridospermae. Global distribution, Late Devonian to Cretaceous, but an especially important part of Carboniferous floras.

**Pterobranchia:** a still-extant class of small, worm-like colonial animals in the subphylum Hemichordata. Phylogenetic analysis indicates that they are related to the graptolites, but they differ in morphology and habits. The benthic pterobranchs usually secrete tube-stalks which they extend to filter-feed. Families: Atubaridae, Cephalodiscidae, and Rhabdopleuridae. Global distribution, early Cambrian to Recent.

**Pterodactyloidea:** a large suborder of flying archosaurs in the order Pterosauria; generally tail-less and much larger than the basal pterosaurs of the Late Triassic; several later genera were toothless; many had large crests, and their wingspan

ranges from a few inches to as much as 40 feet (see *Quetzalcoatlus*); Europe and China, Middle Jurassic to Late Cretaceous.

**Pterodactylus:** “finger wing,” the type genus of flying pterosaurs of the suborder Pterodactyloidea; Europe and Africa, Jurassic and Cretaceous.

**Pterosauria:** an order of archosaurs distinguished by the leathery membranes stretched between extremely elongated fingers that enabled them to glide or soar. They are traditionally divided into two suborders, the rhamphorhynchoids and the Pterodactyloidea, but only the latter is monophyletic. The wingspan of the pterosaurs ranged from a few inches to as much as 45 feet. Pterosaurs were carnivorous and especially piscivorous, and many families were toothless.

They were not dinosaurs and not birds, but evolved along with dinosaurs from a common ancestor in the Late Triassic. Because their bones were bird-like — thin-walled and slender — the fossil record is less complete for some pterosaurs than for most archosaurs. Their eggs are extremely rare, but several discoveries since 2004 have shown that the parents may have buried eggs; whether they were altricial or not is also unclear. The exact shape of their “wings” and their mode of flying is still unclear. Some investigators believe they had unusually large flocculi, brain lobes that link brain activity with body movement, and that their flocculi may have enabled them to fly more efficiently than modern birds and bats.

About 100 species are known, the earliest being dated at the Carnian-Norian boundary in the Late Triassic, about 230 Ma. They flourished worldwide during the Jurassic but were dying out by the late Cretaceous.

**Pterygotidae:** a family of marine arthropods in the extinct order Eurypterida. Large sea scorpions, they had 2 pairs of eyes and a short, flattened telson ending in a short spine. They swam with their tail and two paddle-like appendages, for which they were named. The largest known is *Jaekelopterus*, estimated at 8 feet, and a 2009 discovery, *Ciurcopterus*, may be larger. Global distribution, Silurian to Late Devonian.

**Pterygota:** the winged insects, a subclass of the class Insecta; the pterygote insects are unrelated to the Pterygotidae, sea scorpions, except as arthropods; traditionally divided into the infraclass Neoptera and the paraphyletic group Palaeoptera but now reclassified in different ways which are still unsettled.

**pterygote:** referring to winged or secondarily apterous insects.

**pterygotid:** referring to the marine arthropods in the family Pterygotidae.

**Pterygotus:** a genus of large marine arthropods in the family Pterygotidae; its specimens are 5–6 feet long; North and South America, Europe, and Australia; Silurian to Devonian.

**Ptilodontoidea:** a group of multituberculate mammals in the suborder Cimolodonta; generally small and rodent-like, poorly known but probably derived from the Plagiaulacida; North America and Europe, Late Cretaceous to Eocene.

***Ptilodus***: a North American multituberculate in the family Ptilodontidae; squirrel-like and 1–2 feet long, it was widespread across North America, early to late Paleocene.

***Ptychagnostus***: a genus of very small, blind agnostid trilobites in the family Ptychagnostidae; less than half an inch long, it is characterized by 2 segments in the glabella and 3 in the pygidium; it was nektonic, generally living in the water column; global distribution, middle Cambrian.

***Ptychodus***: “layer tooth,” a genus of early sharks in the extinct superfamily Hybodontoidae and family Ptychodontidae; about 30 feet long, *Ptychodus* was characterized by its unusual dentition, which consisted of thousands of flat molar teeth, evidently used to crush bivalves and crustaceans; cosmopolitan, Cretaceous to Paleocene.

***Ptychopariida***: a large early order of trilobites that appeared, along with the Redlichiida and Corynexochida, early in the Cambrian; diverse but generally characterized by an oval shape and small pygidium; global distribution, early Cambrian to Late Ordovician.

***Ptyctodontidae***: “folded teeth,” a family of placoderm fish in the monotypic order Ptyctodontida, related to the Arthrodira and Phyllolepidia; weakly armored on head and shoulders and the only sexually dimorphic placoderms, the males having hook-like claspers on their pelvic fins; they had large eyes, heads, and bodies; now considered the most derived placoderms, they may be ancestral to the jawed vertebrates; cosmopolitan, Middle to Late Devonian.

***Puertasaurus***: a genus of titanosaurian sauropodomorph dinosaurs closely related to *Argentinosaurus*; known only from skeletal fragments of one individual, it is estimated to have been massive and 100–130 feet long; Argentina, Late Cretaceous, Cenomanian or Maastrichtian.

***Pugnax***: a genus of articulate rhynchonellid brachiopods in the family Pugnacidae; about 1 inch wide, generally characterized by a sub-triangular shape and strong central ribs, often with a smooth shell; global distribution, Devonian to Permian.

***Puijila***: a genus of ancestral pinnipeds, the most primitive relative of the Phocidae, the earless seals; otter-like and semi-aquatic, it had a tail and four legs with enlarged feet; see also *Enaliarctos*; Canada, late Oligocene to Miocene.

***Pulmonoscorpius kirktonensis***: a species of giant terrestrial scorpions more than 2 feet long; Scotland, Carboniferous, 320 Ma.

**punctate**: pierced by pores; in brachiopods, a condition in which elongated, regularly arranged cavities extend from the inside of the shell to the outside; although all terebratulids are punctate and all atrypids and pentamerids are impunctate, the condition cuts across the other systematic boundaries.

**punctuated equilibrium:** the evolutionary model that sees most change as occurring in brief bursts of evolutionary diversification, with longer periods of stasis in between; see also **phyletic gradualism**, **anagenesis**, and **uniformitarianism**.

***Purgatorius:*** a genus of small mammals in the order Plesiadapiformes; possibly the last common ancestor of primates and plesiadapids; North America, Late Cretaceous to early Paleocene.

***Purpuroidea:*** a genus of Mesozoic prosobranch gastropods in the clade Littorinimorpha and extinct family Purpurinidae; traditionally classified in the Mesogastropoda; generally characterized by a thick, robust shell almost 3 inches high, with a series of short, blunt spines on the top half and fine spiral ribs on the bottom; cosmopolitan, Jurassic and Cretaceous.

**Pycnodontiformes:** “flattened tooth,” an order of laterally compressed actinopterygian fish; flourishing in the Jurassic and Cretaceous, the pycnodonts were small to medium-sized fish, characterized by their almost circular shape and round and flattened teeth; global distribution, Late Triassic to Eocene.

**Pycnogonida:** the sea spiders, a class of marine arthropods usually placed in the subphylum Chelicerata; not arachnids but closer to them than to other arthropods, they have small bodies and generally 4 pairs of long legs; their size ranges from less than an inch to 3 feet; cosmopolitan but especially large in the Antarctic, late Cambrian to Recent.

**Pygasteridae:** Mesozoic sea urchins, a family of irregular euechinoids in the extinct order Pygasteroidea; in the type genus *Pygaster*, the large periproct is keyhole-shaped; Europe, Middle Jurassic to Late Cretaceous.

**pygidium:** the tail segment of an arthropod, such as a trilobite.

**pygostyle:** the ploughshare-shaped element of fused bones at the base of the tail of modern birds.

**Pyrotheria:** an order of large South American ungulates that includes two small families, the Pyrotheriidae and the Colombitheriidae; sometimes called “false elephants,” they were characterized by short, columnar limbs and snouts a foot long; Paleocene to Oligocene.

## Q

**Quadrijugatoridae:** a family of palaeocopan ostracods in the order Beyrichicopina and superfamily Hollinoidea; Canada, Late Ordovician.

**Quagga:** a subspecies of African plains zebras, perissodactyls in the genus *Equus*, that became extinct in the middle of the nineteenth century.

**Quaternary extinctions:** the relatively abrupt extinctions of most of the large mammals in all continents during the middle and late Pleistocene; most of these extinctions occurred after the arrival of hominins, although some researchers have pointed also to climate change or other factors as partial causes.

**Quaternary Period:** the current division of geologic time, including essentially the Pleistocene Epoch and the current historical epoch, which is often referred to as the Holocene and dated from about 12,000 years before the present. The Quaternary is of course marked by the spread of modern hominins, and by the extinction of many large terrestrial animals.

**Quetzalcoatlus:** a genus of large pterosaurs in the suborder Pterodactyloidea and family Azhdarchidae; characterized by a very long neck and a sharp-pointed beak, *Quetzalcoatlus* had a wingspan of 40 feet; it closely resembles the Romanian discovery *Hatzegopteryx*; North America, Late Cretaceous, 68–66 Ma.

# R

**radiation:** the evolutionary pattern of rapid appearance and dispersal of many diverse species of a lineage.

***Radinskya*:** an obscure genus of primitive mammals generally placed in the Laurasiatheria; known only from a partial skull and jaw, it was the size of a small dog and is thought to be evidence of the radiation of the perissodactyls from Asia; China, late Paleocene.

**Radiolaria:** a subclass of marine protists in the phylum Retaria, from 0.1 to 0.2 mm in diameter; radiolarians are important stratigraphically in the absence of calcareous microfossils, but even their siliceous skeletons are dissolved by high concentrations of carbon dioxide in the ocean; global distribution, Cambrian to Recent.

***Radiolites*:** a genus of rudistid bivalves in the order Hippuritoida and family Radiolitidae; up to a foot long, with valves that were unequal in size and shape, it was one of the unusual horn-shaped bivalves that were important reef-forming organisms in the Cretaceous; Europe, Asia, and North and South America; Early to Late Cretaceous.

**radiometric dating:** the technique of using the known rate of decay of radioactive isotopes to establish, within certain limits of certainty, the absolute age of strata of Earth's surface; used with biostratigraphic information to establish the geologic time scale.

**radula:** a row of rasping chitinous teeth on a tongue-like structure behind the mandible of mollusks, a synapomorphy of the phylum.

***Ramapithecus*:** see *Sivapithecus*.

**rangeomorphs:** a group of fern-shaped Ediacaran forms which may have been either the first true animals or an extinct stem group related to animals. Dated at 575–560 Ma, just before the Cambrian Explosion of multivariate animal forms, they



may also be related to the even earlier sponges. At least two described species, *Rangea schneiderhoehoni* and *Fractofusus misrai*, are considered valid. Global occurrences, notably Russia, Canada, and Australia; Precambrian,

**Raoellidae:** a still poorly known family of cetartiodactyl mammals in the clade Whippomorpha; the semi-aquatic *Indohyus*, the best-known genus, may represent a step in the transition of whale ancestors back to an aquatic environment; Southeast Asia, Eocene.

**Rapetosaurus:** a monospecific genus of titanosaurian sauropod dinosaurs in the family Nemegtosauridae; *R. krausei* is known from an unusually complete skeleton of a juvenile and parts of three other individuals; adults are estimated to have been up to about 50 feet long, somewhat smaller than the largest titanosaurs; the juvenile is estimated to have grown fast, probably without any parental care, from about 8 pounds at hatching to about 90 pounds when it died about two months later, probably from starvation; Madagascar, Late Cretaceous, 70–66 Ma.

**Raphidonema:** a genus of calcareous sponges in the still-extant subclass Calcareonida and order Pharetronida; cup-shaped and often twinned, *Raphidonema* forms large sponge beds in the Early Cretaceous of England; Europe and Asia, Cretaceous to Eocene.

**Raphinae:** a subfamily of birds in the order Columbiformes that became extinct less than 300 years ago with the disappearance of the dodo (*Raphus cucullata*) and the Rodrigues solitaire (*Pezophaps solitaria*) from islands in the Western Indian Ocean.

**Raphiophoridae:** a family of blind trilobites in the order Asaphida and superfamily Trinucleoidea; characterized by very long, trailing genal spines and a single spine extending forward from the triangular cephalon; cosmopolitan, Ordovician to middle Silurian.

**Raptorex kriegsteini:** a dubious species of dinosaurs known from a single fossil, once considered a possible ancestor of *Tyrannosaurus rex* but now thought to be an unclassifiable juvenile specimen, possibly related to *Tarbosaurus*; China, Late Cretaceous.

**Rastrites:** a short-lived genus of scandent graptolites in the order Graptoloidea; characterized by long, slender, isolated thecae standing out from a single linear stipe, each theca hooked at the tip; global distribution, early Silurian.

**ratites:** large, flightless birds of the still-extant infraclass Palaeognathae. Mostly of Gondwanan origin, they include the modern rheas in South America, ostriches in Africa, emus in Australia, and probably the extinct moas of New Zealand. The name is derived from the Latin *rat*is (raft), chosen because ratites have a flat breastbone with no keel on their sternum, and significant because the keel is crucial to anchoring wing muscles for flight. Although no fossils are known from the Cretaceous, genetic research indicates that the order probably originated before the end-Cretaceous extinction. The earliest-known ratites appeared in the Paleocene

(see *Diogenornis*). Several giant genera, such as *Dinornis* and *Aepyornis*, became extinct after the arrival of humans in their habitats.

**rauisuchians:** a group of crocodylian archosaurs of the Triassic, included in the clade Pseudosuchia; up to 20 feet long, they were generally carnivorous and among the largest predators of the period; North and South America and Europe, Early to Late Triassic.

***Razanandrongobe:*** a monospecific genus of sebecosuchian crocodylians described in 2017 as a mesoeucrocodylian and the earliest notosuchian; on the basis of several cranial fragments and several large, serrated teeth, *R. sakalavae* is estimated to have been large enough to prey on large dinosaurs; Madagascar, Middle Jurassic, 170 Ma.

**Receptaculitidae:** a family of benthic marine organisms, currently classified as an alga; in the past it has been referred to the Porifera and is still controversial; see e.g. *Ischadites*; global distribution, late Cambrian to Early Triassic.

**Red Gulch Dinosaur Track Site:** a location in the Sundance Formation in Northern Wyoming, displaying numerous footprints made by Middle Jurassic ceratosaurs walking on a beach of fine, well-sorted sand.

**Redlichiida:** an early order of relatively flattened trilobites; characterized by a large cephalon, a many-segmented thorax, and a small pygidium; the Redlichiida appeared at about the same time as the Ptychopariida and Corynexochida; global distribution, early to late Cambrian.

**Remingtonocetidae:** a family of archaocete whales in the family Protocetidae; similar in appearance to amphibians like the crocodile, they had short limbs and a long, narrow skull with nostrils near the front; they could walk on land but were mainly aquatic; see also *Ambulocetus* and *Kutchicetus*; Asia, early to middle Eocene.

***Repenomamus robustus:*** a small eutriconodont mammal in the family Gobiconodontidae. About the size of an opossum or badger, it is especially notable for a Jehol specimen of *R. robustus* with the remains of a baby psittacosaur in its stomach, the first direct evidence that mammals were competing for food with dinosaurs at the beginning of the Cretaceous. Bearing characteristics of reptiles as well as mammals, *Repenomamus* existed also as a much larger species, *R. giganticus*, which was 3 feet long and weighed more than 30 pounds. China, Early Cretaceous, 130 Ma.

**replacement:** the complete supplanting of minerals in a fossil by different minerals coming from the surrounding sediment, usually resulting in increased mass and hardness, and often preserving anatomical structure in detail; in exceptional circumstances, the organism may be replicated in three-dimensional detail, especially by pyrite, marcasite, calcium phosphate, kaolinite, or other relatively soft minerals; see also **taphonomy**.

**Reptilia:** a paraphyletic class of tetrapod animals that includes snakes, lizards, crocodiles, and turtles; reptiles are characterized by a tough, horny skin covered with scales, scutes, or plates; the class excludes some descendants of tetrapods, namely mammals and birds; global distribution, Late Carboniferous to Recent.

**reticulate or reticulated:** having veins, threads, fibers, scales, or pigment creating a net-like appearance.

**Reticuloceratidae:** an important family of ammonoids in the order Goniatitida and superfamily Gastrioceratoidea; several species of the genus *Reticuloceras* are index fossils in the Carboniferous; see also *Arkanites*; North America, Europe, and Asia; Late Carboniferous.

**Revueltosaurus:** a genus of pseudosuchians originally considered an ornithischian dinosaur but now classified as a sister taxon of the aetosaurian suchians; well-armed with a coat of bony plates and a tail club, it is known principally from several partial skeletons found in or near the *Revueltosaurus* Quarry in Petrified Forest National Park; Southwestern United States, Late Triassic, 230–205 Ma.

**Rhabdinopora:** a genus of planktic colonial graptolites in the early order Dendroidea and family Anisograptidae; *Rhabdinopora* is thought to be the ancestor of the large order Graptoloidea; characterized by a conical reticulate colony with many parallel stipes that branch and bifurcate; the stipes are connected by dissepiments, forming a net-like surface and superficially resembling the bryozoan *Fenestella*; global distribution, Early Ordovician.

**Rhabdinopora flabelliformis:** “fan-shaped,” a well-known species of graptolites long considered benthic and classified as *Dictyonema flabelliforme* but now known to be planktic; important index fossil in determining the date of the Cambrian-Ordovician boundary; Europe, Early Ordovician.

**Rhabdopleura:** a still-extant genus of small benthic colonial animals in the class Pterobranchia and family Rhabdopleuridae; it is a worm-like, sessile suspension feeder, probably related to the extinct graptolites; global distribution, Cambrian to Recent.

**Rhachitomi:** a group of late Paleozoic amphibians in the order Temnospondyli; probably derived from the Eutemnospondyli and ancestral to the Stereospondyli; cosmopolitan, Early Carboniferous to Early Cretaceous.

**rhamphorhynchoids:** the basal pterosaurs that gave rise to the pterydactyloids in the Middle Jurassic. Previously considered a suborder, the group is paraphyletic, but the term is still used to refer in general to the early pterosaurs. Although all could fly, they were generally much smaller than the pterydactyloids, and they also differed in having a long tail; most were well-toothed. The rhamphorhynchoids appeared about 230 Ma; among the earliest species are *Preondactylus*, *Peteinosaurus*, *Dimorphodon* (*q.v.*), and possibly the poorly known *Faxinalipterus*. The best known of the group is *Rhamphorhynchus*, which appeared later, about 151 Ma. Global distribution, Late Triassic (Norian) to Cretaceous.

**Rhamphorhynchus:** a genus of fish-eating pterosaurs in the family Rhamphorhynchidae; *Rhamphorhynchus* was only slightly larger than a crow but had a wingspan of 4–5 feet and a very long tail, which ended in a characteristic diamond-shaped vane; Europe and Africa, Late Jurassic, 152–150 Ma.

**Rhenanida:** an order of scaly marine placoderms; flattened and ray-like, they were bottom-dwelling predators, with armor consisting only of unfused tubercles and scales; their fossil record is sparse but worldwide, Early to Middle Devonian.

**Rhenops:** an unusual genus of phacopid trilobites in the large family Acastidae; characterized by stout genal spines, protruding eyes, and two dozen pairs of legs; Europe and South America, Middle to Late Devonian.

**Rhineuridae:** a still-extant family of burrowing squamates in the suborder Amphisbaenia; this family of worm-like lizards is found in Cenozoic strata across North America but is now known only as one genus in Florida; middle Paleocene to Recent.

**Rhinocerotidae:** a still-extant family of large perissodactyl mammals in the suborder Ceratomorpha and superfamily Rhinoceroidea; this large family comprises about 40 extinct genera as well as the modern rhinoceroses; late in their evolution, the latter group developed horns; North America, Europe, Asia, and Africa; Eocene to Recent.

**Rhipidistia:** a still-extant subclass of lobe-finned bony fishes in the class Sarcopterygii; it includes the lungfishes, which are still represented by several genera, and also includes numerous diverse extinct orders; probably ancestral to the tetrapods; Early Devonian to Recent.

**Rhizobiales:** “root life,” an order of symbiotic bacteria, one of several groups involved in the process of producing the ammonium and nitrates used in fertilizers and gunpowder. These bacteria benefit certain plant subfamilies of the order Fabales (principally the Papilionoideae and Mimosoideae) by enabling them to fix atmospheric nitrogen in the form of ammonium and nitrates, eventually enriching the soil; the bacteria benefit from flavonoids secreted by the plants. The rhizobia are known to have existed in the Precambrian, possibly for billions of years, and the type species *Rhizobium leguminosarum* has been thoroughly studied. Worldwide, Precambrian to Recent.

**Rhizodontida:** an order of large predatory freshwater fish in the class Sarcopterygii; one species, *Rhizodus hibberti*, was about 23 feet long, probably the largest freshwater fish known; North America and Europe; Middle Devonian to Late Pennsylvanian.

