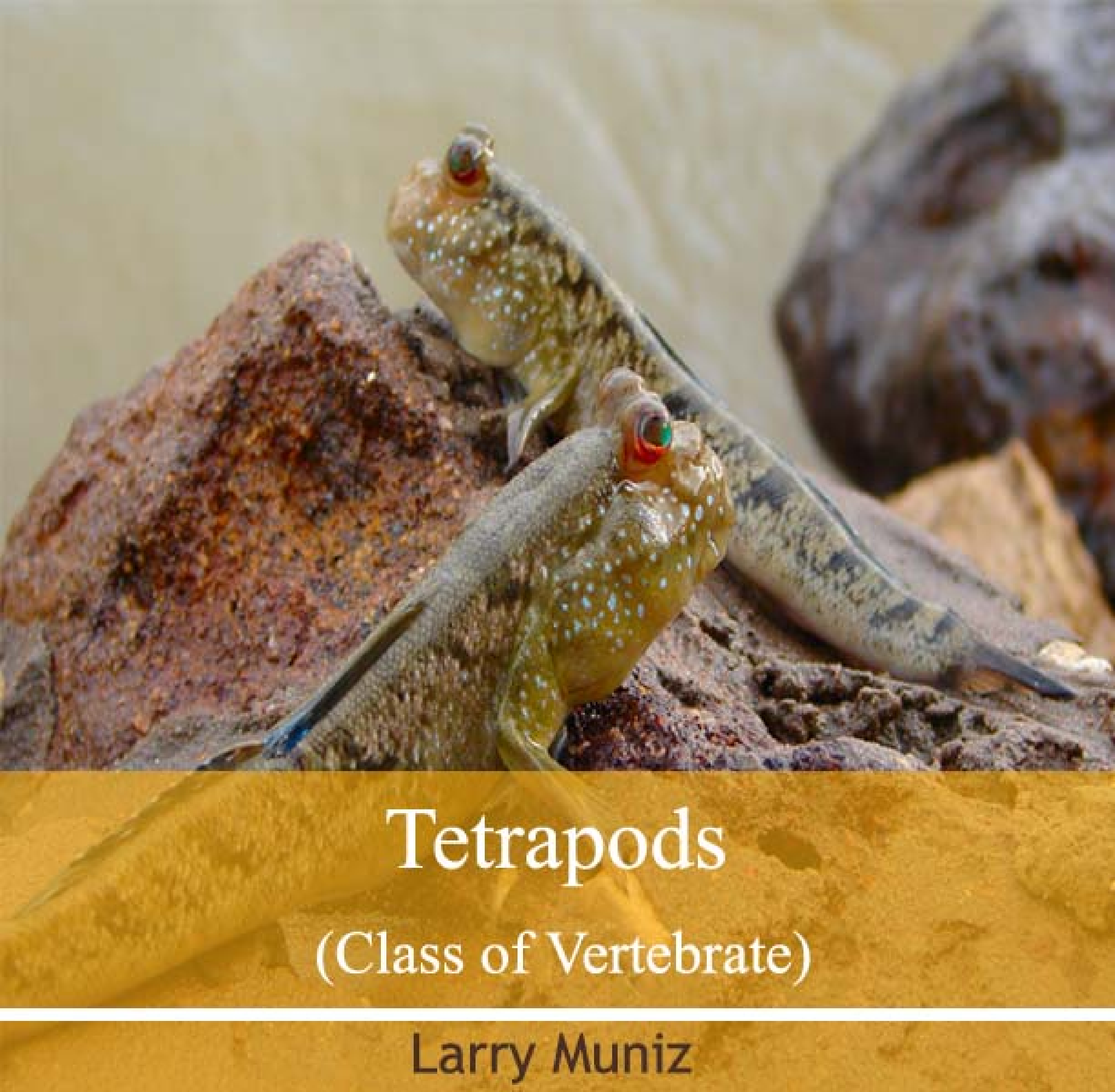

Tetrapods

(Class of Vertebrate)

Larry Muniz

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Chapter 1

Tetrapod

Tetrapods

Temporal range: Middle Devonian - Recent, 395–0 Ma

The four classes of extant tetrapods, (clockwise from upper left), *Rana* (amphibian), *Opisthocomus* (bird), *Eumeces* (reptile) and *Mus* (mammal)

Scientific classification [e]