**rhizome:** a root-like plant stem that generally grows horizontally, on or under the ground.

**Rhizomyinae:** a still-extant subfamily of myomorph rodents in the family Spalacidae, including the Asian bamboo rats and some African mole rats; Miocene to Recent.

**Rhombifera:** a class of blastozoan echinoderms in the superclass Cystoidea, characterized by perforated plates in the calyx and rhombic thecal plates shared equally between adjacent plates; similar to the Diploporita; North America, Europe, and Asia; Early Ordovician to Late Devonian.

**Rhynchocephalia:** an order of lizard-like reptiles in the subclass Lepidosauria; it includes the once-numerous sphenodonts, which are now extant only in the tuatara (two species of *Sphenodon*) of New Zealand; global distribution, Middle Triassic to Recent.

**Rhyncholepis:** a genus of early jawed fish in the order Anaspidia; named “beaked scale” for its thick, bony scales; Scandinavia, late Silurian, 426–423 Ma.

**Rhynchonellata:** a large, still-extant class of articulate brachiopods in the subphylum Rhynchonelliformea, generally with biconvex calcite shells; global distribution, early Cambrian to Recent.

**Rhynchonellida:** a still-extant order of articulate brachiopods in the class Rhynchonellata and superfamily Rhynchonelloidea; characterized by the absence of brachidia and by astrophic hinges; generally wedge-shaped, often resembling a nut; global distribution, Ordovician to Recent.

**Rhynchonelliformea:** term now given to the articulate brachiopods, replacing the class Articulata and revised as a subphylum comprising the extinct classes Chileata, Kutorginata, Obolellata, and Strophomenata, and the extant Rhynchonellata; in addition to articulation, they are characterized by a fibrous secondary shell layer.

**Rhynchosauria:** “beak lizard,” an order of herbivorous diapsid reptiles, primitive archosauromorphs; the early genera were small and lizard-like, while some toward the end of the period grew to more than 6 feet long; these later genera had bulky bodies, a strong beak, and wide skulls, with some teeth becoming broad toothplates for cutting up plant material; global distribution, Early to Late Triassic.

**Rhynia:** a genus of early vascular land plants in the class Rhyniopsida; known only from the Rhynie Chert, where it is a common rhizomatous plant with stems up to 8 inches high; Scotland, Early Devonian.

**Rhynie Chert:** a Lower Devonian Konservat-Lagerstätte that contains many early arthropod and plant fossils. It is especially important because it represents an early stage of the colonization of land by marine life, even the first evidence of herbivory by sap-sucking mites. A short turf a few inches high was created by early land plants, including bryophytes and the first vascular plants (see *Rhynia*), as well as pre-vascular plants with mixed bryophytic characteristics, such as *Aglaophyton* and *Horneophyton*. The informal term “rhyniophytes” is often used to refer to the Rhynie flora in general. The Rhynie fossils are mainly found in chert deposited around hot springs, and many are three-dimensional. Some of the significant animals are the earliest-known insect (*Rhyniognatha hirsti*), crustaceans (see *Lepidocaris*), trigonotarbid, the oldest mites (see *Acari*), and harvestmen (see *Opiliones*). Scotland, 410–405 Ma.

***Rhyniella praecursor***: a famous hexapodal arthropod of the Rhynie Chert, placed in the order Collembola; among the earliest-known proto-insects, 2 mm long and wingless; Scotland, Early Devonian.

***Rhyniognatha hirsti***: the oldest known insect, a species known from specimens found in the Rhynie Chert, especially a dicondylic pair of mandibles; the presence of condyles and the short, triangular mandibles may indicate that *R. hirsti* had wings; Scotland, Early Devonian.

**Rhyniopsida**: a class of primitive leafless plants in the division Tracheophyta; among the simplest of all vascular plants, they bore sporangia near the tips of branches; first known from the Rhynie Chert assemblage; global distribution, Early Devonian.

***Richthofenia***: a genus of articulate strophomenid brachiopods in the order Productida and family Richthofeniidae; similar to cup-shaped corals in shape and also in its reef-forming habit, with specializations for encrustation on hard substrates; North America, especially Texas, early Permian.

***Riojasaurus***: a genus of middle-sized early sauropod dinosaurs in the family Riojasauridae, probably related to the slightly smaller melanorosaurs of South Africa. Herbivorous and with a heavy body and massive legs, *Riojasaurus* was one of the very few sauropods in South America. About 33 feet long and weighing about 10 tons, it was mainly quadrupedal but also bipedal. Argentina, Late Triassic, 230–210 Ma.

**Rissooidea**: a still-extant paraphyletic superfamily of very small marine and freshwater gastropods in the clade Littorinimorpha; generally cylindrical or conical in shape, the group is extremely diverse and widespread; global distribution, Jurassic to Recent.

**Riversleigh**: a Cenozoic Konservat-Lagerstätte in northwestern Queensland that has produced exceptionally well-preserved specimens of bats, marsupials, insects, and other Australian fauna and flora; many of the fossils are three-dimensional, having been preserved in soft, uncompressed limestone; Australia, late Oligocene to late Miocene.

***Robertia***: an early monospecific genus of herbivorous dicynodont therapsids in the family Pylaecephalidae; about a foot long, *R. broomiana* had two sharp canine teeth and a horny beak, probably used in digging; related to *Diictodon*; South Africa, middle to late Permian, 265–260 Ma.

**rock varnish**: a dark biogeochemical encrustation on exposed rock in almost any terrestrial weathering environment, but most commonly found as desert varnish in arid or semi-arid sites; consisting primarily of iron and manganese oxides, clay, and carbonates secreted by bacteria, it is useful in identifying paleoenvironments.

***Rodhocetus kasrani***: a species of archaeocete whales in the family Protocetidae, an important recent discovery in strata deposited in deep water about 50 Ma,

representing the earliest-known deep-ocean whale. Notable for its unfused vertebrae that allowed it to swim principally with its tail, as do modern whales, *Rodhocetus* still bore short but powerful hindlimbs and a pelvis connected to its sacrum. Similar to the slightly more recent *Protocetus* except that the latter could not have supported its own weight on land, whereas *Rodhocetus* may have been able to do so and therefore represents the farthest-known evolution of ancestral whales before they lost all useful terrestrial characteristics. It is also notable because its blowhole was high on its head, a step in the direction of modern whales, all of which have a blowhole on top of the head. Pakistan, early Eocene.

**Rodinia:** “Motherland,” name given to a Proterozoic supercontinent that existed between 1300 and 650 Ma; it consisted of fragments from an earlier supercontinent called Columbia or Nuna that had drifted apart between 1800 and 1500 Ma; Rodinia centered on Laurentia, which was on the Equator.

**Rodrigues solitaire:** see *Pezophaps solitaria* and **Raphinae**.

**Romer’s Gap:** the paucity of tetrapod and arthropod fossils in the period between 361 and 340 Ma at the beginning of the Carboniferous period, also called the Tournaisian Gap. The first terrestrial vertebrates appeared at the end of the Devonian, around 370 Ma, but their fossil record in the early Mississippian is very thin. (See also **Tetrapoda** and *Tulerpeton*.) Terrestrial vertebrates appear in great numbers in the middle Mississippian, so their radiation at the beginning of the period must have been quite rapid. This radiation has drawn many researchers since Alfred Romer himself, especially Robert Carroll, Per Ahlberg, and Jennifer Clack at the end of the twentieth century.

**Rosamygale grauvogeli:** a species of funnel spiders in the infraorder Mygalomorphae and extant family Hexathelidae; less than half an inch long, *R. grauvogeli* is the oldest known mygalomorph spider; known only from the Grès à Voltzia, France, Early Triassic.

**Rostroconchia:** a class of mollusks superficially similar to bivalves and once proposed as ancestral to them; both, however, along with the brachiopods, appeared close to the same time in the Cambrian Explosion near the beginning of the Paleozoic Era, and their inter-relationships remain unclear. From 1 to 6 inches wide, the rostroconchs had a taco-like shell and a rostrum, a tube extending outside the shell, possibly to filter the water. They diversified rapidly worldwide through the Ordovician, then declined in comparison to the bivalves, and became extinct at the end of the Permian.

**Rotalipora globotruncanoides:** a species of planktic foraminiferans whose first appearance marks the beginning of the Late Cretaceous at 100.5 Ma; France.

**Rubeosaurus:** a genus of ceratopsian dinosaurs in the subfamily Centrosaurinae; named “thornbush” for an array of horns and spikes, with a single short horn on its snout and longer horns on its neck frill; known from two specimens of skull fragments, it is estimated at about 19 feet and 2 tons; North America, Late Cretaceous, 75 Ma.



***Rubidgea*:** a monospecific genus of therapsids in the family Gorgonopsidae; as long as 11 feet, *R. atrox* is notable for canine teeth longer than those of *Tyrannosaurus rex*; known only from two skulls; South Africa, late Permian.

**rudists:** see **Hippuritoida**.

***Rugops primus*:** a species of ceratosaurian theropod dinosaurs in the family Abelisauridae; known only from a single skull, it is estimated at 15–20 feet long and thought to be carnivorous but probably a scavenger; Niger, Late Cretaceous, 96–94 Ma.

**Rugosa:** the “wrinkled” corals, a large order of anthozoan cnidarians in the subclass Hexacorallia; also called Tetracoralla. The Rugosa and the Tabulata were the most diverse and widespread coral reef-builders of the Paleozoic. Mainly solitary and conical or horn-shaped, but also often colonial, the rugose corals were composed of calcite, as opposed to the more easily dissolved aragonite of the modern Scleractinia. The first undoubted Rugosa appeared in the Middle Ordovician, and they became extinct along with the Tabulata at the end of the Permian.

***Rugosodon eurasiaticus*:** a species of multituberculate mammaliaforms in the order Paulchoffatiidae; found in the Tiaojishan Formation and dated at about 160 Ma, *Rugosodon* is so called because of its distinctively wrinkled teeth; it was omnivorous, and its chipmunk-sized body was 6–7 inches long and adapted to tree-dwelling; China, Late Jurassic.

**Ruminantia:** a suborder of artiodactyl ungulates that have a four-part stomach to digest tough plant material. The Ruminantia include cattle, sheep, goats, antelopes, deer, pronghorns, giraffes, and many extinct pecorans. A smaller group of ungulates that includes tylopods (the camelids), and macropods (kangaroos and wallabies) are considered “pseudo-ruminants” with a slightly different digestive system. Global distribution, early Eocene to Recent.



# S

***Sacabambaspis***: a genus of early pteraspidimorph craniates in the order Arandaspidiformes, closely related to *Arandaspis* and among the earliest whole-body specimens of ostracoderms. Jawless and 10 inches long, it had a laterally flattened body and an extended tail with a small fin web at the end, but no paired fins. Its head was armored with bony plates and the body was covered with scales. First found in Bolivia, it is known from several Gondwanan locations: Argentina, Australia, and the Arabian Peninsula; Middle to Late Ordovician.

***Saccorhytus coronarius***: the oldest known species of deuterostomes, described in 2017 from a group of 45 individuals; only 1 mm long, its globular body seems to have only one opening, which is surrounded by conical protuberances; China, early Cambrian, 540 Ma.

**saddle**: an anterior-pointing fold in the suture line of an ammonoid.

***Sagenocrinites***: a genus of crinoids in the order Sagenocrinida; characterized by an ovoid crown and a conical cup half the height of the crown and about an inch in diameter, with branching arms well differentiated from the calyx; North America and Europe, Silurian.

***Sagenopteris***: a genus of seed-fern leaves in the family Caytoniaceae; global distribution, Early Triassic to Early Cretaceous.

***Saghatherium***: a genus of primitive hyracoid mammals in the extinct family Pliohyracidae and subfamily Saghatheriinae; it was scansorial and herbivorous, and somewhat similar to the modern hyraxes of the Procaviidae; Fayum, Egypt, late Eocene or early Oligocene.

***Saharagalago***: a genus of lorisiid primates in the suborder Strepsirrhini and family Galagidae; discovered in 2002 in Fayum, Egypt; dated between 40 and 37 Ma, the early bushbabies *Saharagalago* and a cousin *Karanisia* pushed back the date of the earliest lorisiiforms by 20 million years; they represent the earliest-known examples of the characteristic strepsirrhine toothcomb; Fayum, Egypt, middle Eocene.

***Sahelanthropus tchadensis***: a species of hominids found near Lake Chad in 2001; this early hominid lies near the divergence of humans from chimpanzees, although probably predating it slightly; it shows a mix of human and chimpanzee characters and at 6.9 million years old is the oldest known hominid.

**St. George Dinosaur Discovery Site**: a set of exceptionally well-preserved Early Jurassic dinosaur tracks now enclosed in a museum on the Johnson Farm in southwestern Utah.

**Salientia**: “jumpers,” the clade that includes the modern frogs, Anura, and their most closely-related ancestors.

***Saltasaurus loricatus***: a species of titanosaurian sauropod dinosaurs in the monospecific family Saltasauridae; about 40 feet long and weighing 8 tons, it was unusual for a sauropod in having osteoderms and armor plates covering its upper body and sides; Argentina, Late Cretaceous, 71–69 Ma.

***Salterella***: an enigmatic small, conical fossil, widespread in North America in the Cambrian; its stratified walls are composed of agglutinated grains of calcite; it superficially resembles some early cephalopods but is now tentatively referred to the proposed short-lived phylum Agmata; North and South America and Europe, early Cambrian to Late Ordovician.

***Saltoposuchus connectens***: the type species of a genus of relatively small, bipedal sphenosuchian reptiles in the superorder Crocodylomorpha, 3–5 feet long and weighing less than 35 pounds; Europe, Middle Triassic.

***Saltopus***: “leaping foot,” a monospecific genus of early dinosauriform reptiles, placed by some in the family Silesauridae. The enigmatic *S. elginensis* is poorly known from a partial skeleton, mainly cast impressions. It has been studied intensively since its discovery in 1910 and classified variously as a stem-dinosaur or a dinosauriform outside the clade Dinosauria. In a re-classification proposal in 2017, it figures as possibly ancestral to dinosaurs. Scotland, Late Triassic, 228 Ma.

***Samotherium***: a genus of early giraffes similar in appearance to the modern okapi, with two ossicones extending upward from the skull; larger than the okapi but smaller than modern giraffes, *Samotherium* is a good example of a transitional genus; Europe, Asia, and Africa; Miocene to Pliocene.

***Sanmiguelia lewisii***: a species of early plants that may belong to a stem-group of angiosperms, known from several localities in Western North America. One especially well-preserved autochthonous specimen was found in a Late Triassic stream-side paleosol near Palo Duro Canyon in Northwest Texas. Buried in its growth position, it has several structures similar to angiosperms. North America, Late Triassic to Early Jurassic.

**Santa Maria Formation**: a Triassic site in Southern Brazil with strata dating from the Ladinian to Carnian Stages, similar to those of the Chañares Formation of northwestern Argentina; notable for specimens of early dinosaurs, aetosaurs, and cynodonts; Middle to Late Triassic.

**Santana Formation:** a Lower Cretaceous Konzentrat-Lagerstätte in the Araripe Basin of Northern Brazil. It is dated uncertainly between 112 and 106 Ma, slightly later than the neighboring Crato Formation. The Santana fossils, occurring inside limestone concretions, include complete specimens of fish in great numbers; partial specimens of pterosaurs with soft-tissue preservation of webbing; dinosaurs, including spinosaurids and coelurosaurs; reptiles (see **Araripesuchus**); and a few insects and other invertebrates.

**Sarcopterygii:** “flesh fin,” lobe-finned fish in the superclass Osteichthyes, the bony fishes. Previously called Crossopterygii, the Sarcopterygii appeared in the late Silurian along with other osteichthyans. They dwindled during the Mesozoic, eclipsed by the many very successful osteichthyans and chondrichthyans. The Sarcopterygii are still represented by several genera, including the coelacanth in the subclass Actinistia and the lungfishes in the subclass Rhipidistia. Among the many extinct sarcopterygian taxa, the closely related tetrapod lobefins of the Late Devonian are especially significant evolutionarily as the first terrestrial vertebrates. See also **Actinopterygii** and **Tetrapoda**.

**Sarcosuchus imperator:** a very large crocodylian of the Cretaceous, first discovered in 1964 in Niger in the Ténéré Desert. From 37 to 40 feet long, with a head more than 5 feet long and jaws about 4 feet long, it weighed around 9 tons, about 1.5 times as much as an African elephant. *Sarcosuchus* had a bulbous protuberance on the end of its snout, probably used to locate prey by smell or sound. North Africa and South America, Early to Late Cretaceous.

**Sarmientosaurus musacchioi:** a species of titanosaurian sauropod dinosaurs found in Patagonia and described in 2016; estimated at about 40 feet long and 10 tons, it is known from an almost complete skull and several articulated vertebrae that may indicate a drooping posture of the head; also characterized by very large eyes; Argentina, Late Cretaceous, about 95 Ma.

**Sasayamamylos:** a genus of basal eutherian mammals in the order Asioryctidae; insectivorous, known only from a skull found in Japan in 2007 and described in 2013, *S. kawaii* may be the earliest-known example of a modern mammalian dentition; Early Cretaceous, 112 Ma.

**Saurichthyidae:** a speciose family of Mesozoic ray-finned chondrosteian fish in the order Saurichthyiformes. They were about 3 feet long and very slender, with symmetrical dorsal and anal fins near the tail, a shape that probably made them fast and efficient predators. They may have originated toward the end of the Permian but were common throughout the Triassic and persisted at least to the Middle Jurassic (see **Saurorhynchus**). North America, Europe, Asia, Australia, and Madagascar; Early Triassic to Middle Jurassic.

**Saurischia:** one of the basic divisions of dinosaurs, characterized by a three-pronged pelvic structure similar to that of most reptiles, with a pubis bone pointing downward and slightly forward. The earliest saurischians (such as *Eoraptor* and the Guaibasauridae) appeared during the Carnian Age of the Late Triassic. The

sauropods are the most prominent group within the Saurischia, while the theropods are variously considered as saurischians or part of some other division (see **Ornithoscelida**). Global distribution, Triassic to Late Cretaceous.

**Saurolophus:** “lizard crest,” a genus of large hadrosaurid dinosaurs in the subfamily Saurolophinae; 30–40 feet long, they were characterized by a “duck bill” and a backward-extending cranial crest of unknown function; see also **Parasaurolophus**; North America and Asia, Late Cretaceous, 71–68 Ma.

**Sauropoda:** an infraorder of quadrupedal saurischian dinosaurs in the suborder Sauropodomorpha. Semi-aquatic and herbivorous, the sauropods had very long necks, long tails, and a heavy body supported by four pillar-like legs. Estimates of sauropod weight vary greatly, but conservative estimates range from 50 to 70 tons for the largest. Global distribution, Late Triassic to Late Cretaceous.

**Sauropodomorpha:** a clade of herbivorous saurischian dinosaurs that includes the infraorders Plateosauria and Sauropoda and their immediate ancestors; with representatives dated between 231 and 66 Ma, the sauropodomorphs were the dominant terrestrial herbivores worldwide from the Late Triassic to the Late Cretaceous.

**Sauroposeidon:** a genus of titanosaurian sauropod dinosaurs; at about 60 feet high it was possibly the tallest dinosaur, and it had a longer neck than any other dinosaur, conservatively estimated as 40 feet long, with some vertebrae 5 feet long; weighing about 60 tons, it was significantly larger than *Brachiosaurus*; North America, Early Cretaceous, about 110 Ma.

**Sauropterygia:** a superorder of aquatic diapsid reptiles characterized by pectoral and pelvic girdle adaptations that supported strong flippers. Including the nothosaurs, plesiosaurs, and pliosaurs, the sauropterygians arose at the beginning of the Triassic and diversified worldwide, with the plesiosaurs surviving into the Jurassic and the pliosaurs appearing in the Early Jurassic. The last of the sauropterygians disappeared at the end of the Cretaceous, except that some research now indicates that modern turtles may be distant descendants. Early Triassic to Late Cretaceous.

**Saurorhynchus:** a genus of chondrosteian fish in the order Saurichthyiformes and family Saurichthyidae; formerly called *Acidorhynchus*; gar-like in appearance, it was 2–3 feet long and slender, with symmetrical dorsal and anal fins near the tail; North America and Europe, Early to Middle Jurassic.

**savanna:** term used to refer to a wide range of environments between dense forest and desert, usually referring to openly wooded grassland.

**Savannasaurus:** a monospecific genus of titanosaurian sauropod dinosaurs described in 2016; *S. elliottorum* was 50 feet long and is the most complete specimen of a sauropod found in Australia; Cenomanian, Late Cretaceous, 100–94 Ma.

**scandent:** of vines and graptolites: having a climbing habit.

**scansorial:** of animals: able to climb trees, spending at least part of the time in an arboreal environment.

**Scansoriopteryx:** see *Epidendrosaurus*.

**Scaphites:** a genus of small, loosely coiled ammonoids in the order Ammonitida and suborder Ancyloceratina, known worldwide. Its species are generally characterized by a boat-shaped shell 2–5 inches long, with an involute and compressed juvenile stage, then a straight segment in the middle, and an erect terminal stage bending back over the juvenile stage like a hook. Probably a slow swimmer, mainly benthic; several species are index fossils in the Late Cretaceous.