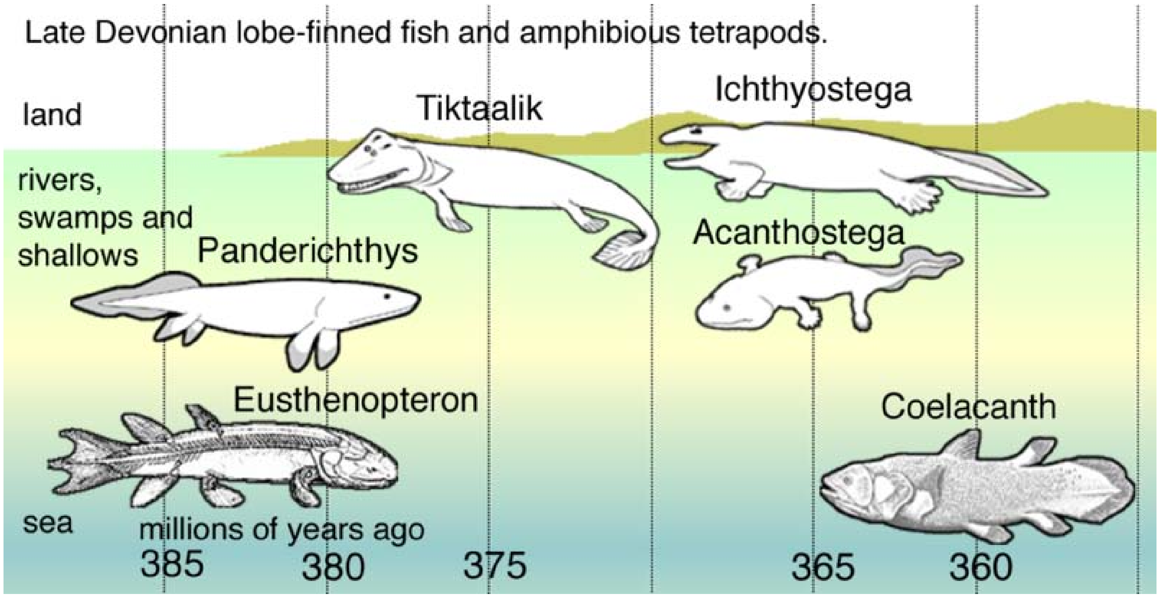
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Infraphylum:	Gnathostomata
(unranked):	Eugnathostomata
(unranked):	Teleostomi
Superclass:	**Tetrapoda** Broili, 1913

Subgroups

- Amphibia
- Reptiliomorpha

Tetrapods are vertebrate animals having four limbs. Amphibians, reptiles, birds and mammals are all tetrapods; even snakes and other limbless reptiles and amphibians are tetrapods by descent. The earliest tetrapods evolved from the lobe-finned fishes in the Devonian. They are now a dominant part of the terrestrial fauna, representing all known larger land animals. Some groups have even returned to an aquatic existence, including the largest animal known, the blue whale.