**Scaphopoda:** “boat foot,” a still-extant class of infaunal marine mollusks; called “tusk shells,” they are characterized by a tooth-shaped, curving, tapering shell, open at both ends; from 1 to 4 inches long, they live in the soft substrate offshore, beyond the intertidal zone; they are probably the latest class of mollusks to appear; global distribution, Ordovician to Recent.

**Scenella:** an enigmatic genus of limpetlike animals variously considered monoplacophorans, gastropods, helcionellids, and even hydrozoans; about half an inch across, it is characterized by a high, curving, cap-shaped shell with radial and concentric striations; global distribution, Cambrian to Ordovician.

**schizochroal:** a type of compound eye found only in some phacopid trilobites; it has up to 700 lenses with separate corneas, with larger lenses than in the holochroal eyes of most trilobites.

**Schizoneura:** a genus of small, slight sphenophyte trees in the order Equisetales, related to the Calamitaceae; global distribution, early Permian to Late Jurassic.

**Schloenbachiidae:** a family of ammonoids in the order Ammonitida and superfamily Hoplitoidea; characterized by a complex ammonitic suture and a compressed form; irregular, some genera smooth and involute and others strongly ribbed and evolute; North America, Europe, and Asia; Cretaceous, 113–94 Ma.

**Schubertellidae:** a family of foraminiferans in the superfamily Fusulinoidea; they diversified greatly toward the end of the Permian but became extinct at the end of the period; North America, Europe, and Asia; Pennsylvanian to late Permian.

**Schwagerinidae:** a family of large, complex foraminiferans in the superfamily Fusulinoidea; the genus *Schwagerina* is important in petroleum geology, providing several index fossils in lower Permian strata; North and South America, Europe, and Asia; Late Carboniferous to late Permian.

**Sciuridae:** the still-extant family of rodents that includes modern squirrels, so similar to their Miocene ancestors that they can be considered “living fossils”; global distribution, Oligocene to Recent.

**Sciurumimus albersdoerferi:** “squirrel mimic,” a species of feathered theropod dinosaurs in the suborder Coelurosauria; reported in 2012 and known only from a juvenile specimen, 28 inches long; the tail feathers resemble a squirrel’s tail fur; Germany, Late Jurassic, 150 Ma.

**Scleractinia:** “hard-rayed,” a still-extant order of anthozoan cnidarians, corals placed in the subclass Hexacorallia but with obscure origins. Often called stony corals, they are mostly colonial in relatively shallow water, with some solitary genera found in deeper water, some even abyssal. When the mainly calcitic tabulate and rugose corals disappeared at the end of the Permian, there were no important reef-building animals until the aragonitic scleractinians appeared in the Middle Triassic and became a dominant reef-builder late in the period; barely escaping extinction, they began to spread globally in the Cretaceous. Only one purely calcitic genus, *Coelosimilia* (Late Cretaceous, about 70 Ma), is known. Middle Triassic to Recent.

**scolecodonts:** the chitinous jaws of marine polychaete annelid worms; as large as a few millimeters, scolecodonts appeared in the Cambrian, were common in Ordovician and middle Paleozoic strata, became rare at the end of the Permian, recovered in the Mesozoic, and again became rare at the end of the Cretaceous; at least seven families of modern polychaetes have chitinous teeth that would be considered scolecodonts if fossilized; Cambrian to Recent.

**Scolosaurus:** a monospecific genus of armored ornithischian dinosaurs in the subfamily Ankylosaurinae; called “horned toad dinosaur” for the many spines of various sizes that protrude from its head, body, and tail, *S. cutleri* grew as long as 20 feet and weighed 2 tons; it is the oldest known North American ankylosaur, known only from a single skeleton dated at about 76.5 Ma; Alberta, Late Cretaceous.

**scute:** an external ossicle, a plate of bone embedded in the skin and covered with horn, common in many dinosaurs and some mammals.

**Scutosaurus:** a genus of large pareiasaurian reptiles, the largest herbivore of the late Permian; about 10 feet long, it was heavily armored with scutes, osteoderms, and small skull spikes; Russia, late Permian.

**Scyphozoa:** the jellyfish, a class of cnidarians; they probably date back to the Precambrian, but fossils are rare because of the lack of hard parts; one of the earliest well-identified is *Essexella*, 3–4 inches wide, which is known from many specimens in the Mazon Creek fauna of the Late Carboniferous.

**sea lilies:** common name for crinoids that are attached to the substrate by a stalk.

**sea pens:** see **Pennatulacea**.

**sea squirts:** see **Tunicata**.

**sectorial tooth:** a single-cusped, pointed tooth, especially of non-human primates, often with a cutting edge capable of a scissors-like action in occlusion.

**seed fern:** see **Pteridospermatophyta**.

**Segnosaurus:** a genus of herbivorous theropod dinosaurs in the family Therizinosauridae; about 20 feet long and weighing a little more than a ton, they are characterized by long, flattened claws on the large forelimbs, strong hindlimbs, and cutting denticles on the edges of some teeth; Asia, Late Cretaceous, 90 Ma.

***Seismosaurus***: see *Diplodocus*.

***Seitaad***: a monospecific genus of sauropodomorph dinosaurs found in Southern Utah in 2004 and described in 2010, probably an early sauropod; *S. ruessi*, known only from a headless but articulated skeleton, was 10–25 feet long and was probably herbivorous; United States, Early Jurassic, 185 Ma.

**Selachii**: the sharks, a superorder of chondrichthyan fish in the subclass Elasmobranchii. The only Paleozoic elasmobranchs, the first sharks appeared about 420 Ma and diversified rapidly, becoming the dominant predators in the oceans in the Devonian. The best-known early shark is the North American *Cladoseleche*, and another genus similar in appearance to modern sharks is *Denaëa*. Two with very unusual characters were *Stethacanthus* and *Falcatus*, *q.v.* The selachians declined in the Carboniferous and Permian but rebounded in the Jurassic. Most modern sharks have their roots in the Cretaceous, along with the other elasmobranchs. Global distribution, Silurian to Recent.

***Selaginella***: a still-extant genus of spikemosses in the division Lycopodiophyta and class Isoetopsida, related to the extinct giant club mosses of the Mesozoic; global distribution, Silurian to Recent.

**selenodont dentition**: “crescent tooth,” low-crowned teeth with a hard chewing surface and cusps forming a crescent shape if viewed from above; common in ruminant mammals.

***Selenopeltis***: an Ordovician genus of trilobites in the order Odontopleurida and family Odontopleuridae; from 4 to 6 inches long, characterized by many long pleural spines and a rectangular carapace; Europe and North Africa, Early to Late Ordovician.

***Selkirkia***: a genus of predatory priapulid worms in the family Selkirkiidae, known primarily from the Burgess Shale; about 3 inches long, it lived in a tube, oriented vertically in the sediment, extending its proboscis to capture prey; North America (possibly also South America and Antarctica), middle Cambrian.

***Semionotus***: the type genus of a family of early neopterygian fish in the order Semionotiformes; only 5 inches long, it was mainly freshwater but is also found in marine deposits; it is notable for its peg-like teeth and an almost-square dorsal fin pointing backward; cosmopolitan, Middle Triassic to Early Cretaceous.

**septum**: a partition inside the skeleton of an animal, especially in corallites and the shells of ammonoids, belemnites, and nautiloids.

***Sequoia jeholensis***: the earliest-known sequoia; North America, Europe, and Asia; Jurassic to Oligocene.

***Serridentinus***: see *Gomphotherium*.

**sessile**: stationary on the bottom sediment and often anchored directly to the substrate.

**setae**: slender, rigid, bristle-like extensions on living organisms, usually referring to bristles or hairs on animals; see also **chaetae**.



**sexually dimorphic:** having distinguishing features between male and female individuals; dimorphism has often resulted in male and female forms being interpreted as different species, a mistake usually corrected by examination of a greater number of specimens.

**Seymouria:** a genus of semi-aquatic stem-amniotes in the family Seymouriidae; it was about 3 feet long and had several reptilian adaptations; related to *Discosauriscus*, *q.v.*; known only from Central North America and Germany, early Permian, 280–270 Ma.

**Seymouriamorpha:** an order of reptile-like stem-tetrapods, generally placed in the clade Batrachosauria; North America, Europe, and Asia; early to late Permian.

**Shansisuchus:** a genus of crocodylians in the family Erythrosuchidae; well-known from several specimens, *Shansisuchus* was about 6 feet long; China, Middle Triassic.

**Shantungosaurus:** a genus of hadrosaurid dinosaurs in the subfamily Saurolophinae; as long as 54 feet and weighing 16 tons, it is the largest known hadrosaurid and one of the largest ornithischians; China, Late Cretaceous, 70 Ma.

**Sharktooth Hill:** one of the largest bone-beds, a densely packed layer of 15-million-year-old fossils. The site has yielded 40-foot *Carcharodon megalodon* remains, mainly teeth, and thousands of other marine species, as well as some terrestrial tapirs and ancestral horses. The remains were deposited over a period of about 700,000 years along the southeastern shore of the Tumbler Sea, which covered California's long inland valley. United States, middle Miocene.

**Sharovipteryx:** a genus of small gliding reptiles in the order Protorosauria; known from one specimen found in the Madygen Formation of Kyrgyzstan in 1965 and dated at 225 Ma; notable for the membrane attached to its elongated hindlimbs; Kyrgyzstan, Late Triassic.

**Shastasaurus:** a genus of ichthyosaurs in the family Shastasauridae. Known from specimens in California, Oregon, British Columbia, and China, the type species is *S. pacificus*. Since *Shastasaurus* is very different from other ichthyosaurs found in North America, it is one of the many pieces of evidence of the degree to which terranes of Western North America have originated in the Pacific Ocean and been accreted by tectonic forces to the North American continent. North America and Asia, Late Triassic, 236–204 Ma.

**shipworm:** see **Teredinidae**

**Shonisaurus:** a genus of ichthyosaurs in the family Shastasauridae; about 50 feet long, they were bulky and dolphin-shaped, with a long, thin snout; known primarily from a large bone-bed in Nevada that contains 30–40 relatively complete specimens, all lying in the same position; the causes of their deaths are uncertain; North America and Europe, Late Triassic, 225–210 Ma.

**Shumardiidae:** a family of minute, blind trilobites in the order Ptychopariida; about 5 mm long, characterized by a semicircular glabella with deep furrows and conspicuous lateral lobes; global distribution, late Cambrian to Late Ordovician.



***Shuotherium***: a genus of Mesozoic mammals in the family Shuotheriidae; known from several dental fragments, they share characteristics with monotremes and eutherians; England and China, Middle to Late Jurassic.

***Shuvosaurus***: see *Effigia*.

***Siamopithecus eocaenus***: a genus of primitive anthropoid primates in the family Amphipithecidae, found in the 1990s in Thailand; reconstructions based on skull, jaw, and dental fragments indicate similarities to *Aegyptopithecus* and *Pondaungia*; late Eocene.

**Siberian Traps**: an area of lava flows, about 870 miles in diameter, northeast of Lake Baikal in Siberia; the eruptions occurred over a period of less than 1 million years, beginning about 248 Ma, and have been intensively studied because their date is so close to the end of the Permian; some researchers believe the eruptions may be related to the causes of the great extinction that occurred then.

***Sidneyia***: a monospecific genus of flattened stem-arthropods of the Burgess Shale fauna; 2–5 inches long, *S. inexpectans* is one of the larger arthropods at the site; its glabella was wide and shaped like a ram, and it probably preyed on trilobites, brachiopods, and hyoliths; Canada, middle Cambrian, 508 Ma.

***Sigillaria***: “seal-marked,” a genus of large lycopodiophyte trees in the order Lepidodendrales; ranging from 50 to 100 feet high, they are characterized by leaves growing directly from the trunk and branches; the leaves are indistinguishable from those of the related genus *Lepidodendron*, but the leaf-scars are arranged in parallel vertical rows instead of the spiral arrangement of *Lepidodendron*; global distribution, Devonian to Permian.

**Silesauridae**: a family of dinosauromorphs in the clade Dinosauriformes; the family includes several genera of archosaurian reptiles that seem close to the line of descent to dinosaurs, such as *Silesaurus*, *Asilosaurus*, *Diodorus*, *Lewisuchus*, and probably *Agnosphytis*; South and North America, Africa, and Europe; Middle to Late Triassic, 245–203 Ma.

**Silurian**: the third period of the Paleozoic Era, from 444 to 416 Ma. Agnathans and placoderms were the most abundant vertebrates, but by the end of the period all principal groups of vertebrates had evolved. Stromatolite and coral reefs covered large areas of the shallow seas; Silurian strata are mostly calcitic, with some sandstones and graptolite shales. The first vascular plants appeared in the middle Silurian, and plants such as rhyniophytes and clubmosses increased their colonization of the land, creating a great diversity of new terrestrial ecosystems.

***Silvacola acares***: a species of very small hedgehogs in the still-extant family Erinaceidae, found in 2014 in northern British Columbia. It is only 2–3 inches long but is otherwise similar to modern hedgehogs; whether *Silvacola* had spines cannot be determined from the specimens. Canada, early Eocene, 50 Ma.

**Simoedosauridae**: see **Choristodera**.

***Sinoceratops***: an Asian genus of short-frilled ornithischian dinosaurs in the family Ceratopsidae; they were herbivorous, medium-sized, and quadrupedal, and are still the only ceratopsians known from Asia; two species found in 2008 in China have been identified as *S. zhuchengensis* and *S. formosensis*; China, Late Cretaceous, 72–66 Ma.

***Sinoconodon***: a genus of early mammals in the suborder Cynodontia; one of the earliest cynodonts, it is probably ancestral to Morganucodon; although similar in many ways to the non-mammalian synapsids (such as polyphyodonty), it also has several characters that mark it as a basal mammal (especially in the jaw joint); China, Early Jurassic, 193 Ma.

***Sinodelphys szalayi***: a species of metatherians, the earliest-known mammal to display marsupial traits; about 6 inches long, fur-bearing, and weighing about one ounce; known from only one specimen found in the Yixian Formation; China, Early Cretaceous, 125 Ma.

***Sinopterus***: a genus of small pterodactyloid pterosaurs in the family Tapejaridae; dated at 120 Ma, it had a wingspan of almost 4 feet; the first tapejarid found outside Brazil, *Sinopterus* is known from three specimens found in the Jiufotang Formation; China, Early Cretaceous.

***Sinornithosaurus millennii***: a species of theropod dinosaurs in the family Dromaeosauridae; they were turkey-sized and had bird-like features and short, downy proto-feathers, but probably did not fly; characterized by single large claws on hind feet and long claws on its arms, possibly poisonous; one of several feathered dinosaurs in the Jehol biota; China, Early Cretaceous, 120 Ma.

***Sinosauropteryx prima***: a species of small theropod dinosaurs that seems to have had rings of different-colored feathers on its tail and a colored stripe across its eyes. Researchers base this conclusion on melanosomes, cells that contain the pigment melanin; the color itself is not visible in the fossil, but electron-microscope analysis of melanosomes in the follicles gives indirect evidence of a russet color. The feathers were as long as 1.5 inches and were evidently bristly like those of the modern kiwi. *Sinosauropteryx* was about 3 feet long but weighed only about 6 pounds; it had 64 vertebrae in its tail, more than any other theropod. One of several feathered dinosaurs in the Jehol biota, Early Cretaceous, 127–125 Ma.

***Siphonia***: a genus of demosponges in the polyphyletic order Lithistida and extinct family Hallirhoidae; globular, cylindrical, or pear-shaped, they were anchored to the sea floor by a stalk and a root system or holdfast; the name refers to the main feeding tube, which runs through almost the whole length of the body; Europe, Early Cretaceous to late Eocene.

***Siphonodella sulcata***: a species of conodonts whose first appearance marks the beginning of the Early Carboniferous (Mississippian) at 358.9 Ma; France.

***Siphonotretoidea***: a small superfamily of inarticulate brachiopods in the order Siphonotretida; similar to the Obolellida and still-extant Acrotretida, they are char-

acterized by a teardrop-shaped, chitinophosphatic shell and an elongate or apical pedicle valve; global distribution, middle Cambrian to middle Permian.

**Sirenia:** an order of fully aquatic mammals, some freshwater, placed in the clade Tethytheria. In addition to several extinct families such as the Prorastomidae and Protosirenidae, extinct genera of the still-extant Dugongidae and Trichechidae are known from the Miocene. Global distribution, early Eocene to Recent.

**Sirius Passet:** a locality in Greenland that has produced soft-bodied fossils similar to those of the coeval Chengjiang biota; known especially for *Halkieria*, *q.v.*; early Cambrian.

**sister group:** a phylogenetic term referring to the most closely related taxa in an evolutionary lineage, those more closely related to each other than either is to other taxa; the term is used most often in relation to species and genera, but it may also designate most closely related clades as sister clades.

**Sivapithecus:** a genus of hominoid primates in the subfamily Ponginae, known from fossils found at several sites in Asia; formerly called *Ramapithecus* and *Brahmapithecus*. About 5 feet long, they probably spent some time in trees but were mainly ground-dwelling. There is still disagreement as to their place in hominoid evolution, but they may be close to the ancestry of modern orangutans. India, middle to late Miocene, 12.5–8.5 Ma.

**Sivatherium:** a genus of artiodactyl mammals in the family Giraffidae; similar to the modern okapi but larger, about 10 feet high and 7 feet at the shoulder, weighing at least half a ton; it had a pair of wide, antler-like ossicones at the back of its skull and a smaller pair above its eyes; Africa and India, Pliocene to about 8000 years ago.

**Skolithos:** a trace fossil ichnogenus, burrows of diameters up to 1.6 inches in mainly marine and sometimes freshwater strata; the often-vertical burrows are straight, helical, or slightly curved; they are made by phoronids, worms, insect larvae, other arthropods, and even small vertebrates; Ediacaran to Recent.

**“small, shelly fauna”:** a “catch-all name that spells frustration” according to Stephen Jay Gould. The phrase refers to an enigmatic assemblage of spines, plates, caps, and cups that represent the first steps toward hard skeletons in animals. Occurring globally from the end of the Ediacaran into the early Cambrian, these fragmentary bits and pieces have long been a puzzle, but whole specimens have now been discovered of some of the animals that bore the fragments in life; see for example *Microdictyon sinicum*.

**Smilodectes:** a genus of small adapoid primates in the order Strepsirrhini and subfamily Notharctinae; it weighed 4–6 pounds and was scansorial; North America, early Eocene.

**Smilodon:** “knife-tooth,” a genus of cats in the subfamily Machairodontinae; one of several genera of large sabertooth cats that flourished in the Pliocene and Pleistocene but disappeared about 10,000 years ago; global distribution except Australia and Antarctica; see also *Megantereon*, *Homotherium*, and *Machairodontinae*.

***Smilodon fatalis***: the species of sabertooth cats found in the La Brea Tar Pits in Los Angeles; middle Pleistocene to about 11,000 years ago.

***Smilodon gracilis***: an early California sabertooth, Pliocene to about 1 Ma.

***Smilodon populator***: a South American sabertooth cat, the largest known felid at 500–800 pounds; late Pleistocene.

**Smith, William**: an English geologist, Smith is considered the founder of biostratigraphy for his ground-breaking geologic map of England of 1815, which revolutionized the study of layers of rock, brilliantly combining paleontology, petrology, and geology. By establishing the principle of faunal succession, Smith's work immediately inspired widespread use of his techniques in comparing fossils in widely separated rock outcrops to understand the strata underlying the earth's surface.

**Solanaceae**: the nightshades, a large family of still-extant plants in the order Solanales; a 2017 description of early Eocene (52 Ma) lantern fruits in the genus *Physalis* reports the earliest-known occurrence of the family, in Patagonia before the breakup of South America from Antarctica; Argentina, Eocene.

***Solenopora***: a disputed genus of calcite-secreting organisms, some seeming to be algae in the division Rhodophyta and extinct family Solenoporaceae; however, most specimens are now recognized as chaetetid sponges; most were nodular masses, while some late Paleozoic and Mesozoic forms occur as encrusting mats; they appeared in the Cambrian, and some forms may still be extant.

**Solitaire**: see **Raphinae**.

**Solite Quarry**: an important Triassic Konservat-Lagerstätte in Virginia, noted especially for insects and small reptiles; its lakebed deposits were laid down over a period of less than 50,000 years; North America, Late Triassic, late Carnian to Norian.

**Solnhofen Limestone**: a Late Jurassic Konservat-Lagerstätte in Bavaria, where several quarries produce lithographic limestone, with fossils of the best quality coming from those near the towns of Solnhofen and Eichstätt. The extremely fine-grained limestone layers of the Solnhofen Formation were laid down in a protected lagoon on the northern edge of the Tethys Sea over a period of half a million years. The stagnant lagoon contained anoxic and hypersaline areas with few benthic organisms, and most of the 600 species of fossils are allochthonous, probably washed into the lagoon by storms. Several crustacean fossils lie at the end of "death trail" trackways, one 30 feet long (see *Mesolimulus* and *Mecochrinus*). Only one dinosaur, *Compsognathus*, is known here; it has several skeletal similarities to *Archaeopteryx*, the best-known of the Solnhofen fossils. Marine vertebrates such as ichthyosaurs are known only from poorly preserved fragments, having reached the lagoon through the coral reefs at its edge during severe storms. Other well-preserved fossils include pterosaurs, some with toe-webbing and hair-like covering of wing membranes intact; fish; amphibians; insects; and many arthropods. Germany, Late Jurassic (Kimmeridgian, 150 Ma).

**Solo man:** see **Ngandong fauna**.

**Sonorasaurus:** a mid-Cretaceous sauropod of North America, a monospecific genus of large sauropod dinosaurs in the family Brachisauridae; notable for its extremely long neck, *S. thompsoni* grew as long as 55 feet and 30 feet high, its neck evidently almost as long as the rest of its body and tail; Sonora Desert, Albian to Cenomanian.

**Soomaspis:** a monospecific genus of trilobite-like arthropods in the order Nektaspida; *S. splendida* resembles a soft-bodied agnostid trilobite, isopygous and eyeless, and with only three thoracic segments; known only from the Soom Shale of South Africa, Late Ordovician.

**Soom Shale:** a Konservat-Lagerstätte near Cape Town, South Africa; several sites contain exceptionally well-preserved fossils in cold-water deposits of the Upper Ordovician, 445–444 Ma. Although the formation is unusual for the almost complete absence of benthic organisms, its biota includes several organisms familiar from the Cambrian Lagerstätten as well as some that became more prominent later in the Paleozoic, such as the eurypterid *Onychopterella*. Among other important specimens are the conodont *Promissum pulchrum* and the nektaspid *Soomaspis*, as well as brachiopods, lobopods, orthocone cephalopods, and chitinozoans.

**Soricidae:** the shrews, a still-extant large family of small, mouse-like mammals in the order Eulipotyphla, mainly insectivorous; they first appeared in the late Eocene and have diversified worldwide.

**Spatangoida:** the heart urchins, a still-extant order of atelostomate echinoids, characterized by an oval shape and a deep groove into the mouth, and by the absence of a lantern; global distribution, Early Cretaceous to Recent.

**speciation:** development of new species through lineage splitting, resulting in reproductively isolated branches.

**species:** 1. biological species concept: a group of actually or potentially interbreeding organisms that are almost completely isolated reproductively from other organisms, exchanging only a few genes. 2. evolutionary species concept: a single lineage of ancestor-descendant populations that maintains its own identity distinct from other lineages.

**species duration:** The length of time that a species persists varies widely, with some long-lived species lasting many millions of years, but the average duration is estimated to be about 4 million years.

**speciose:** species-rich, containing many species.

**Sphaeractinoidea:** Mesozoic marine hydrozoans possibly related to the stromatopoids and the spongiomorphs; they have long been called “Mesozoic stromatopoids,” but the discovery of spicules in some species has resulted in those species being reclassified as demosponges and raised the possibility that all sphaeractinoids may eventually be reclassified.

**Sphaerirhynchia:** a genus of articulate brachiopods in the still-extant order Rhynchonellida and extinct superfamily Rhynchonelloidea; strongly biconvex and almost spherical, less than an inch across, they attached to the soft substrate with a functional pedicle; global distribution, Silurian and Devonian.

**Sphenacodon:** “wedge-point tooth,” the type genus of the synapsid family Sphenacodontidae; 6–10 feet long, *Sphenacodon* was slightly smaller than its cousin *Dimetrodon* and had only a low sail about a foot high; North America, Late Pennsylvanian to middle Permian.

**Sphenacodontidae:** a family of large, advanced pelycosaurian synapsids; they were characterized by relatively long and narrow snouts and skulls; most genera have tall, sometimes greatly elongated neural spines; the most familiar sphenacodontid is *Dimetrodon*, which is well-known for its sail more than 3 feet high; North America and Europe, Late Carboniferous to middle Permian.

**Spheniscidae:** the penguins, a family of large flightless birds of the Southern Hemisphere; they first appeared in the middle Eocene and diversified rapidly; notable for having retained the bone structure and musculature of flying birds despite being flightless, penguins adapted these flight structures to swimming, essentially flying underwater; middle Eocene to Recent.

**Sphenodon:** “wedge tooth,” the tuatara, a still-extant genus of lizard-like reptiles in the family Sphenodontidae, represented by two species in New Zealand, *S. punctatus* and *S. guntheri*; they are as long as 3 feet and weigh up to 3 pounds; New Zealand, Miocene to Recent.

**Sphenodontidae:** a still-extant family of lizard-like reptiles in the order Rhynchocephalia. Sphenodonts were numerous in the Jurassic but are represented today by only one genus, the tuatara of New Zealand (*Sphenodon*); see also *Planocephalosaurus*. Global distribution, Triassic to Recent.

**Sphenophyllales:** “wedge leaf,” an extinct order of articulate vascular plants in the class Equisetopsida, related to the modern horsetails; small and slender, they grew only up to about 3 feet, with jointed stems and linear, forked, or wedge-shaped leaves; common as fossils in the Carboniferous and early Permian; global distribution, Early Devonian to Late Triassic.

**Sphenopteris:** a form genus of leaves from late Paleozoic and Mesozoic plants, generally of seed plants such as *Lyginopteris* but also of some ferns, in which the leaves produced spores; global distribution, Devonian to Late Cretaceous.

**Sphenosuchia:** an order of basal crocodylomorph reptiles; between 1 and 2 feet long and characterized by an upright posture and long, slender legs, they were fast runners; the monophyly of the order is in question; global distribution, Middle Triassic.

**sphinctozoans:** a polyphyletic group of hypercalcified sponges that grow as a series of chambers, one on top of the next; they originated in the Cambrian and flourished in the late Paleozoic and the early Mesozoic; absent from the fossil record

since the Late Cretaceous, but a single surviving species, *Vacletia crypta*, was discovered in Australia in 1977; global distribution, Cambrian to Recent.

***Spiclypeus shipporum***: a species of chasmosaurine dinosaurs in the family Ceratopsidae, found in Montana in 2005 and described in 2016; known from a partial skull and bones of the spine, legs, and hips, it was about 15 feet long and weighed up to 4 tons, a medium-sized ceratopsian; like other chasmosaurs, it had a very large and highly ornamented neck frill; North America, Late Cretaceous, 76–75 Ma.

**spicule**: a pointed mineral structure that is part of an animal's skeleton, as in some sponges and brachiopods; most often of silica or calcium carbonate.

***Spinosaurus aegyptiacus***: the type species of a genus of very large carnivorous dinosaurs characterized by sturdy 6-foot-long vertebral spines and by crocodile-like teeth as long as 7 inches. It was possibly the largest known carnivore at 36–50 feet long, with its weight centered on its neck. Study of various fossils, including a partial skeleton from the Kem Kem beds of Morocco — described in 2013 — seems to prove that *Spinosaurus* spent a large part of its life in North African rivers, preying on the numerous large species of fish and turtles. It was discovered about 1913 by Ernst Strömer, who may have suspected its riverine habit but could not prove it. See also *Bahariasaurus*, *Baryonyx*, *Carcharodontosaurus*, *Suchomimus*, and **Strömer's Riddle**. North Africa, Late Cretaceous, 112–94 Ma.

**Spiriferida**: an order of articulate brachiopods in the class Rhynchonellata. Strongly ribbed and either punctate or impunctate, spiriferides are characterized externally by a long, straight hinge line that is the widest part of the body, so that the animal appears to be winged. Their name refers to the laterally directed spiral brachidia, which support the lophophore. The Spiriferida appeared in the Ordovician, were still rare in the Silurian, widespread in the Devonian and Carboniferous, survived the end-Permian extinction, and persisted to the Early Jurassic.

**Spiriferidina**: the larger of the two suborders of brachiopods in the order Spiriferida (the other is Delthyridina, early Silurian to Permian); characterized by strong ribbing; global distribution, Late Ordovician to late Permian.

***Spiriferina walcotti***: a species of articulate brachiopods in the order Spiriferinida; characterized by a broad, ribbed shell with a wide hinge line and folds at the edge; from 1 to 2 inches wide with faint concentric growth lines; Europe, Early Jurassic.

**Spiriferinida**: an order of later articulate brachiopods in the class Rhynchonellata, similar to Spiriferida but generally smooth-shelled; global distribution, Early Devonian to Early Jurassic.

***Spondylus***: a still-extant, large, and diverse genus of spinose bivalve mollusks in the family Spondylidae, and in the same superfamily as scallops, the Pectinoidea; they cement themselves to rocks and are often called spiny oysters, although unrelated; up to 4 inches wide, they have several eyes around the edges of the shell; global distribution, Middle Triassic to Recent.



**sponges:** see **Porifera**.

**Spongiomorphidae:** the single family of colonial hydrozoans in the extinct order Spongiomorphida; their massive colonies are characterized by longitudinal rods perpendicular to the growth surface and connected by horizontal bars parallel to the surface; global distribution, Late Permian to Eocene.

***Spriggina*:** an enigmatic genus of soft-bodied organisms known definitively only from the Ediacara Hills; from 1 to 2 inches long, it is segmented, with a small head; it superficially resembles an arthropod, but several characters seem to mark it as unarthropod; it also resembles sea pens and some rangeomorphs; Australia, 560 Ma.

**Squalodontidae:** a possibly polyphyletic family of large toothed whales in the superfamily Platanistoidea; although poorly understood, they seem to be intermediate between the Archaeoceti and the Odontoceti; the type genus *Squalodon* is the only unquestioned member of the family; global distribution, Oligocene to Pleistocene.

***Squaloraja*:** a genus of chimaerid fish in the family Squalorajidae that seems to be transitional between sharks and rays; known from a specimen collected by Mary Anning and one from Italy; Europe, Early Jurassic.

**Squamata:** the order of reptiles that contains the snakes (Serpentes), lizards (Lacertilia), and worm lizards (Amphisbaenia); the second-largest order of vertebrates, after the perciform fish, its sister group is the Rhynchocephalia; global distribution, Early Jurassic to Recent.

**Staffellidae:** a family of benthic, semi-infaunal foraminiferans in the superfamily Fusulinoidea, related to the Ozawainellidae; the test is generally circular; global distribution, Late Carboniferous to late Permian.

**stage:** see **Geologic Time Scale**.

***Stagonolepis*:** a genus of herbivorous aetosaurian reptiles in the family Stagonolepididae; quadrupedal and slow-moving, it was about 10 feet long and well-armored, with osteoderms covering most of its body; *Stagonolepis* had no teeth at the front of its mouth but cheek teeth adapted for chewing vegetation; Europe and possibly North and South America, Late Triassic, 237–227 Ma.

**Staphylinidae:** the rove beetles, the largest family of beetles, in the order Polyphaga; staphylinids are carnivorous or omnivorous scavengers; probably the oldest is *Leehermania prorova*, found in the Solite Quarry of Virginia and described in 2012; global distribution, Late Triassic to Recent.

***Staurikosaurus*:** a genus of early theropod dinosaurs in the family Herrerasauridae; dated at 225 Ma, it is one of the earliest-known dinosaurs; it was 7 feet long and weighed about 66 pounds; Brazil, Late Triassic.

**Stauropteridae:** a group of enigmatic Carboniferous plants usually placed in the order Cladoxylopsida and considered ancestral ferns; poorly known but characterized by forked, spore-bearing branches, similar to the ancestral *Cooksonia* of the Silurian; cosmopolitan, Late Devonian to Late Carboniferous.



**stegocephalians:** a paraphyletic group of choanatan lobe-fins, formerly considered rhipidistian fish but now identified as tetrapods (such as *Tiktaalik* and *Ventastega*), which are transitional forms leading to the first terrestrial animals; cosmopolitan, Middle to Late Devonian.

**Stegodontidae:** a family of proboscideans in the extinct suborder Mammutoidea, considered by some to be a subfamily in the Elephantidae; they had low-crowned teeth with thick enamel but like modern elephants had lost their lower tusks; Africa and Asia, middle Miocene to late Pleistocene.

**Stegosauria:** “plate lizard,” a suborder of herbivorous ornithischian dinosaurs; they were well-armored, with a row of plates along the spine and scutes elsewhere; the head was small and narrow, and they had long hindlimbs but were quadrupedal; global distribution, Jurassic to Cretaceous.

**Stegosauridae:** a family of large ornithischian dinosaurs in the suborder Stegosauria; this family was larger than the earlier stegosaurs, the type genus *Stegosaurus* weighing more than 5 tons; North America, Europe, Asia, and Africa; Middle Jurassic to Early Cretaceous.

**Steinheim skull:** a fairly well-preserved hominin skull without the lower jaw, found at Steinheim, Germany; it has characteristics of Neanderthals and of *Homo heidelbergensis*, and is estimated to be between 250,000 and 350,000 years old.

**stem group:** a paraphyletic grouping of organisms that consists only of extinct species, excluding all members of the crown group.

**Steneosaurus:** a genus of thalattosuchians in the family Teleosauridae; the species in the genus provide an example of niche partitioning, being divided into two groups, one with short, broad jaws, and the other with long, very narrow jaws; especially good specimens of the latter species are known from the Holzmaden Shale; Europe and Madagascar, Early Jurassic to Early Cretaceous.

**stenohaline:** not tolerant of a wide range of salinity; trilobites and brachiopods, for example, are stenohaline and less able to tolerate changes in salinity than bivalves, which are generally more euryhaline.

**Stenolaemata:** the oldest class of marine bryozoans. Characterized by sac-shaped, tubular, or conical exoskeletons, stenolaemates were the dominant bryozoans throughout the Paleozoic, contributing to reefs in many places. One order, the Cyclostomatida, is still extant; the Cystoporata and Cryptostomata became extinct at the end of the Permian and the Trepostomata in the Triassic. See also **Gymnolaemata**. Global distribution, Early Ordovician to Recent.

**Stenophlebiidae:** a family of damsel-dragonflies in the order Odonata; medium-sized to large, distinguished by their wing venation pattern and long, slender wings; a 2015 discovery in northwestern China represents the earliest specimen of the family; Europe, Asia, and South America; Early Jurassic to Early Cretaceous.

**Stenopterygius:** “narrow wing,” a genus of thunnosaurian ichthyosaurs known from well-preserved specimens from Holzmaden and other Lower Jurassic sites;

up to 12 feet long, with a long, narrow beak and long, thin pectoral fins; a famous Holzmaden specimen is a mother and fetus which died before childbirth, with the fetus in a position to be born tail-first; Europe, Early Jurassic.

**Stensioellida:** a monospecific order of primitive fish, generally considered the most primitive placoderms. The order consists of one species, *Stensioella heintzi*, known only from the Hunsrück Slate. It has a whip-like tail and large pectoral fins, and its elongate body has no large bony plates but is armored by a covering of small dermal tubercles. Germany, Early Devonian.

**Stenurida:** a small order of primitive asterozoan echinoderms in the class Ophiuroidea; this group of brittle stars includes widely disparate families and may be polyphyletic; cosmopolitan, Early Ordovician to Late Devonian.

**Stephanodiscus yellowstonensis:** a species of diatoms in the order Thalassiosirales with a unique history. Recent research shows that it evolved within a short span of time in the Yellowstone area of Wyoming, between 12,000 and 8000 years ago. Once found in many lakes of the area, it is now restricted to Yellowstone Lake. It has not evolved further in the last 8000 years and now seems to be becoming less abundant.

**stereom:** the sponge-like network of calcium carbonate crystals that composes the body tissue of all echinoderms.

**Stereospondyli:** a large suborder of late temnospondyl reptiles, the largest about 7 feet long; characterized by a broad, flat head, they were among the last of the temnospondyls; known only from Gondwana up to the end of the Permian, they radiated worldwide in the Triassic; late Permian to Early Cretaceous.

**Steropodon:** one of several extinct genera of monotremes in the family Steropodontidae; closely related to the modern platypus (*Ornithorhynchus anatinus*), it had teeth and grew as long as 2 feet, large for a Mesozoic mammal; New South Wales, Australia, Early Cretaceous, 110–105 Ma.

**Stethacanthus:** “chest spine,” a genus of Devonian sharks in the order Symmoriida, notable for a mysterious structure on a male’s back in place of the first dorsal fin; it is a flattened area covered with dermal denticles, looking like a narrow, toothed anvil, and its purpose is unclear; North America and Europe, Late Devonian to Early Carboniferous.

**Sthenurus:** “strong tail,” a genus of kangaroos in the family Macropodidae and extinct subfamily Sthenurinae; short-faced and with a tail shorter but stronger than modern kangaroos, they grew as long as 10 feet and weighed more than 500 pounds; Australia, Pliocene to Pleistocene, becoming extinct later than 19,000 years ago.

**Stigmaria:** a form genus of the rooting structures of lycopsid trees such as *Lepidodendron* and *Sigillaria*; global distribution, Carboniferous.

**stipe:** the branch of a graptolite, to which the individual thecae are attached; also, the stem of algae connecting the holdfast to the upper parts.

**Stolonoidea:** a group of encrusting or sessile animals generally considered graptolites, but possibly belonging to the pterobranch family Rhabdopleuridae; global distribution, Ordovician.

**stratigraphy:** the descriptive study of rock strata and interpretation of geological history, including deposition, relative age, and correlation between outcrops that may be separated by great distances; see **biostratigraphy**.

**Strawberry Bank:** a Lower Jurassic Lagerstätte in Somerset, England. It is one of four Lagerstätten dated near the boundary of the Pliensbachian and Toarcian Stages of the Early Jurassic, along with the well-known Holzmaden deposits in Germany, the Osteno deposits of Italy, and the recently explored Ya Ha Tinda site in Canada. Strawberry Bank is especially notable for its nearshore deposits containing 20 species of insects as well as its specimens of nektic organisms (ichthyosaurs, fish, and cephalopods). It differs from other sites also in having predominantly three-dimensional specimens inside calcareous nodules. England, Early Jurassic, 183 Ma.

**Strepsirrhini:** a suborder of primates that includes the lemuroids, galagos, and lorises, and their extinct adapiform primate relatives; formerly called Prosimii; distinguished from haplorrhines by the moist area around their nostrils; see also **Haplorrhini**; widespread in Laurasia from the Eocene to the Miocene but now found only in tropical Asia and Africa; early Eocene to Recent.

**Strepsodiscus:** one of the earliest mollusks, a genus of primitive snail-like mollusks generally considered bellerophonitid gastropods; two species are known, with an asymmetrical shell about an inch high; see also **Chippewaella**; North and South America and Antarctica, late Cambrian to Ordovician.

**Streptognathodus isolatus:** a species of conodonts in the family Polygnathidae; its first appearance, in Kazakhstan, marks the beginning of the Permian at 298.9 Ma; several other species of *Streptognathodus* are important for stages of the Late Carboniferous and early Permian.

**Streptospondylus:** a genus of medium-sized theropod dinosaurs in the family Megalosauridae; one of the first dinosaurs to be discovered, its fossils were found in the late eighteenth century in France and described variously for several decades until finally recognized as dinosaurs; France, Middle Jurassic.

**stridulation:** see **Orthoptera**.

**strobilus:** a cone; a common form genus of many cone-bearing plants.

**stromatolites:** layered, often bulbous, accretionary structures formed by microorganisms in a process of microbial growth, decomposition, and lithification. They accumulate grains of sediment of many kinds in bio-chemical films called laminae, whose morphology varies according to water depth and wave action. Some as much as 3.5 billion years old, they occur in varied shapes from conical to horizontal, often forming reefs. Global distribution, Archaean to Recent.

**Stromatoporoidea:** a group of primitive reef-building organisms now generally considered poriferans, either demosponges or sclerosponges, but their precise affin-

ities are still in dispute; see also **Sphaeractinoidea**; cosmopolitan, Precambrian to Cretaceous, but especially important reef-builders in the Silurian and Devonian.

**Strömer's Riddle**: the question why so many large predatory dinosaurs inhabited the riverine environments of North Africa in the middle of the Cretaceous although relatively few herbivores (such as *Aegyptosaurus*) were present in the fossil record. Ernst Strömer, of the University of Munich, raised the question in the course of his extensive excavations in North Africa in the early twentieth century; most of his specimens were lost in a bombing raid in Munich in 1944. Some research between 2010 and 2014 indicates that the large carnivores were supported by a large population of gigantic aquatic animals, such as a variety of very large turtles, 8-foot lungfish, 13-foot coelacanths, and 25-foot sawfish. If further research confirms that *Spinosaurus* and other large predators did in fact spend most of their time in the water, the riddle may have been solved.

**strophic**: of brachiopods, having a well-defined and elongated hinge line.

**Strophomenida**: the largest and most diverse brachiopod order, articulate brachiopods in the class Strophomenata; the type genus *Strophomena* appeared in the Ordovician but became abundant only in the Triassic; the order is generally characterized by one convex valve and the other flat or concave; they are usually wider than they are long, with a strophic hinge line; but see also the aberrant horn-shaped *Prorichthofenia* and conical *Richthofenia*; global distribution, Ordovician to Early Jurassic.