Evolution

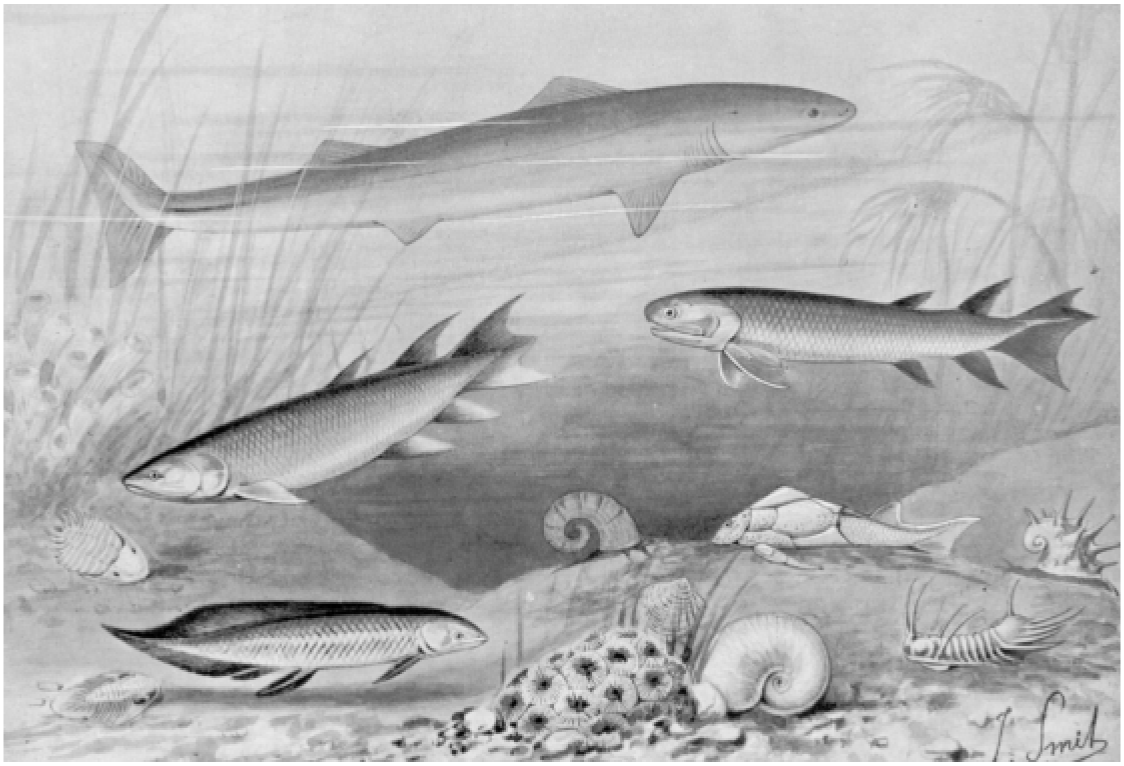


In Late Devonian vertebrate speciation, descendants of pelagic lobe-finned fish — like *Eusthenopteron* — exhibited a sequence of adaptations:
•*Panderichthys*, suited to muddy shallows;
•*Tiktaalik* with limb-like fins that could take it onto land;
•Early tetrapods in weed-filled swamps, such as;
 •*Acanthostega*, which had feet with eight digits,
 •*Ichthyostega* with limbs.
Descendants also included pelagic lobe-finned fish such as coelacanth species.

Origin

The evolution of the first tetrapods marked the moment when the two basic forms of vertebrates, fishes and tetrapods, diverged. This transition, from a body plan for breathing and navigating in water and a body plan enabling the animal to move on land, involved a series of changes taking place throughout most of the 57 million years that make up the Devonian period. While it is one of the most profound evolutionary changes known, it is also one of the best understood, largely thanks to a number of amazing fossil finds in the late 20th century combined with improved phylogenetic analysis.

"The Age of Fishes"



Devonian fishes, including an early shark Cladoselache, *Eusthenopteron* and other lobe-finned fishes, and the placoderm *Bothriolepis*, 1905.

The Devonian period is traditionally known as the "Age of Fishes", marking the diversification of numerous extinct and modern major fish groups. Among them were the early bony fishes, who diversified and spread in freshwater and brackish environments at the beginning of the period. The early types resembled their cartilaginous forefathers in many aspects of their anatomy, including a shark-like tailfin, spiral gut, large pectoral fins stiffened in front by skeletal elements and a largely unossified axial skeleton.

They did however have certain traits separating them from cartilaginous fishes, traits that would become pivotal in the evolution of terrestrial forms: The gills did not open singly to exterior like in sharks, rather they were hidden behind a bony operculum, and bound posteriorly by a stout cleithrum bone, also functioning as anchoring for the pectoral fins. As part of the overall armour of rhomboid cosmin scales, the skull had a full cover of dermal bone, constituting a skull roof over the otherwise shark-like cartilaginous inner cranium. Importantly, they also had a swim bladder/lung, a feature lacking in all other fishes.

Lungs before land

The primary function of the swim bladder/lung is not entirely certain. One consideration is buoyancy. The heavy scale armour of the early bony fishes would certainly weigh the animals down. In cartilaginous fishes, lacking a swim bladder, the open sea sharks need to swim constantly to avoid sinking into the depths, the pectoral fins providing lift. Another factor is oxygen consumption. Ambient oxygen was relatively low in the early Devonian, possibly about half of modern values. The partial pressure of oxygen is necessarily much higher in air than in water, and vertebrates are active animals with high energy requirement compared to invertebrates of similar sizes. The Devonian saw increasing oxygen levels, opening up ecological niches as active, large bodied animals for groups able to exploit aerial oxygen. Both factors may have been important, modern fishes with open swim bladders do indeed use their bladders both for buoyancy and for breathing.

In order to function in gas exchange, lungs need to be supplied by blood. In cartilaginous fishes and teleosts, the heart pumps blood forward through the ventral aorta which splits up in a series of paired aortic arches, each corresponding to a gill arch. The aortic arches then merge to form a dorsal aorta supplying the body with oxygenated blood. In lungfishes, bowfin and bichirs, the swim bladder is supplied by paired pulmonary arteries branching off from the hindmost (6th) aortic arch. The same basic pattern is found in the lungfish *Protopterus* and in terrestrial salamanders, and was likely the pattern found in the tetrapods' immediate forefathers as well as the first tetrapods. In most other bony fishes the swim bladder is supplied by the dorsal aorta.

Skull morphology

The tetrapods have their root in the early Devonian tetrapodomorph fish. Primitive tetrapods developed from an osteolepid tetrapodomorph lobe-finned fish (sarcopterygian-crossopterygian), with a two-lobed brain in a flattened skull. The coelacanth group represent marine sarcopterygians that never acquired these shallow-water adaptations. The sarcopterygians apparently took two different lines of descent and are accordingly separated into two major groups: the Dipnomorpha (including the Dipnoi or lungfishes) and the Tetrapodomorpha (which include extinct lines of lobe-finned fishes that evolved into the Tetrapoda).