**Strunius**: a genus of unusual lobe-finned fish in the order Onychodontida; only 4 inches long, *Strunius* had the articulated skull characteristic of the rhipidistians and the coelacanths; its fins were not so muscular as those of other lobe-fins, being stiffened by bony rays like the fins of actinopterygians; Europe, Late Devonian.

**Struthiomimus**: “ostrich mimic,” a genus of medium-sized saurischian dinosaurs in the family Ornithomimidae; they were bipedal and bird-like, with a small, slender head and long neck; the type species, *S. altus*, was about 14 feet long and weighed about 330 pounds; Canada, Late Cretaceous, 78–68 Ma.

**Stylasterina**: an order of delicate, lacy cnidarians in the class Hydrozoa; like the milleporines, they are colonies of soft-bodied polyps but different from other Hydrozoa in having calcareous parts that fossilize; New Zealand, Asia, Australia, and North America; Cretaceous to Recent.

**Stylemys**: a genus of small terrestrial tortoises in the family Testudinidae; the earliest-known land turtle in North America, up to 3 feet long; forelimbs too weak for burrowing; North America, Europe, and Asia; late Eocene to Miocene.

**Stylemys nebrascensis**: a species of North American tortoise in the family Testudinidae; about 2 feet long, with an unusually high-domed shell; Nebraska, late Eocene to early Oligocene.

**Styracosaurus**: a genus of North American ornithischian dinosaurs in the family Ceratopsidae; characterized by large armor plates on the head, a robust nasal horn,

and a large neck frill crested with long spikes; rhinoceros-sized, about 18 feet long and weighing more than 3 tons; Alberta and Montana, Late Cretaceous, 76–74 Ma.

**Subulitidae:** a family of marine siphonate gastropods in the clade Caenogastropoda and superfamily Subulitoidea; from 1 to 2 inches long, generally awl-shaped; global distribution, Ordovician to Carboniferous.

**Suchomimus:** a monospecific genus of primitive, crocodile-like dinosaurs in the family Spinosauridae and subfamily Baryonychinae, closely related to *Baryonyx*. A striking example of convergent evolution, *S. tenerensis* was bipedal and had a long tail and strong forearms. Its long, flattened skull was very similar to that of a crocodile and was well-adapted to catching fish. *Suchomimus* had 120 cone-shaped teeth and was 40 feet long and 10–12 feet high at the hip. North Africa, Early Cretaceous, 121–113 Ma.

**sulcus:** a shallow groove or furrow on the surface of some part of an organism's body; in brachiopods, a characteristic furrow in the pedicle valve, usually corresponding to a fold or ridge in the brachial valve; in vertebrates, usually referring to a fold separating parts of the brain.

**Sundance Formation:** a mostly sandstone Middle Jurassic formation in Western North America; composed of mainly marine deposits laid down in the inland waterway called the Sundance Sea, it contains few but important fossils of the period.

**Supersaurus:** a genus of very large sauropodomorph dinosaurs in the family Diplodocidae; on the basis of specimens from Colorado and Wyoming, which account for about 35 percent of the skeleton, its length is estimated at 110–112 feet and its weight at up to 40 tons; see also **Sauropoda**; United States and Portugal, Late Jurassic, 152–150 Ma.

**suture line:** of ammonoids, the pattern of lobes and saddles on the edge of a septum, often used in classification of genera.

**Swanscombe Man:** three skull fragments found at Swanscombe, England, anatomically similar to *Homo sapiens* with a cranial capacity of around 1300 cc; dated at about 450,000 years ago.

**Sycidiales:** an extinct order of charophytic algae in the class Charophyceae and division Charophyta; notable for its uncommon gyrogonites, which have porous vertical walls, as opposed to the characteristically spiral walls of later charophytes; the oldest known species, *Sycidium siluricum*, is considered the oldest known bisexual plant; global distribution, Silurian to Early Carboniferous.

**Sylvian sulcus:** the lateral sulcus of the human brain, a shallow furrow between three lobes and the most prominent human sulcus; deeper in most primate brains, it is a deep cleft in the most primitive monkeys.

**Symbos cavifrons:** a species of North American woodland musk ox, an artiodactyl ruminant mammal in the family Bovidae; it is known from the early Pleistocene and was one of many large ruminants whose extinction at the end of the Pleistocene was probably human-related.

**symmetrodonts:** formerly considered an order of primitive mammals, but the term is now used in an informal sense to refer broadly to a large number of early mammals close to the line of descent from cynodonts to mammals; the name refers to the symmetrical arrangement of the upper and lower molar teeth; see also *Kuehniotherium* and *Morganucodon*; North America, Europe, and Asia; Late Triassic to Late Cretaceous.

**Symphysurus:** a genus of asaphid trilobites in the family Nileidae; medium-sized, about 3 inches long; global distribution, Early to Late Ordovician.

**synapomorphy:** an apomorphy shared by a group of lineages to the exclusion of other groups, a key to inferring evolutionary relationships by identifying common ancestors.

**Synapsida:** the advanced amniotes formerly called mammal-like reptiles. They are a sister group of reptiles but are now considered part of the clade Reptiliomorpha. Synapsids are identified primarily by a lateral temporal fenestra (a single opening in the skull behind each eye). The Synapsida include the pelycosaurs (Permian) and the more advanced therapsids (chiefly Triassic, descendants of pelycosaurs and ancestors of mammals). Middle Pennsylvanian to Recent .

**synonyms:** two or more different names referring to the same taxon.

**Syntrophiidina:** one of two suborders of impunctate articulate brachiopods in the extinct order Pentamerida; more primitive than the second suborder, the Pentameridina; characterized by an almost circular shell with a pronounced dorsal fold; global distribution, early Cambrian to Early Devonian.

**syntypes:** a set of several specimens that serve together as name-bearers for a species if no holotype has been designated.

**Synziphosurina:** a paraphyletic group of chelicerate arthropods in the still-extant class Xiphosura, related to the modern *Limulus*; characterized by free abdominal segments; cosmopolitan, Ordovician to Devonian.

**Syringophyllidae:** a family of tabulate corals in the extinct order Sarcinulida, with a horizontal and tubulate structure; global distribution, Ordovician and Silurian.

**Syringopora:** a genus of tabulate corals in the order Auloporida and family Syringoporidae. *Syringopora* is phaceloid, with a sub-colonial structure of long and vertical cylindrical corallites, interconnected irregularly by horizontal tubuli, so that there was no contact in life between the polyps living at the top of the column of corallites. As the colony grew, it expanded horizontally. Because of this structure, *Syringopora* is often called organ-pipe coral. Global distribution, Ordovician to Permian.

**Syringothyris:** a genus of articulate brachiopods in the superfamily Spiriferinida and family Syringothyrididae; characterized by an internal tube around the pedicle valve, a punctate shell, and a pyramidal shape; about 2 inches across and semi-infaunal in lime substrates; global distribution, Silurian to Permian.

# T

**tabula:** (plural tabulae) a transverse septum between the walls of tabulate corals and some archaeocyathans.

**Tabulata:** one of the two dominant Paleozoic corals, an order of wholly colonial cnidarians in the subclass Hexacorallia. The Tabulata are distinguished by tabulae within each of the corallites, which are almost always hexagonal. Appearing along with the rugose corals and stromatoporoids at the beginning of the Ordovician, they are characteristic of Silurian and Devonian shallow seas. Less common after the Devonian, they became extinct at the end of the Permian. Global distribution, Early Ordovician to Permian.

**Tachypleus:** one of two surviving genera of horseshoe crabs, chelicerates in the order Xiphosurida and family Limulidae; see also **Limulus**; China and Southeast Asia, Late Jurassic to Recent.

**Taeniodonta:** a suborder of non-placental eutherian mammals in the order Cimolesta; the taeniodonts varied greatly in size, from rat-sized to bear-sized (*Stylinodon*, of the Eocene); some became highly specialized for digging, but efforts to categorize them on that basis are still tentative because of a sparse fossil record; Western North America, Late Cretaceous to Eocene.

**Taeniolabidoidea:** a suborder of primitive mammals in the order Multituberculata; although mostly small and rodent-like, some were the largest of the multituberculates; *Taeniolabis taoensis* weighed more than 200 pounds, similar to *Castoroides*, the largest beaver of the Pleistocene; North America and Asia, Late Cretaceous to early Eocene.

**Taeniopteris:** a genus of Mesozoic tree-like plants in the Pentoxylales with leaves as long as 16 inches; global distribution, Carboniferous to Late Cretaceous.

**Taimyr wolf:** According to a DNA analysis in 2015, a 35,000-year-old fossil of a wolf on the Taimyr Peninsula is a previously unknown species that indicates a date between 27,000 and 40,000 years ago for the splitting off of dogs from wolves, earlier than previous estimates; Siberia.



***Tanystropheus***: a genus of large archosauromorph reptiles in the extinct order Protosauria and family Tanystropheidae; notable for a very long neck (10 feet) composed of only 13 elongated vertebrae, while its body and tail together were only about 10 feet long; probably a semi-aquatic piscivore; Europe and Asia, Middle Triassic.

***Tanytrachelos***: a genus of small amphibious reptiles in the extinct order Protosauria and family Tanystropheidae; the type species *T. ahynis* is a long-necked archosauromorph only 1–2 feet long; United States, Late Triassic, 225–220 Ma.

**Tapejaridae**: a family of pterodactyloid pterosaurs, probably related to the Azhdarchidae; characterized by a large bony crest and better vision than most pterosaurs; many possessed a distinctive rounded crest, sometimes as wide as 3 feet; global distribution, Early to Late Cretaceous.

**taphocoenosis**: a taphonomic association of fossils, either autochthonous or allochthonous. The term is sometimes used to refer specifically to an allochthonous assemblage of fossils transported after their death and deposited together, so that the assemblage does not represent a functional community in life. The term thanatocoenosis, on the other hand, specifically refers to an autochthonous death assemblage of organisms that died together.

**taphonomic artifact**: a product of artificial character resulting from some accident during the process of fossilization and thus not indicative of the actual structural relationships of the parts of the organism.

**taphonomy**: the study of an organism's history between its death and the time of its discovery. Three taphonomic stages are recognized: necrosis (death), biostratinomy, and diagenesis. Biostratinomy refers to what happens to the organism between necrosis and burial, while diagenesis refers to what happens to it after burial, principally the process of mineralization. Taphonomy is especially concerned with transported allochthonous deposits and with biases present in deposition and fossilization, such as scavenger activity, different rates of disintegration and decomposition, displacement of the fossil by soil movement, and dissolution or mineral replacement of bones.

**Tapiroidea**: a still-extant superfamily of perissodactyl mammals in the suborder Ceratomorpha. Probably related to the early Eocene *Homogalax* and *Hyracotherium*, the tapiroids spread throughout the northern continents and diversified slightly in the middle Eocene into four short-lived families: the Isectolophidae in North America, the Lophiodontidae in Europe, and the Deperetellidae and Lophialetidae in Asia. Spreading globally in the Oligocene with little evolutionary change, the tapiroids became extinct in the northern land masses, persisting in some places to about 10,000 years ago. Several genera are still extant elsewhere. See also *Cambaytherium* and *Heptodon*.

***Tapirus californicus***: a species of tapir known from New Mexico to Southern California in the early and middle Pleistocene; one specimen is known from the Oregon



coast, a well-preserved jaw with teeth; it is either *T. californicus* or the better-known *T. haysii*, which is common in lower Pleistocene deposits in Eastern North America.

**Tapocyon:** a genus of primitive mammals in the family Miacidae; coyote-sized, it had retractable claws and was partly arboreal; Southwestern United States, Eocene.

**Tarbosaurus bataar:** a species of large carnivorous dinosaurs in the subfamily Tyrannosaurinae. A close Asian relative of *Tyrannosaurus rex*, it was 33–39 feet long and weighed 5 tons or more. Two elongated eggs discovered in 1993, purportedly of this species, are at 16.5 inches long the largest dinosaur eggs known; Northern China, Late Cretaceous.

**Tardigrada:** The “water bears,” a still-extant minor phylum of almost microscopic animals, called tardigrades because of their slow, lumbering gait. There are about 400 modern species, most of them living in water films on lichens and other plants, and some living on the bottom of ponds and ocean basins. They have eight legs, most of which are only 0.1 to 0.5 mm long. They are notable for their ability to survive long periods of cryptobiosis, complete dormancy; a large group in a European Space Agency experiment survived in a vacuum for a week in orbit around the Earth. No fossils were known until their discovery in the 1990s in Cambrian deposits in Siberia, so that the group does seem to have existed as long as most other modern phyla.

**Tarsiidae:** a still-extant family of haplorrhine primates in the infraorder Tarsiiformes; tarsiers, now restricted to Southeast Asia, arose in the middle Eocene and became widespread in North America, Europe, and Asia, with two disputed African species from the Eocene and Oligocene (see *Afrotarsius*).

**Tasmanian tiger:** see *Thylacinus*.

**Taxideinae:** the American badgers, a subfamily of caniform omnivores in the family Mustelidae; North America, Miocene to Recent.

**Taxocrinida:** an order of crinoid echinoderms in the extinct subclass Flexibilia; characterized by a small, conical cup and crown; global distribution, Middle Ordovician to Late Carboniferous.

**taxon:** a group of organisms sharing unique features that differentiate the group from other taxa.

**taxonomy:** the study of the nomenclature and classification of organisms in groups according to their descent and evolutionary relationships.

**Teilhardina:** a genus of marmoset-like haplorrhine primates tentatively placed in the family Omomyidae, but probably polyphyletic and currently being reassessed; North America, Europe, and Asia; early to middle Eocene.

**Teilhardina magnoliana:** the earliest-known primate in North America; mouse-sized, weighing about an ounce, it resembled a small marmoset; discovered in 2008 and estimated to have lived at the boundary of the Paleocene and Eocene; United States.

***Teleoceras***: a genus of perissodactyl mammals in the family Rhinocerotidae; standing 9 feet high and weighing 1 ton, it resembled the hippopotamus but bore a small nasal horn; North America and France, early Miocene to early Pliocene.

***Teleosauridae***: a family of aquatic crocodylomorphs in the clade Thalattosuchia; generally characterized by elongate snouts and forelimbs only half as long as the hindlimbs, they resembled the modern gharial; they ranged in length from 6 to more than 16 feet, with some estimates much higher; North and South America, Europe, Africa, and possibly China; Early Jurassic to Early Cretaceous.

***Teleostei***: an infraclass of actinopterygian fishes in the superclass Osteichthyes. The teleosts comprise 50 percent of all known vertebrate species and 96 percent of all extant species of fish. They are characterized by movable upper-jaw bones, which allow the jaw to protrude forward; fully homocercal (symmetrical) tail fins; and thin, bony scales. Most teleosts reproduce by external fertilization of eggs, with generally no paternal care; a few genera are viviparous and somewhat altricial. Early Triassic to Recent.

***Telephinidae***: a family of nektic trilobites in the order Proetida; see also *Opipeuterella*; global distribution, Ordovician.

***telson***: the terminal section of the body of many arthropods.

***Temnospondyli***: “cut vertebra,” a large, diverse, and long-lived order of semi-aquatic and marine tetrapods, generally considered primitive amphibians. They include the first vertebrates to fully adapt to terrestrial life. Ranging in size from very large (*Mastodonsaurus*) to very small, they flourished in the late Paleozoic and the Triassic, and some genera survived into the Cretaceous. Whether they are ancestral to modern amphibians is unclear. (See *Amphibamus*.) Global distribution, Carboniferous to Cretaceous.

***Tempskya***: a genus of Cretaceous ferns, the only genus in its family, Tempskyaceae; it grew to about 15 feet and appeared tree-like, but its false trunk consisted of thin rhizomatous stems intertwined with small adventitious roots; its leaves grew directly from the upper parts of the trunk, not on branches or in a crown; global distribution but primarily Northern Hemisphere, Early to Late Cretaceous.

***Tentaculitida***: an enigmatic order of mollusk-like lophophorates, *incertae sedis*; less than an inch long but abundant in some localities, their ribbed calcitic shell is straight and conical; global distribution, Early Ordovician to Early Carboniferous.

***Teratophoneus curriei***: a species of carnivorous tyrannosaurid dinosaurs known only from a partial skull and post-cranial skeleton found in 2010 in the Kaiparowits Formation of Southern Utah; about 12 feet tall and 20 feet long; Late Cretaceous, about 76–74 Ma.

***Teratornithidae***: a family of vulture-like birds that includes the largest known flying birds, known principally from the Americas. The North American genera (at least four species in three genera identified so far) on average were about 40 percent

larger than the modern condor. *Teratornis merriami*, the best-known teratorn because of many specimens recovered from the La Brea Tar Pits, had a wingspan of 12 feet but weighed only 30–35 pounds. The largest known of the family is *Argentavis magnificens*, known from several partial specimens found in South America; it had a wingspan of 20–26 feet and may have weighed up to 170 pounds. (For the largest wingspan of a flying bird, see *Pelagornis sandersi*.) Predators and scavengers, the last of the teratorns became extinct about 10,000 years ago. North and South America, Miocene to late Pleistocene.

**Terebratellidina:** a still-extant small suborder of articulate brachiopods in the class Rhynchonellata and order Terebratulida; characterized by a long loop, a punctate shell, and a median septum; global distribution, Triassic to Recent.

**Terebratulidina:** a still-extant suborder of large articulate brachiopods in the class Rhynchonellata and order Terebratulida; characterized by a short loop, internal spicules, and a punctate and generally biconvex, egg-shaped shell; the widespread modern genus *Terebratula* grows as long as 4 inches; global distribution, Late Devonian to Recent.

**Teredinidae:** the shipworms, a family of marine bivalve mollusks; they are worm-like except that they use two small shells at the anterior end of the body to bore through wood, living inside their tunnel; known worldwide, they range from 2 inches to 3 feet long and are very destructive; they live worldwide but are less active in brackish water, such as the Baltic Sea; Early Jurassic to Recent.

**Teredo:** the most common genus of shipworms, marine bivalve mollusks in the family Teredinidae; global distribution, Late Jurassic to Recent.

**Ternifine man:** fossil bones found in Algeria in 1954 in a stratum about 700,000 years old, originally named *Atlanthropus mauritanicus* but later recognized as an example of *Homo erectus*.

**terrane:** a large fragment of continental crust differing from the surrounding crustal material because it originated a considerable distance away and was accreted to the continent by tectonic forces.

**Tertiary:** a discarded term formerly used to refer to the first part of the Cenozoic, from the end-Cretaceous extinction to the end of the Pliocene.

**Tessarolax:** a genus of gastropods in the still-extant family Aporrhaidae; characterized by thin, curving spines 1–3 inches long, growing from the edge of the lip; North America, Europe, Africa, and Madagascar; Cretaceous to Paleocene.

**test:** the external skeletal covering of echinoderms, composed of calcium carbonate; the internal walls and external covering in foraminiferans, composed of either calcium carbonate or agglutinated grains of sediment.

**Testudines:** the turtles, a still-extant order of mainly aquatic reptiles, characterized by a hard dorsal carapace above the rib cage and a hard ventral plastron attached to the rib cage. Whether their origin was terrestrial or marine is still debated. The order

was once called Chelonii, and the term *chelonian* refers to turtles in general. The earliest turtles are usually placed in a slightly different order or clade; see for example *Archelon*, *Desmatochelys*, *Odontochelys* and *Proganochelys*. See also **Cryptodira** and **Pleurodira**. Global distribution, Late Triassic to Recent.

**Testudinidae:** the modern land tortoises, a family of cryptodire tortoises in the still-extant order Testudines; global distribution, Cretaceous to Recent.

**tetanurans:** the large group of dinosaurs (including tyrannosaurids, ornithomimids, and others) that are more closely related to modern birds than to the ceratosaurs.

**Tethys Sea:** a chiefly tropical body of water to the east of Pangaea from the late Permian to the Miocene, with Laurasia to the north, Gondwana to the south, and the land masses that became China and Southeast Asia to the east.

**Tethytheria:** a clade of ungulate mammals containing the proboscideans, the sirenians, and the extinct desmostylians.

**Tetraceratops:** an obscure genus of small synapsids represented by a single 4-inch skull found in Texas in 1908; despite its four-horned name, *T. insignis* has six small horns on its face; *incertae sedis*, it appears to be a transitional genus midway between pelycosaurs and therapsids, the precursors of mammals; North America, early Permian.

**Tetragraptus:** an early genus of dichograptid graptolites in the order Graptoloidea; planktic, with four stipes, pendent or horizontal, and no bithecae; important index fossil because of its many widely distributed species in the Early Ordovician.

**Tetralophodon:** a genus of elephant-like proboscideans in the extinct family Gomphotheriidae; about 8 feet high, with four tusks and a trunk, but named for its specialized four-cusped teeth; North America, Europe, and Asia; middle Miocene to early Pliocene.

**Tetrapoda:** a superclass of vertebrate animals that includes many living and extinct taxa. The earliest tetrapods appeared in the fossil record in the Devonian period, at about 370 Ma. Various environmental pressures — including intense competition among the many marine animals, the growing presence of terrestrial plants along the shorelines, and climatic changes — led some marine organisms to be attracted to habitats along shallow shorelines, evolving into species that could adapt to terrestrial habitats. Anatomical changes in some Middle Devonian rhipidistian fish such as *Eusthenopteron* gave rise to lobe-finned sarcopterygians such as *Tiktaalik*, some of which evolved in the Late Devonian into an amphibian lifestyle. Especially notable are the bones of the lobe fins, which correspond closely to the arm, wrist, and hand bones of later vertebrates. These bones are a homologous trait in all vertebrates descended from the lobefin fish, including humans and even snakes (considered tetrapods because they are descended from diapsids, which had four limbs like other vertebrates). The only modern sarcopterygians are

the coelacanths and lungfish. See also *Acanthostega*, *Ichthyostega*, *Koilops*, *Latimeria*, *Perittodus*, **Romer's Gap**, *Tiktaalik*, *Tulerpeton*, and **Whatcheeridae**.

**Tettrarhynchia:** a genus of articulate brachiopods in the still-extant order Rhynchonellida; characterized by coarse ribs, incurved beak, and a width greater than the length; Europe, Asia, and North America; Jurassic.

**Texas Red Beds:** a series of lower-Permian formations in Texas and Oklahoma, one of the most prolific sites for a range of reptiles, sharks, stem-tetrapods, temnospondyls, and other amphibians; North America, early Permian.

**Thalassocnus:** a genus of xenarthran sloths in the family Megatheriidae. It is represented by several species living off the coasts of Peru and Chile; herbivorous and about the size of a human, it is one of the few tetrapods that have returned to the sea and then become extinct (see also *Neovison*). The earlier species were probably semi-aquatic and the later species fully aquatic. South America, late Miocene to late Pliocene.

**Thalattosauria:** "ocean lizard," an order of primitive marine reptiles, difficult to classify but generally considered archosauromorph diapsids; growing as long as 13 feet, they had a broad body, flattened tail, and paddle-shaped limbs; North America, Europe, and Asia; Middle to Late Triassic.

**Thalattosuchia:** "sea crocodile," a clade of marine crocodylomorphs consisting of the Metriorhynchidae and the Teleosauridae; cosmopolitan, Early Jurassic to Early Cretaceous.

**thanatocoenosis:** see **taphocoenosis**.

**Thaumaptilon:** an enigmatic organism of the Burgess Shale, possibly a cnidarian; it resembles a sea pen and may be the earliest pennatulacean, although some Ediacaran organisms may be even earlier pennatulaceans; Canada, middle Cambrian, 508 Ma.

**thecae:** cases, receptacles, or sheaths in various animals such as graptolites and echinoderms; especially the chitinous structures protruding from a graptolite's stipes, often resembling the teeth of a saw blade, which are the tubular skeletons of the individual zooids of a rhabdosome, a graptolite colony.

**Thecideidina:** a still-extant small suborder of brachiopods in the class Rhynchonellata, exact relationships unclear; very small, cemented to the undersides of corals or in coral debris, they are the only extant tropical brachiopods; cosmopolitan, Triassic to Recent.

**thecodonts:** "socket tooth," a paraphyletic group of basal archosaurs that appeared in the Permian and diversified widely in the Triassic; formerly classified as an order, the group includes the ancestors of dinosaurs, crocodylians, and pterosaurs; similar in appearance to a more upright crocodile or to a four-legged theropod dinosaur, they became abruptly extinct at the end of the Triassic; global distribution, Permian to Triassic.

***Thecosmilia***: a genus of stony corals, colonial scleractinian corals in the still-extant suborder Faviina; the corallites are phacelo-dendroid and about half an inch in diameter; an important reef-builder, especially in the Jurassic; global distribution, Middle Triassic to Cretaceous.

***Thectardis avalonensis***: a species of triangular fossils known only from the Mistaken Point biota; it is *incertae sedis* but has been suggested as the earliest sponge; probably cone-shaped in life, it grew to 2.5 inches wide and 7 inches high; Canada, Ediacaran, 575–560 Ma.

***Thelodonti***: a contentious group of jawless fish still considered a class by some but probably polyphyletic; 6–8 inches long, they resembled the heterostracans and anaspids but are characterized especially by their thelodont scales, tiny, oval dermal denticles with ridges, furrows, and spikes; global distribution, Middle Ordovician to Late Devonian.

***Thelodus***: an obscure genus of thelodont agnathan fish in the family Coelolepididae; characterized by a broad, blunt head and thick, bony, pear-shaped scales covering its body; estimates of its size vary from a few inches to 3 feet long; global distribution, Silurian.

***Theosodon***: a genus of litoptern mammals in the family Macraucheniidae; similar in appearance to the modern guanaco, they were almost 7 feet long and weighed about 200 pounds; South America, early Miocene.

***Therapsida***: a group of synsapsids that includes the dominant predators of the Permian, becoming a transitional link between their reptile ancestors and the early mammals of the Triassic, which probably evolved from a therapsid group called cynodonts. The earliest therapsid may be the still-controversial *Tetraceratops* of the early Permian, and other basal therapsids like the *Biamrosuchia* appeared in the middle Permian. Developing from the sphenacodontid pelycosaur, therapsids became the dominant predators, replacing the pelycosaurs in the middle Permian and diversifying globally in the late Permian and Early Triassic. Only a few genera, including the cynodonts, persisted into the Jurassic, as the dinosaurs gradually replaced most of the therapsids.

***Theria***: the principal subclass of mammals, including the Metatheria (marsupials) and Eutheria (placentals) but excluding the Prototheria (egg-laying monotremes); the earliest-known therians (see *Juramaia* and *Montanalestes*) appeared in the Middle Jurassic, but there is some evidence of their existence in the Early Jurassic.

***Theridomyoidea***: a superfamily of rodents possibly related to the sciuriforms; Europe and Africa, Eocene to Miocene.

***Theriodontia***: an important group of advanced carnivorous therapsids, including the therocephalians and gorgonopsians in the late Permian, and then in the Early Triassic the more advanced cynodonts, from which the ancestors of mammals evolved; cosmopolitan, middle Permian to Recent.

***Theriognathus***: a genus of therapsids in the family Whaitsiidae; about 3 feet long with a long, narrow snout, it exhibits mixed reptile and mammal characteristics; a close relative may have survived the end-Permian extinction; Africa and Russia, late Permian.

**Therizinosauridae**: a large family of feathered herbivorous theropod dinosaurs, related to the sharp-clawed, carnivorous raptors; species in the group varied in length from 3 to 33 feet and weighed up to 5 tons; they were basically bipedal, with claws as long as 3 feet on their robust forelimbs; numerous eggs have been found that indicate little if any care by parents; also called segnosaurids; North America and China, Early to Late Cretaceous.

***Theropithecus***: a still-extant genus of large monkeys in the family Cercopithecidae; weighing from 25 to 40 pounds, three species are known from the Pliocene; East Africa.

**Theropoda**: a large group of dinosaurs that spanned a great range of types and sizes. Traditionally considered saurischians, in a proposed reclassification in 2017 they are considered a separate suborder. The theropods were generally carnivorous and were the principal terrestrial carnivores of the Jurassic and Cretaceous. They were among the earliest dinosaurs, dating back to 231 Ma, and their clade includes all modern birds. The most important theropod families are the Allosauridae, Compsognathidae, Dromaeosauridae, Spinosauridae, Therizinosauridae, and Tyrannosauridae. Global distribution, Late Triassic to the end of the Cretaceous.

***Thescelosaurus***: “marvelous lizard,” a parrot-beaked genus of bipedal ornithischian dinosaurs in the herbivorous family Thescelosauridae, usually classified as ornithomimids. About 12 feet long, it appeared in North America at the very end of the Cretaceous, about 66 Ma. In a specimen found in 1993 the heart was preserved well enough that computer tomographic scans seemed to reveal a four-chambered heart and an aorta, significant because close to the evolutionarily advanced heart structure of birds and mammals, and more efficient than the three-chambered heart of snakes and crocodylians. A more thorough examination in 2011, however, disputed these interpretations, indicating that the “heart” may be simply a concretion.

**Thlipsuridae**: a family of podocopid ostracods in the suborder Platycopina and superfamily Thlipsuroidea; North America and Europe, early Silurian to Late Devonian.

***Thrinaxodon***: “trident tooth,” a genus of early cynodont therapsids in the family Thrinaxodontidae; a fox-sized carnivore, probably in the line of descent to mammals; *Thrinaxodon*'s features are transitional between the reptilian traits of early synapsids and the mammalian traits of advanced cynodonts; South Africa and Antarctica, Early Triassic, 250–245 Ma.

***Thylacinus cynocephalus***: a species of carnivorous marsupials in the still-extant order Dasyuromorphia and extinct family Thylacinidae. One of the “Tasmanian tigers,” superficially dog-like but unrelated to the Canidae, it is a prime example of



convergent evolution. It was the size of a large dog (6 feet long), with a long muzzle and striking posterior dorsal stripes. The family appeared in the Oligocene and became a top predator in Meganesia. *T. cynocephalus* is the only species to survive into the twentieth century, evidently becoming extinct in the 1930s. Meganesia; early Pliocene to Recent.

***Thylacoleo*:** “pouch lion,” a genus of Australian marsupials in the still-extant order Diprotodontia and extinct family Thylacoleonidae; resembling a small lion, it weighed up to 350 pounds and was about 4 feet long; it was probably carnivorous, but ambivalent dentition has led to intense debate about its diet and habits; *Thylacoleo* became extinct between 45,000 and 40,000 years ago, shortly after the arrival of humans in the continent; late Pliocene to late Pleistocene.

***Thylacosmilus*:** a genus of scansorial carnivores in the order Sparassodonta; not a felid, it was more closely related to marsupials than placentals; the leopard-sized *Thylacosmilus* was similar by convergent evolution to the sabertooth cats of the Oligocene and Miocene on other continents; Argentina, late Miocene.

***Tianyulong*:** a monospecific genus of ornithischian dinosaurs in the family Heterodontosauridae; the specimen of *T. confuciusi* was only about 28 inches long but probably a juvenile; it was bipedal and had tufts of fuzz that seem to be primitive feathers; China, Late Jurassic, 158 Ma.

**Tiaojishan Formation:** a series of interspersed volcanic and sedimentary rocks in northeastern China, dated between 165 and 153 Ma; an important source of fossil fauna and flora well-preserved by volcanic eruptions; especially notable for specimens of the stem-mammaliaforms *Juramaia*, *Castorocauda*, *Agilodocodon*, and *Docofossor*; China, Late Jurassic.

***Tiktaalik roseae*:** a species of stegocephalians known from several skeletons found on Ellesmere Island. The predatory *Tiktaalik* is a significant link between earlier sarcopterygians and the first four-legged land animals. It was 6–8 feet long and possessed a suite of characters adapted to moving on land as well as in water, especially its strong shoulders, bendable wrists and neck, and weight-bearing fins. It lived in shallow coastal waters about 375 Ma, possibly making brief forays onto land. See also *Ventastega* and **Tetrapoda**. Canada, Late Devonian.

**Tillodontia:** a suborder of eutherian mammals in the order Cimolesta, probably related to the pantodonts; they were quadrupedal, and the largest was about 3 feet long; they combine ungulate, rodent, and carnivore features, such as gnawing teeth and clawed feet; North America, Europe, and Asia; early Paleocene to late Eocene.

***Timurlengia*:** a genus of early tyrannosaurs intermediate between the first tyrannosaurs and the larger ones of the Late Cretaceous; discovered in 2004 and described in 2016, *T. euotica* was still only horse-sized but was similar in several ways to its large cousin *Tyrannosaurus rex*, notably in having similar brain and ear features; it is dated at 90 Ma in the early Late Cretaceous, in the middle of a 20-million-year gap in tyrannosaurid fossils; Uzbekistan.



***Titanis walleri***: a North American genus of large, flightless phorusrhacid birds in the order Cariamiformes; like the other Phorusrhacidae, it probably attacked smaller animals from ambush; known from fragments but no skull, it is estimated to have been 8 feet tall and up to 350 pounds; Florida, early Pliocene to early Pleistocene.

***Titanites***: a genus of ammonoids in the order Ammonitida and family Dorsoplanitidae; strongly ribbed, it is one of the larger ammonoids, the largest species more than 4 feet in diameter; England, Late Jurassic (end Tithonian).

***Titanoides***: a genus of herbivorous mammals in the extinct order Pantodonta; about 3 feet long and 350 pounds, these were unusual herbivores in having large canine teeth and five-clawed feet, although otherwise resembling a small modern rhinoceros; North America, late Paleocene.

***Titanophoneus***: a genus of large carnivorous therapsids in the order Dinocephalia and family Anteosauridae; the type species, *T. potens*, was as much as 10 feet long, with the typical long, heavy snout and interlocking incisors typical of dinocephalians; Russia, middle Permian.

**Titanoptera**: an order of neopteran insects in the subclass Pterygota; large, some species having wingspans up to 16 inches; although related to grasshoppers, they could not jump; Europe, Early to Late Triassic.

**Titanosauria**: a clade of large, herbivorous saurischian dinosaurs in the suborder Sauropodomorpha. They had a long tail, a fairly long neck, spoon-like or peg-like teeth, and solid vertebrae. The largest specimen, found in 2012 in Patagonia, was among the largest of all dinosaurs at 130 feet long and about 90 tons, and several juvenile specimens found there appear to be longer than 120 feet. A very large colonial nesting ground has been found in Patagonia, consisting of hundreds of titanosaur nests containing an average of 25 eggs each; other similar nesting grounds have been found in Madagascar, India, and Spain. Global distribution but principally in southern continents, Early to Late Cretaceous.

**Titanotheriidae**: see **Brontotheriidae**.

***Titanotylopus***: a genus of even-toed ungulates in the family Camelidae; the largest camelid, about 13 feet high at the shoulder; North America, Miocene to Pleistocene.

***Tomarctus***: a genus of canids in the extinct subfamily Borophaginae; 3 feet long and about 40 pounds, it had very powerful jaw muscles, indicating bone-crushing ability, a hallmark of scavengers; probably close to the ancestry of modern dogs; North America, early to middle Miocene.

**Tommotian biota**: an assemblage of invertebrates of the early Cambrian, named for the area where they were first discovered in Siberia but probably occurring worldwide; there are a few entire skeletons, but the assemblage consists mainly of fragments known collectively as a “**small, shelly fauna**,” *q.v.*; 535–520 Ma.

***Tongtianlong limosus***: a species of maniraptoran oviraptorosaurs, one of many similar recent Chinese discoveries; the specimen named in 2016 died in a

splayed-limb and raised neck posture; feathered and bipedal, it has a sharp beak and a dome-like skull roof with a low crest; China, Late Cretaceous, 71–66 Ma.

**toothplate:** a specialized biting or crushing structure in the occlusal areas of the mouth of several types of fish, including placoderms and several genera of rays, lungfishes, and chimaeroids; even some rhyrachosaurian reptiles have a type of toothplate.

**Torosaurus:** a genus of chasmosaurid ornithischian dinosaurs in the family Ceratopsidae; very similar to *Triceratops*, *Torosaurus* is characterized by a skull 9 feet long and by two large openings in its 5-foot-wide neck frill which give it its name; it had two large horns projecting forward above its eyes and other smaller horns behind its frill; the herbivorous *Torosaurus* weighed about 5 tons and was about 30 feet long; North America, Late Cretaceous, 68–66 Ma.

**Torrejonia:** a genus of plesiadapiform primates generally considered in the family Paromomyid but proposed as a member of a new family Palaecthonidae; one of the oldest known primates, *Torrejonia* had a body length of 15 inches; it was arboreal, with long legs, fingers, and toes; see also **Plesiadapiformes**; North America, Paleocene.

**Torvosaurus:** a genus of large carnivorous saurischian dinosaurs in the family Megalosauridae. Found in Utah, Colorado, Portugal, and possibly China, the genus appeared at the time that North America and Europe were drifting apart. The largest species, *T. gurneyi*, weighed almost 5 tons and was about 33 feet long; it is the largest theropod known from Europe. A nest of eggs found in Portugal contains the most primitive dinosaur embryos known. United States, Europe, and Asia; Late Jurassic, 153–148 Ma.

**Toxasteridae:** a family of sea urchins, irregular euechinoids in the order Spatangoida; they were atelostomate and had an elongated oval shape; North America, Europe, and Asia; Early to Late Cretaceous.

**Toxodon platensis:** a South American ungulate in the suborder Toxodonta, the type species of the family Toxodontidae; 8 feet long and 5 feet high, it was similar to the modern rhinoceros; southern South America, Pliocene to Pleistocene.

**Toxodonta:** a suborder of mostly South American ungulates in the order Notoungulata; the toxodonts were between 4 and 10 feet long, the larger genera being similar to a modern rhinoceros in appearance and size; some species have nasal openings on the top of the skull; research in 2014 suggests that the toxodonts may be related to the perissodactyls (odd-toed ungulates); South and North America, late Paleocene to Pleistocene.

**Toxodontidae:** a family of large notoungulates in the suborder Toxodonta; principally South American but known also from the Pleistocene in Central America and the Southwestern United States; Oligocene to Pleistocene.

**trace fossil:** see **paleoichnology** and **fossil**.

**Trachodon:** a dubious genus of dinosaurs, known only from teeth and dental fragments, some of which are now known to be from a ceratopsid and some from a hadrosaur; see also *Edmontosaurus*; North America, Late Cretaceous, 77 Ma.

**Tragulidae:** a still-extant family of primitive hornless artiodactyls in the suborder Ruminantia; commonly called chevrotains or mouse deer, they appeared in the Eocene, descended from the Hypertragulidae; currently represented by three genera in Asia and Africa; Europe, Asia, and Africa, late Eocene to Recent.

**transitional species:** a species that bears traits clearly indicating the sequential phases in the evolution of a new species, specifically traits common to both its ancestors and its descendants; see for example *Amphistium*, flatfish, *Heteronectes*, *Tetraceratops*, and **Theropoda**.

**Traversodontidae:** a family of sheep-sized herbivorous therapsids in the suborder Cynodontia; the traversodonts appeared in the Early Triassic, diversified widely throughout the period, and became extinct in the Early Jurassic; mainly Gondwana but also Laurasia.

**Tremarctinae:** a subfamily of carnivorous short-faced bears, still extant only in one species, *Tremarctos ornatus*, found in limited places in the Andes; South and North America, late Miocene to Recent.

**Trematosauroida:** a superfamily of labyrinthodont amphibians in the suborder Stereospondyli; medium-sized fish-eaters, some almost completely marine; one of only two or three groups of temnospondyls that survived the Triassic extinction; global distribution, Early Triassic to Middle Jurassic.

**Trepostomata:** an order of colonial bryozoans in the still-extant class Stenolaemata; characterized by long, curving, impunctate, calcareous tubes, filled with closely spaced diaphragms; tree-like colonies, seldom preserved intact, the fragmented branches forming a major part of some Ordovician limestones; global distribution, Ordovician to Triassic.

**Treptichnus pedum:** a trace fossil that marks the GSSP for the beginning of the Cambrian Period and the Paleozoic Era; one of the earliest complex trace fossils, it is the burrow of an animal similar to modern priapulid worms; Newfoundland, Canada, 541 Ma.

**Triadobatrachus:** a genus of frog-like amphibians in the order Proanura and family Triadobatrachidae; the earliest-known frog, *Triadobatrachus* was 4 inches long and had 14 trunk vertebrae, a transitional feature since the typical amphibian had 24 and modern frogs only 4–9; it also had frog-like pelvic characteristics; Madagascar, Early Triassic.

**Triarthrus:** “three-jointed,” a genus of ptychopariid trilobites in the family Olenidae, it was the last of its family. One of the few trilobites found with intact appendages, it was about 2 inches long and characterized by jointed, inward-facing spines on the legs and a smoothly rounded pygidium. Good examples are known

from Beecher's Trilobite Bed in New York, especially notable for the spine details and for information about the protaspis and meraspis phases. Researchers in 2017 also reported the first known direct evidence of trilobite reproduction in a cluster of very small pyritized eggs near the head of a *Triarthrus* specimen from Beecher's. North America, Europe, and Asia; Late Ordovician.

***Triassaraneus***: a genus of true spiders (Araneae), the first found in South Africa; known from several specimens of varying completeness; South Africa, Late Triassic (Carnian), 235 Ma.

**Triassic**: the first period of the Mesozoic Era, from 252.2 to 201.3 Ma, divided into Early, Middle, and Late Epochs. It was overall a relatively hot and dry period, dominated by a great diversity of reptiles on land, especially the pseudosuchian archosaurs. Mammaliaforms and dinosaurs appeared in the middle of the period, and the pterosaurs — which were the first flying vertebrates — at the end of the Middle Triassic. Sauropterygians and ichthyosaurs dominated the seas, and scleractinian corals appeared in the Middle Triassic, becoming important reef-builders late in the period. Only one lineage of ammonoids survived the end-Permian extinction, but from it the ceratitid ammonoids diversified rapidly and became very numerous throughout the Triassic. Evolving by the end of the Triassic were also the ammonitids, which were to become the dominant ammonoid group of the Jurassic and Cretaceous. The great coal swamps of the late Paleozoic almost disappeared during the dry Triassic, but conifers, cycads, and corytosperms (see *Dicroidium*) flourished throughout the period.

**Triassic extinction**: the fourth of the five great extinctions, at the end of the Triassic Period. It affected land and sea, causing the extinction of one class of marine animals, the conodonts; one-third of all marine genera; and many families of terrestrial animals. One-third of all known animal species of the Triassic did not survive, creating vacant ecological niches that the dinosaurs could occupy in the Jurassic. However, plant fossils and palynomorphs show no appreciable effects. As with all five mass extinctions, the causes are unclear; paleoclimatological research has found a marked increase in the level of carbon dioxide in the atmosphere near the end of the period, and other possible causes have been suggested. Some researchers have argued that at least two extinction pulses occurred. But the second, between 201.5 and 201.3 Ma at the end of the Rhaetian Stage, is the one usually referred to as the Triassic extinction.

***Triassocheilus***: see *Proganochelys*.

***Tribrachidium heraldicum***: a unique species of soft-bodied benthic organisms in the monospecific phylum Trilobozoa, given its own phylum since it could not be classified in any known phylum; it was limpet-shaped, circular and about an inch in diameter, but its upper surface was a shallow cone with 3 lobes in a triskelion pattern; triradially symmetrical and known only from negative impressions in overlying strata; Australia and Russia, Ediacaran, 558–555 Ma.

**Triceratops:** “three-horned face,” a genus of ornithischian dinosaurs in the family Ceratopsidae. The largest weighed as much as 12 tons and were almost 30 feet long and 10 feet tall. They were characterized by a very large, 10-foot skull with a parrot-like beak; a large, bony neck frill; and three horns. Herbivorous and eating a highly fibrous diet, they had replaceable grinding teeth. Known only from the Late Cretaceous of North America, 68–66 Ma.

**Triconodonta:** see **Eutriconodonta**.

**Trigoniidae:** a still-extant family of articulate bivalve mollusks in the order Trigoniida. They are large and roughly triangular, with striking patterns of ribbing and a very complex articulation with elaborate hinge teeth. Although trigoniids were widespread in the Jurassic and Cretaceous, they were thought to have become extinct at the end of the Cretaceous until a living member of the family (now named *Neotrigonia*) was discovered in 1802 in Australia. Global distribution, Late Carboniferous to Pliocene.

**Trigonostylopidae:** a family of South American hoofed mammals in the order **Astrapotheria**, *q.v.*

**Trigonotarbita:** a large group of primitive arthropods in the order Arachnida, superficially resembling spiders. They were probably predators on other arthropods, and some Devonian genera developed armor, spines, and tubercles. They did not have spinnerets and probably did not produce venom. Trigonotarbitids are well-known, especially from the European Coal Measures of the Late Carboniferous. Europe and North and South America, early Silurian to early Permian.

**trilobites:** a very large group of mostly small marine arthropods, generally referred to as a class called Trilobita. The earliest definitive arthropods (see also *Spriggina* and *Parvancorina*), the trilobites were characterized by a hard exoskeleton, a longitudinally three-lobed body, and a series of biramous limbs. The body is also divided in three parts from head (cephalon) to thorax to tail (pygidium), generally also having a post-segmental part called the telson. They are sometimes found enrolled, curled into a ball. Although trilobites averaged around an inch in length, a few species grew as long as 28 inches (see *Isotelus rex*). Mostly benthic and sometimes burrowing in the top layers of sediment, but some small species were evidently planktic.

Trilobites arose in the early Cambrian and flourished in the late Cambrian and the Ordovician. Since the hard exoskeleton fossilized relatively easily, they are among the most abundant fossils of the Paleozoic. Their abundance and their worldwide distribution make them stratigraphically important through the middle of the Paleozoic; they dwindled in numbers thereafter up to their extinction at the end of the Permian.

**Trimerellida:** a superfamily of inarticulate brachiopods, formerly called Trimerellacea; they have a strong calcite shell and a pedicle, sometimes attached to another brachiopod; global distribution, Middle Ordovician to late Silurian.

***Trimerocephalus***: a genus of eyeless trilobites in the order Phacopida and family Phacopidae; noted for a 2016 report of a single-file line of individuals in close physical contact with each other, evidently dying suddenly while migrating; Europe, Asia, and Australia; restricted to the Famennian Stage of the Late Devonian, 371–365 Ma.

**Trimerophytopsida**: an extinct class of early vascular plants in the division Tracheophyta; arising in the Early Devonian from the rhyniophytes, the trimerophytes are considered ancestral to the progymnosperms and ferns, and thus to almost all higher plant life today; also called Psilophytopsida, Trimerophytales, and Trimerophyta; global distribution, Devonian to Carboniferous.

***Trimerus***: a genus of phacopid trilobites in the family Homalonotidae and related to the calymenids; characterized by a wide, shovel-shaped cephalon and small, raised eyes; global distribution, Silurian to Devonian.

**Trinil fauna**: a biostratigraphic faunal assemblage at Trinil, Java, that contains the hominin remains commonly referred to as “Java Man”; the fauna is dated at about 1.8 Ma; the Trinil site is about the same age as the Jetis fauna and considerably older than the “Solo Man” remains at the Ngandong site; all three sites are within 60 miles of each other.

**Trinucleidae**: a family of small, blind trilobites in the order Asaphida and superfamily Trinucleoidea, important as index fossils in the Ordovician; characterized by an almost circular shape up to an inch across, long genal spines, a vaulted glabella, and a ribbed fringe around the large cephalon, which accounts for about half of the body length; the trinucleids went extinct in the Ashgill event, 444 Ma, at the end of the Ordovician; the type genus is *Trinucleus*, but see also *Cryptolithus*; global distribution, Middle to Late Ordovician.

**Trinucleoidea**: a superfamily of trilobites in the order Asaphida; the only asaphids to survive the Ordovician extinction into the Silurian; Ordovician to late Silurian.

***Trionyx***: a still-extant genus of softshell freshwater turtles in the order Cryptodira; 3 feet long, with a long, narrow head; global distribution, Early Cretaceous to Recent.

***Triops cancriformis***: a still-extant species of tadpole shrimps, notostracans in the family Triopsidae; 2–4 inches long and resembling a small *Limulus*, it is known from the Grès à Voltzia Lagerstätte and remains almost unchanged today; Europe, Early Triassic to Recent.

**Trithelodontidae**: a family of advanced cynodonts in the infraorder Eucynodontia; formerly called Ictidosauria; among the longest-lived non-mammalian therapsids, they were probably replaced in the Jurassic by early mammals; mainly carnivorous or insectivorous, the largest species were less than 10 inches long; South America and Africa, Late Triassic to Middle Jurassic.

**Tritylodontidae**: a family of mammalian morph therapsids in the suborder Cynodontia; tritylodonts were generally herbivorous, characterized by protruding incisors and three rows of grinding cheek teeth; they had a prominent sagittal crest and are estimated to have been about 2 feet long; global distribution, Triassic to Cretaceous.

**Trochiliscales:** an early order of charophytic algae characterized by dextrally coiled gyrogonites; cosmopolitan, Silurian to Carboniferous.

**Troodon:** a genus of small, agile theropod dinosaurs in the family Troodontidae; up to 8 feet long and 150 pounds, it is notable for evidence of bird-like nesting and egg-laying behavior, including possible brooding behavior by males; China, Russia, and North America, found recently even in Northern Alaska; Late Cretaceous, 78–76 Ma.

**Trucherognathidae:** “ragged jaw,” a family of conodonts characterized by fibrous, platelike teeth resting in a depression on the jaw ramus rather than grasping the ramus or the jaw tip; North America, Europe, and Asia; Ordovician.

**Tryblidium:** a large genus of monoplacophorans in the family Tryblidiidae; from 1 to 2 inches long with a pear-shaped shell, in some species composed of an outer calcitic and an inner aragonitic layer; North America and Europe, Ordovician to Silurian.

**Tsidiyazhi abini:** a species of sparrow-sized birds in the still-extant family Coliidae (the mousebirds), described in 2017 as the oldest known tree-dwelling bird; found in New Mexico, it is dated at 62.5 Ma and is evidence of a rapid speciation in birds following the end-Cretaceous extinction; United States, early Paleocene.

**tuatara:** see **Sphenodontidae**.

**Tubuliporina:** still-extant, the largest suborder of bryozoans in the order Cyclostomatida; global distribution, Late Triassic to Recent.

**Tulerpeton curtum:** a species of early tetrapods in the order Ichthyostegalia, closely related to *Acanthostega* and *Ichthyostega*; *Tulerpeton* lacked gills and had six digits on each limb; one of the few well-known labyrinthodonts from the period of time called Romer’s Gap; Russia, Late Devonian, 365–361 Ma.

**Tullimonstrum gregarium:** the famous “Tully monster,” a soft-bodied chordate in the class Hyperoartia; possibly a stem lamprey, it is known only from the Mazon Creek site southwest of Chicago and is the Illinois state fossil; 6–8 inches long, it has stalked eyes and a notochord; United States, Late Pennsylvanian.

**Tunicata:** a large, still-extant subphylum of basal marine chordates, also called Urochordata; tunicates have a notochord only in their free-swimming larval phase; as adults they are benthic and sessile; the main group is the Ascidiacea, commonly called sea squirts; global distribution, Cambrian to Recent.

**Tuojiangosaurus:** a monospecific genus of ornithischian dinosaurs in the family Stegosauridae; similar to the better-known *Stegosaurus*, *T. multispinus* was 24 feet long and weighed about 3 tons; it is notable for 17 pairs of spikes and plates along its backbone; China, Late Jurassic, 161–155 Ma.

**Turkana Boy:** the name given to a nearly complete hominin skeleton found in 1984 near Lake Turkana, tentatively assigned to *H. ergaster*; the most complete early hominin skeleton known; Kenya, 1.6 Ma.



***Turrilites*:** an unusual genus of ammonoids in the order Ammonitida, suborder Ancyloceratina, and family Turrilitidae; characterized by its resemblance to gastropods, a strongly ribbed surface, and a high-spired, tightly coiled helical shell; global distribution, Late Cretaceous, 100–90 Ma.

**turtles:** see **Testudines**.

***Tuzoia*:** a genus of bivalved organisms tentatively classified as stem-arthropods; probably nektonic, it had a circular carapace from 6 to 8 inches in diameter and a pair of large stalked eyes; North America, Europe, Asia, and Australia; early to middle Cambrian.

**Two Medicine Formation:** an important geologic formation of the Campanian, encompassing a large area of Northwestern Montana and Southern Alberta; laid down along the western shore of the Western Interior Seaway between 80 and 74 Ma, the Two Medicine strata contain many fossils of Late Cretaceous dinosaurs as well as many freshwater and terrestrial animals; North America, Late Cretaceous.

***Tylocidaris*:** a genus of sea urchins, echinoids in the order Cidaroida and family Psychocidaridae; notable for club-shaped spines, narrow at the proximal end and bulbous at the distal end; Europe and North America; Early Cretaceous to late Eocene.

**Tylopoda:** “swollen foot,” a still-extant suborder of artiodactyl ungulates, originating in North America in the middle Eocene and found only there until the early Pliocene; although once placed in the Ruminantia, they are not true ruminants; the modern representatives are the Camelidae, the camels and camelids of Asia and South America.

***Tylosaurus proriger*:** a large species of mosasaurs in the subfamily Tylosaurinae; the type species of the genus, *T. proriger* was almost 50 feet long and weighed up to 11 tons; characterized by an elongated, cylindrical snout, it inhabited the shallow Western Interior Seaway in the middle of North America in the Late Cretaceous, with a diet including fish, shellfish, and small aquatic birds; although most *Tylosaurus* specimens have been found in North America, they are known also from Spain, New Zealand, and Antarctica; 85–70 Ma.

**type species:** as defined by the ICZN, the name-bearing type of a genus or subgenus, considered the typical representative of a genus with which the name is permanently taxonomically associated; a type genus has the same relationship to a family.

**type specimen:** see **holotype**.

**typostrophism:** a saltationist theory of evolution espoused by the German paleontologist Otto Schindewolf in the middle twentieth century; stressing catastrophically destructive events as the principal cause of mass extinctions and of the subsequent emergence of new taxa, typostrophism downplays natural selection as the basic mechanism of evolution. See also **Unspecialized Descent**.



**Tyotheria:** a possibly paraphyletic suborder of South American ungulates in the extinct order Notoungulata, possibly including the hegetotheres; ranging from rabbit-like to bear-sized, the tyotheres shared several characters with rodents; the Intertheriidae and Mesotheriidae are the largest of the five families in the suborder; late Paleocene to middle Pleistocene.

**Tyrannosauridae:** a family of large predatory dinosaurs in the superfamily Tyrannosauoidea; restricted to North America and Asia, Early to Late Cretaceous.

**Tyrannosauoidea:** a superfamily of theropod saurischian dinosaurs; arising in the Middle Jurassic, the early tyrannosauroids, such as *Guanlong* and *Eotyrannus*, were relatively small and had well-developed forelimbs with three fingers; the later genera became the largest known land predators ever; global distribution, 165–66 Ma.

***Tyrannosaurus rex*:** the type species of the family Tyrannosauridae, *T. rex* reached lengths up to 45 feet and 12–15 feet high at the hips; estimates of its weight vary from 7 to 18 tons. Like the more recently discovered *Albertosaurus*, a close relative, *T. rex* was among the most powerful predators in the history of life. It was characterized by a large skull more than 3 feet long, with several dozen serrated teeth up to 6 inches long. It had broad skull attachments for its powerful jaw muscles, and very large vertebrae that supported its massive head. Bipedal, with very strong hindlimbs, it had relatively weak forelimbs only 3 feet long; each manus had two claws. Although the teeth did not meet, coprolites indicate that *T. rex* may have chewed and crushed even the bones of small prey by a shearing action of its teeth.

*T. rex* is noteworthy for an unusual pattern of holes in its skull that may indicate a more advanced nervous system than most other dinosaurs, and it may have had stereoscopic color vision, although nothing is known of its visual acuity. Its life-span has been estimated at 27–30 years, and its normal walking speed was about 5 miles an hour, but it probably reached speeds as high as 18 miles an hour. The first partial skeletons of *T. rex* were found in Montana by Barnum Brown in 1900 and 1902, and about a dozen partial skeletons have been found since in South Dakota, Wyoming, Montana, and Alberta. One of the most complete skeletons, referred to as “Sue,” is now in the Field Museum in Chicago. North America, Late Cretaceous, 68–66 Ma.

# U

***Ugrunaaluk***: a monospecific genus of hadrosaurs in the subfamily Saurolophinae; described in 2015, *U. kuukpikensis* was a duckbill dinosaur that lived above the Arctic Circle; several thousand bones belonging to the species have been found on the Colville River in Northern Alaska in strata from 69 Ma; it was 25–30 feet long and 7 feet high at the hip, and bore crests along its spine; it is so similar to *Edmontosaurus* that some researchers consider them the same species; Late Cretaceous.

**Uintacrinida**: a small order of stemless crinoids that includes only two genera, *Uintacrinus* and *Marsupites*; North America and Europe, Late Cretaceous, 87–84 Ma.

**Uintatheriidae**: a family of large, primitive herbivorous mammals in the order Dinocerata; the uintatheres were replaced in their large-browser niche late in the Eocene by the brontotheres; North America and China, late Paleocene to late Eocene.

***Uintatherium***: the type genus of the mammal family Uintatheriidae; up to 13 feet long and weighing as much as 2 tons, *Uintatherium* resembled the modern rhinoceros in shape but was not related; its skull was very thick and bore 6 frontal ossicones; United States and China, middle to late Eocene.

***Umoonasaurus***: a monospecific genus of Early Cretaceous plesiosaurs in the family Leptocleididae; *U. demoscyllus* was identified by Australian researchers in 2006 along with the larger plesiosaur *Opallionectes*; it was about 8 feet long and had three crest-like ridges on the skull; it swam in a shallow sea of Central Australia about 115 Ma.

**ungulates**: a general term for the many herbivorous hoofed mammals of the Cenozoic; Late Cretaceous to Recent.

**uniformitarianism**: Until the eighteenth century, the accepted view was that life on Earth has been affected throughout its history by sudden catastrophic events — such as great floods, widespread volcanic eruptions, and rapid formation of mountain chains — which led to the more or less universal destruction of all life forms but

which no longer occur. In the period after such catastrophes, new and completely different life forms were thought to have appeared to repopulate the devastated regions. As knowledge of the fossil record increased in the eighteenth and nineteenth centuries, this view became untenable and the theory of uniformitarianism gained credibility, advanced especially by James Hutton and Charles Lyell. Uniformitarianism stressed the idea that changes in the past were gradual and were caused by essentially the same forces of change observable in the present. From about 1850 to 1970 this view was almost universally accepted, with gradualism considered a hallmark of evolutionary change. In the last few decades a more complex view has emerged, accepting the importance of occasional catastrophic events that cause relatively rapid changes in the conditions of life. See also **punctuated equilibrium**.

**Uniramia:** “one branch,” a term sometimes used for a grouping of arthropods including myriapods, onychophorans, and hexapods (insects).

**Unspecialized Descent, Law of:** Also called Law of the Unspecialized, it was formulated by E.D. Cope. It holds that the typical taxa of any temporal unit are not closely related to the most highly developed and specialized taxa of the previous epoch but are rather descended from the least specialized taxa. Otto Schindewolf made it an important part of his anti-Darwinian theory of typrostrophism, summarizing it thus: “Evolution builds upon that which has remained simple.” Although the concept contains an obvious general truth, its use in typrostrophism has been widely refuted as over-simplified.

***Uptonia jamesoni*:** a species of ammonoids in the order Ammonitida and family Polymorphitidae, an important index fossil in the Pliensbachian; evolute, strongly ribbed, about 4 inches wide; Europe and Greenland, Early Jurassic.

**Uraraneida:** an order of arachnids in the subclass Tetrapulmonata. As its name indicates, the order contains the earliest araneids. Still poorly known, the uraraneids seem to be proto-spiders, but they may lack spinnerets, and they retain a segmented abdomen and a flagellum resembling that of scorpions. Uraraneida was established for *Attercopus fimbriunguis*, and in 2016 *Permarachne* was assigned to the order. North America and Russia, Middle Devonian to Permian.

**Urochordata:** see **Tunicata**.

**Ursidae:** the bears, a still-extant family of mammals in the clade Caniformia and superfamily Arctoidea; the ursids evolved from canids such as *Cephalogale* in the Miocene and are now found on all continents but Antarctica.

***Ursus spelaeus*:** the cave bear, a species of omnivorous mammals in the family Ursidae; about the size of the largest modern bears and differing only in a few characters, it became extinct between 24,000 and 10,000 years ago; Europe, Pleistocene.

***Utahraptor*:** a genus of theropod dinosaurs in the subfamily Dromaeosaurinae, known from several specimens from Eastern Utah; estimated at up to 23 feet long and half a ton, it is probably the largest known dromaeosaur, and it seems to be of a heavier build than its cousins *Deinonychus* and *Velociraptor*; like other dromaeosaurs, it hunted in packs; United States, Early Cretaceous, 130–125 Ma.

# V

**Vaceletia:** a still-extant monospecific genus of sphinctozoan sponges; the sphinctozoans were thought to be extinct since the Cretaceous until *V. crypta* was discovered off the northeastern coast of Australia in 1977; important because of a rich Mesozoic fossil record, it may be related to the ceractinomorph demosponges; global distribution, Cambrian to Recent.

**Vagaceratops:** a monospecific genus of herbivorous horned dinosaurs in the subfamily Chasmosaurinae; found in Alberta's Dinosaur Provincial Park, *V. irvinensis* was given its "wandering" appellation because of its similarity to *Kosmoceratops*, known only from southern Utah; the similarities extend to the neck frill, square in *Vagaceratops* but topped the same way by several hornlets, some curving forward; it was 15–20 feet long and had no other horns besides those on the frill; Canada, Late Cretaceous, 75 Ma.

**Valenictus chulavistensis:** an extinct species of walrus in the still-extant family Odobenidae and subfamily Odobeninae. Its tusks are only slightly shorter than those of the modern walrus *Odobenus*, and it is very similar to *Odobenus* except that it has no teeth besides the tusks. *Valenictus* is one of at least 24 species of walrus that evolved from bear-like land animals since the late Oligocene, with only one species still surviving. See also *Dusignathus*; Southern California, Pleistocene, 3 Ma.

**Varanops:** a genus of primitive synapsid reptiles in the family Varanopseidae; about 4 feet long, it is a larger version of its relative *Varanosaurus*; global distribution, early Permian.

**Varanosaurus:** a genus of pelycosaurian synapsid reptiles in the family Ophiacodontidae; from 3 to 4 feet long, with a set of sharp teeth, including two pairs of longer teeth at the tip of its long snout, adapted to grasp prey; North America, early Permian.

**Varanus:** a genus of very large monitor lizards in the family Varanidae; synonym: *Megalania*. Ancestral to the modern Komodo dragon, it was about 20 feet long and weighed about a ton. Australia, Asia, Europe, and Africa; Miocene to Recent.

**Variscan orogeny:** the mountain-building process, caused by tectonic shifting, associated with the convergence of Laurasia and Gondwana in the Devonian and Carboniferous to form Pangaea; also called Hercynian orogeny; see **paleogeography**.

**Vaughaniidae:** a family of tabulate corals in the superfamily Favositicae; characterized by shallow, rounded corallites and the absence of tabulae; type species *Vaughania cleistoporoides* Garwood; Europe, Early Carboniferous.

**Vegavis iaai:** a genus of duck-like birds in the suborder Anatoidea, known from only one specimen but generally considered the first anseriform bird; about 1 foot long, *V. iaai* is the oldest known waterfowl; CT scans indicate that it had a voice box and could probably vocalize as modern birds do; found on Vega Island in Antarctica and named for the Instituto Antártico Argentino, which described the first of two specimens in 2005; Late Cretaceous, 68–66 Ma.

**Velociraptor:** a Mongolian genus of turkey-sized carnivorous dinosaurs in the family Dromaeosauridae. About 6 feet long but weighing less than 35 pounds, it was a bipedal feathered predator, characterized by a large, forward-pointing claw on the top of each pes. This sickle claw may have been used for attack, as was probably true of *Utahraptor* and *Achillobator*, larger dromaeosaurs up to 20 feet long. Disagreement continues as to whether the claw was sharp enough to rip skin open or may have been used in tree-climbing to a perch to pounce on prey. Mongolia, Late Cretaceous, 75–71 Ma.

**Vendian:** see **Ediacaran**.

**Ventastega curonica:** a species of early stegocephalian tetrapods; from about 365 Ma, it is similar to *Tiktaalik*, another early tetrapod that was terrestrial as well as aquatic; about 3 feet long, relatively large for the time, it is one of the earliest tetrapods yet found; Latvia, Late Devonian.

**Ventriculites:** a genus of cup- or vase-shaped sponges in the class Hexactinellida; characterized by siliceous spicules fused into a rigid skeleton; North America and Europe, Jurassic to Eocene.

**Verbeekiniidae:** a family of highly specialized foraminiferans in the superfamily Fusulinoidea; characterized by planispirally coiled tests; global distribution, early to late Permian.

**Vernanimalcula:** a monospecific genus of microscopic acritarchs that display some bilateral symmetry; *V. guizhouena*, found in the Ediacaran Doushantuo Formation of China, was dated in 2004 at between 600 and 580 Ma, 40 million years before the earliest undisputed bilaterians; it was first described as a bilaterian,

but the claim has been widely disputed, so that even the kingdom in which *Vernanimalcula* should be placed is in doubt.

**Vertebrata:** the subphylum of chordate animals that have a vertebral column containing the spinal cord, including jawless, bony, and cartilaginous fish and jawed vertebrates. There are about 66,000 species of vertebrates, accounting for 5 percent of all described animals. All vertebrates have an internal skeleton, a central nervous system running dorsally the length of the body, and gills or gill arches. (In mammals the jaw, the thyroid, the larynx, and the ossicles of the ear all correspond to the gill arches of earlier vertebrates.) For the earliest vertebrates, see *Mylokunmingia*, *Haikouichthys*, and *Zhongjianichthys*.

**vertisol:** a clay soil that is subject to extreme shrinking and expanding with environmental changes; taphonomically important in evaluating the original position of fossils deposited in it.

**vestigial structures:** body parts of organisms that seem to have no function, such as hip bones of snakes and rudimentary hindlimbs of whales. Such structures are to be expected in the process of natural selection and are among the more obvious evidences of evolution. See also **analogous** and **homologous structures**.

**Veterupristisaurus:** a genus of theropod dinosaurs in the family Carcharodontosauridae; described in 2011 as the oldest carcharodontosaurid and estimated to have been about 30 feet long, it is known from spinal fragments found in an Upper Jurassic formation dated at around 150 Ma; Tanzania, Late Jurassic.

**Vetulicolia:** an enigmatic group of early to middle Cambrian organisms, tentatively considered deuterostomes. Their size ranges from microscopic to 4 inches long; they are generally elongate, with a larger anterior section which contains several gill-like openings, and a posterior tail-like section. They have no eyes or appendages but do seem to have a notochord and are considered chordates. Cosmopolitan, middle Cambrian.

**Vilevolodon diplomys:** a species of early haramyidan mammals in the family Eleutherodontidae; about 3 inches long, it seems to have been a glider similar to the larger *Maiopatagium*; its complex tooth crown dentition is similar to that of modern squirrels; China, late Jurassic, 160 Ma.

**Vintana sertichi:** a species of groundhog-like mammals in the family Sudamericidae, discovered in Upper Cretaceous strata on the western coast of Madagascar in 2010. The almost intact skull increases what is known of the Gondwanatheria, early mammals known previously only from teeth and fragments of bone from the Late Cretaceous through the Miocene. Dated between 72 and 66 Ma and weighing about 20 pounds, *Vintana* was much larger than other known mammals of the time and is notable for well-developed olfactory bulbs in the brain. Madagascar, Late Cretaceous.

**Viverravidae:** a family of early mammals in the extinct superfamily Miacoidea; related to early carnivores but believed to be unrelated to any modern carnivorans;

characterized by an elongated skull and by having only two molars in the upper and lower jaws; North America, Europe, Asia, and Africa; early Paleocene to late Eocene.

**Viverridae:** a still-extant family of omnivorous small mammals in the order Carnivora and suborder Feliformia; although primitive, they have several living representatives, such as civets, linsangs, binturongs, and in some classifications mongooses; global distribution, late Eocene to Recent.

**Volaticotherium:** a monospecific genus of insectivorous eutriconodont mammals in the proposed subfamily Alticonodontinae. The earliest-known gliding mammal, *V. antiquum* was about the size of a squirrel but is not related to the modern flying squirrel. Mongolia, Middle Jurassic, 164 Ma.

**Volborthella:** a problematic genus of early Cambrian fossils; its fragmentary siliceous specimens are widespread in North America, Greenland, and Europe in lower Cambrian strata, appearing earlier than trilobites and then concurrently with them through the early Cambrian; once suggested as a cephalopod but now simply *incertae sedis*; see also *Salterella*.

**Volchovia:** a genus of ophiocistoid echinoderms in the family Volchoviidae; its turtle-like shell was high in the middle and flattened out toward the edges, like an inverted shallow vase; Russia, Ordovician to Silurian.

**Voltzia:** a genus of early conifers, abundant in the Triassic Grès à Voltzia Lagerstätte, to which it gave its name; generally low-growing and bushy; Europe, North and South America, Europe, and Asia; Carboniferous to Triassic.

**Vombatidae:** a still-extant family of Australian marsupials in the order Diprotodontia; the family diverged from other diprotodonts earlier than the late Oligocene and possibly in the late Eocene; several genera of large Vombatidae became extinct in the late Pleistocene; see *Phascolonus*.

**Voulte-sur-Rhône:** see **La Voulte-sur-Rhône**.

# W

**Waimanu:** a genus of sphenisciform flightless diving birds of the Paleocene, probably a basal penguin; New Zealand, middle Paleocene.

**Walcott, Charles D.:** American paleontologist who discovered and investigated the **Burgess Shale** site, *q.v.*

**Wallace's Line:** the imaginary line between the different fauna characteristic of Southeast Asia on one hand and of islands centered on Australia on the other. The line, named for Alfred Russel Wallace, runs between parts of Indonesia, specifically through the Lombok Strait between Bali and Lombok, eastward between Borneo and Sulawesi, and then south of the Philippines. The deep-water barrier represented by the line is thought to have existed for 50 million years, since the early Eocene. With few exceptions, both mammals and birds have remained separate on the two sides, even though the distance is quite small in places, especially in periods of great ice formation in the polar regions.

**walruses:** see *Valenictus*.

**Waptia:** a genus of shrimp-like arthropods known primarily from *W. fieldensis* of the Burgess Shale; an earlier species is known also from Chengjiang; about 3 inches long, it had a thin exoskeleton and long antennae; China and North America, early to middle Cambrian.

**Weichselia:** a genus of ferns in the still-extant order Gleicheniales and family Matoniaceae; characterized by lobed leaves on 3-foot-long fronds, it spread rhizomatously, forming dense swards over large areas; global distribution, Jurassic to Late Cretaceous.

**Wenlock Series:** a Konservat-Lagerstätte of the middle Silurian, a site in Western England that contains an important biota caught in fine-grained deposits of volcanic ash interwoven with successive strata of carbonate mud; organisms represented include polychaete worms, sponges, graptolites, microscopic radiolarians, and other uncommonly fossilized organisms; Wenlock Epoch of the Silurian.



**Western Interior Seaway:** a shallow sea covering much of Central North America in the Cretaceous; in its largest phase it was 600 miles wide and stretched from the Arctic Ocean to the Gulf of Mexico, and was also connected by the Hudson Seaway across Eastern Canada to the Atlantic Ocean; also called Niobrara Sea and Cretaceous Seaway; Early Cretaceous to early Paleocene.

**Whatcheeridae:** a small family of temnospondyl amphibians of the Early Carboniferous; named for What Cheer, Iowa, where a large deposit of early amphibians was found in the 1990s; about 3 feet long, the type species *Whatcheeria deltae* is dated to 340 Ma, about the same date as *Greererpeton*; the family also includes *Pederpes finneyi*; North America, Early Carboniferous.

**Wheeler Shale:** a Konzentrat-Lagerstätte in the House Range of Western Utah, dated at 507 Ma. Known principally for large numbers of trilobites (see *Elrathia*), it has also produced specimens of *Anomalocaris*, *Wiwaxia*, and other early organisms such as bivalved crustacean arthropods, chancelloriids, vetulicolians, priapulid worms (see *Selkirkia*). The fauna is considered comparable to the coeval Burgess Shale biota. North America, middle Cambrian.

**White River Group:** a large set of lower Oligocene deposits centered on southwestern South Dakota; the volcanoclastic strata have produced many articulated skeletons of mammals from the period of transition from subtropical forests to grassland, including entelodonts, oreodonts (*Merycoidodon*), all three of the rhinocerotoids (see **Amynodontidae**, **Hyracodontidae**, and **Rhinocerotidae**), horses, hyaenodonts, canids, and some of the last of the brontotheres; United States, late Eocene to early Oligocene.

**Wielandiella:** a genus of shrubs in the family Williamsoniaceae; Europe and Asia, Late Triassic to Middle Jurassic.

**Williamsonia:** a genus of trees in the family Williamsoniaceae; known worldwide from cones and fern-like leaves; Late Triassic to Late Cretaceous.

**Williamsoniaceae:** a family of Mesozoic trees in the still-extant division Spermatophyta and extinct order Bennettitales; their reproductive processes are enigmatic, but they were similar in overall appearance to palms, growing as high as 33 feet; global distribution, Triassic to Cretaceous.

**Winneshiek Site:** a Middle Ordovician Lagerstätte in a meteorite crater in Iowa; discovered in 2005, the site has produced significant eurypterids (see *Pentecopterus*), conodonts, phyllocarids (see **Ceratiocarididae**), and other indeterminate fossils; United States, Middle Ordovician.

**Wiwaxia:** a small, slug-like but armored animal of the middle Cambrian; first found in the Burgess Shale group and identified by Walcott as a polychaete worm, it is now sometimes classified as a mollusk, possibly a stem-polyplacophoran; it resembled a miniature sea urchin except that it had only two rows of spikes on its head and eight rows of carbonaceous sclerites covering its body, similar to those of

an isopod; isolated specimens have been found also in the United States, China, and Russia, dated between 513 and 505 Ma.

**Wukongopteridae:** a small family of pterosaurs represented by the genera *Darwinopterus* and *Wukongopterus* (the latter is poorly known); the family is an example of modular evolution, having a long tail and other characteristics of the earliest pterosaurs, combined with the skull features of the more advanced pterodactyloids; China and England, Middle to Late Jurassic, 165–153 Ma.

**Wynyardiidae:** a small extinct family of marsupials in the still-extant order Diprotodontia; similar to the phalangerids, the Wynyardiidae are intermediate between the primitive polyprotodonts and the advanced diprotodonts; Australia, Oligocene to Miocene.

# X

**Xenacanthida:** an order of late Paleozoic freshwater sharks in the superorder Euselachii; formerly called Pleuracanthodii. Eel-like and as long as 13 feet, they are characterized by two-pronged teeth and a large serrated spine extending backward from the rear of the braincase. They appeared in the Carboniferous and spread worldwide in the Permian, but only a few genera survived the Permian extinctions before disappearing in the Middle Triassic.

**Xenarthra:** a clade of unusual placental mammals of the Americas that includes the living sloths, anteaters, and armadillos, as well as many extinct ancestors, including the glyptodonts, pampatheres, and ground sloths. They were formerly referred to as paratheres, or as edentates because of the lack of enamel on their teeth. Many genera are marked by varying degrees of body armor in the form of dermal ossicles. The anteaters of Africa and Asia (such as the aardvarks, echidnas, numbats, and pangolins) are unrelated, having evolved convergently to fill the same ecological niche. North and South America, Paleocene to Recent.

**Xenodiscus:** a genus of ceratitic ammonoids in the superfamily Xenodiscoidea; evolute and thinly discoidal, 2–4 inches wide; North America, Asia, and Madagascar; middle Permian to Early Triassic.

**Xenopithecus:** a proposed genus known only from a disputed jaw fragment, possibly of an early hominoid ape; Kenya, late Oligocene, 28 Ma.

**Xenungulata:** a still-obscure order of large South American ungulates placed in the extinct superorder Meridiungulata; the order currently contains one family, the Carodniidae, with three genera; its inconclusive similarities to several other very different and widespread mammalian groups (such as the primitive Pantodonta, the Uintatheriidae of the Eocene, and the Embrithopoda) leave it *incertae sedis*; Paleocene to Eocene.

**Xenusion:** a genus of basal onychophorans or lobopods in the class Xenusia; poorly known from two specimens found in glacial debris; see also **Onychophora**; Europe, early Cambrian.

**Xiaotingia zhengi:** a species of feathered theropod dinosaurs from the Late Jurassic, about the size of a chicken; described in 2011, its classification and significance are still in doubt; China, 155 Ma.

**Xiongguanlong baimoensis:** a 5-foot-long dinosaur discovered in the southern Gobi Desert and described in 2010. It seems to be an intermediate ancestor of the large tyrannosaurs of the Late Cretaceous. Although earlier fossils of much smaller ancestors of tyrannosaurs are known from England and China, *Xiongguanlong* is an important mid-weight relative that exhibits some of the characteristic features of the effective predator *T. rex*: broader skull attachments that made massive, more powerful jaw muscles possible, and thicker vertebrae to support a larger head. China, Early Cretaceous, 110 Ma.

**Xiphactinus:** “sword-ray,” a genus of large predatory actinopterygian fish in the family Ichthyodectidae; between 15 and 20 feet long, it is characterized by a large gape and four large fangs at the tip of its snout for grasping prey; a specimen at the Royal Tyrrell Museum in Alberta, Canada, is famous for having a well-preserved 6-foot ichthyodectid fish (*Gillicus*) inside its stomach; global distribution, Early to Late Cretaceous.

**Xiphodontidae:** an extinct family of artiodactyl ungulates in the suborder Tylopoda. The xiphodonts were generally slender and camel-like but known only in Europe. Since the early evolution of the camel family is restricted to North America, they probably evolved separately, but a paucity of intermediate specimens makes their relationship unclear. The type genus *Xiphodon* is well-known in the late Eocene, and *Paraxiphodon* from the Eocene to the early Oligocene.

**Xiphosurida:** a still-extant order of marine chelicerate arthropods in the class Xiphosura; the order includes several Paleozoic families and is represented today by *Limulus* and *Tachypleus*, the horseshoe crabs; see also **Lunataspis**; global distribution, Late Ordovician to Recent.

**Xylotitan:** a genus of dwarf brontotheres; the most abundant mammal in the Clarno Nut Beds of Oregon, dated about 44 Ma; North America, middle Eocene.

# Y

**Ya Ha Tinda:** a Konservat-Lagerstätte in Alberta, first described in 2017. Located in the Lower Jurassic Fernie Formation, the site has produced well-preserved articulated marine vertebrates, mollusks, crinoids, crustaceans, and some plant fossils. Like the Holzmaden, Strawberry Bank, and Osteno sites of Europe, it is dated at 183 Ma, near the boundary of the Pliensbachian and Toarcian Stages of the Early Jurassic. Significantly, its fauna is remarkably similar to those of the European sites. Canada, Early Jurassic.

**Yawunik kootenayi:** a species of Cambrian arthropods found in 2014 at the Marble Canyon site of the Burgess Shale; it had an external skeleton, segmented body, and jointed appendages; it could move its frontal appendages backward and forward when swimming, and caught prey in the toothed claws on some appendages; Canada, middle Cambrian, 508 Ma.

**Yinotheria:** a proposed subclass of mammals to include several Mesozoic families and the still-living monotremes, the platypus and four species of echidnas; Late Triassic to Recent.

**Yixian Formation:** a Lower Cretaceous (Barremian to early Aptian) formation in Liaoning Province; Yixian fossils form the larger part of the Jehol biota, underlying the equally important Jiufotang Formation; China, Early Cretaceous.

**Younginidae:** a late Permian family of small diapsid reptiles, formerly placed in the discarded classifications Eosuchia and Younginiformes but now tentatively placed in the clade Neodiapsida; the type species *Youngina capensis* lived in Southern Africa at the end of the Permian and may have survived into the Triassic; Africa and Madagascar, late Permian.

**Yuknessia:** a genus of colonial hemichordate animals in the class Pterobranchia; it extended long branches from a holdfast and is known from the Burgess Shale and other coeval sites; North America and Asia, middle Cambrian.

**Yunnanocopia:** see **Lophogastrida**.

***Yunnanolepis***: a genus of primitive placoderms in the order Antiarchi; China, Early to Middle Devonian.

***Yunnanozoon***: a genus of early Cambrian animals in the Chengjiang biota; *Y. lividum*, similar to *Pikaia* of the Burgess Shale, may be the earliest-known hemichordate; China, 530 Ma.

***Yutyranus huali***: a species of large coelurosaurian dinosaurs in the superfamily Tyrannosauoidea, described in 2012 and dated at 125 Ma. About 30 feet long and weighing 1.5 tons, *Yutyranus* is the largest known feathered dinosaur. The three specimens are also notable for being almost completely articulated fossils with three-fingered hands. Feathers are clearly present in several areas of the body, the longest being 8-inch neck feathers and 6-inch tail feathers. Yixian formation, Liaoning Province, China; Early Cretaceous.

## Z

**Zalambdalestidae:** a family of small, primitive eutherian mammals; now considered stem-eutherians and probably not placental; the shrew-like, mostly insectivorous *Zalambdalestes* was about a foot long; Mongolia, Late Cretaceous, possibly to Paleocene.

**Zhongjianichthys:** a poorly known genus of basal chordate animals; eel-like and jawless, it is about an inch long and has a thick skin and a ventral fin the length of its body; proposed as a relative of *Myllokunmingia*; Chengjiang biota, China, early Cambrian.

**zoarium:** a collection of individual zooids that make up a compound or colonial organism; some bryozoans form zoaria more than a foot wide.

**zone fossil:** see **index fossil**.

**zoecia:** singular zoecium, the chambers constructed by individual bryozoans.

**Zosterophyllum:** a genus of primitive vascular land plants in the subdivision Lycophytina and extinct paraphyletic class Zosterophyllopsida; characterized by kidney-shaped sporangia growing near the ends of the branches; global distribution, Silurian to Late Devonian.

**Zuniceratops:** a monospecific genus of ornithischian dinosaurs in the suborder Ceratopsia; *Z. christopheri* is known from one skull and the bones of several individuals, first found in 1996; only 10 feet long and weighing less than 300 pounds, *Zuniceratops* seems to represent a transitional stage between the earliest ceratopsians and the larger, more familiar ones that were common in North America toward the end of the Cretaceous; New Mexico, 91 Ma.

**Zygentoma:** the silverfish, a still-extant order of insects previously grouped with the Archaeognatha in the obsolete order Thysanura; characterized by an elongate body and at least two cerci and one medial extension on the tail; cosmopolitan,

known definitively from the Middle Devonian but probably originating in the late Silurian.

***Zygodon***: a genus of proboscideans in the family Mammutidae; one of the largest terrestrial mammals, it was 14 feet high at the shoulder, weighed 15–18 tons, and bore a pair of 13-foot tusks; North America, Europe, Asia, and Africa; Miocene to Pleistocene.



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