From fins to feet

The oldest known tetrapodomorph is *Kenichthys* from China, dated at around 395 million years old. Two of the earliest tetrapodomorphs, dating from 380 Ma, were *Gogonasus* and *Panderichthys*. They had a choana and used their fins as paddles in shallow-water habitats choked with plants and detritus. Their fins could also have been used to attach themselves to plants or similar while they were lying in ambush for prey. The universal tetrapod characteristics of front limbs that bend backward at the elbow and hind limbs that bend forward at the knee can plausibly be traced to early tetrapods living in shallow water.

It has been suggested that the evolution of the tetrapod limb from lobe-finned fishes is related to the loss of the proteins actinodin 1 and actinodin 2, which are involved in fish fin development

Denizens of the swamp

The first tetrapods are thought to have evolved in coastal and brackish marine environments, and in shallow and swampy freshwater habitats. Formerly, the timing was thought to be towards the end of the Devonian. In 2010, this belief was challenged by the discovery of the oldest known tetrapod tracks, preserved in marine tidal flat sediments of the southern coast of Laurasia, now Świętokrzyskie (Holy Cross) Mountains of Poland. They were made during the Eifelian stage of the Middle Devonian. The tracks are dated to about 395 million years ago, 18 million years earlier than the oldest known tetrapod body fossils. Some tracks show digits, indicating that the animal had the ability to walk on land. Additionally, the tracks show that the animal was capable of thrusting its arms and legs forward. This type of motion would have been impossible in tetrapodomorphs such as *Tiktaalik*. The animal that produced the tracks is estimated to have been up to 2.5 metres (8.2 ft) long with footpads up to 26 centimetres (10 in) wide, although most tracks are only 15 centimetres (5.9 in) wide.

Devonian tetrapods

Research by Jennifer A. Clack and her colleagues showed that the earliest tetrapods, such as *Acanthostega*, were wholly aquatic and quite unsuited to life on land. This is in contrast to the earlier view that fish had first invaded the land — either in search of prey (like modern mudskippers) or to find water when the pond they lived in dried out — and later evolved legs, lungs, etc.

By the late Devonian, land plants had stabilized freshwater habitats, allowing the first wetland ecosystems to develop, with increasingly complex food webs that afforded new opportunities. Freshwater habitats were not the only places to find water filled with organic matter and choked with plants with dense vegetation near the water's edge. Swampy habitats like shallow wetlands, coastal lagoons and large brackish river deltas also existed at this time, and there is much to suggest that this is the kind of environment in which the tetrapods evolved. Early fossil tetrapods have been found in marine sediments, and because fossils of primitive tetrapods in general are found scattered all around the world, they must have spread by following the coastal lines — they could not have lived in freshwater only.

Excretion in tetrapods

The common ancestor of all present gnathostomes lived in freshwater, and later migrated back to the sea. To deal with the much higher salinity in sea water, they evolved the ability to turn the nitrogen waste product ammonia into harmless urea, storing it in the body to make the blood as salty as the sea water without poisoning the organism. This is the system currently found in cartilaginous fishes and the first bony fishes (acanthodians). Ray-finned fishes (Actinopterygii) later returned to freshwater and lost this ability, while the fleshy-finned fishes (Sarcopterygii) retained it. Since the blood of ray-finned fishes contains more salt than freshwater, they could simply get rid of ammonia through their gills. When they finally returned to the sea again, they did not recover their old trick of turning ammonia to urea, and they had to evolve salt excreting glands instead. Lungfishes do the same when they are living in water, making ammonia and no urea, but when the water dries up and they are forced to burrow down in the mud, they switch to urea production. Like cartilaginous fishes, the coelacanth can store urea in its blood, as can the only known amphibians that can live for long periods of time in salt water (the toad *Bufo marinus* and the frog *Rana cancrivora*). These are traits they have inherited from their ancestors.

If early tetrapods lived in freshwater, and if they lost the ability to produce urea and used ammonia only, they would have to evolve it from scratch again later. Not a single species of all the ray-finned fishes living today has been able to do that, so it is not likely the tetrapods would have done so either. Terrestrial animals that can only produce ammonia would have to drink constantly, making a life on land impossible (a few exceptions exist, as some terrestrial woodlice can excrete their nitrogenous waste as ammonia gas). This probably also was a problem at the start when the tetrapods started to spend time out of water, but eventually the urea system would dominate completely. Because of this it is not likely they emerged in freshwater (unless they first migrated into freshwater habitats and then migrated onto land so shortly after that they still retained the ability to make urea), although some species never left, or returned to, the water could of course have adapted to freshwater lakes and rivers.

Lungs

It is now clear that the common ancestor of the bony fishes (Osteichthyes) had a primitive air-breathing lung -- later evolved into a swim bladder in most actinopterygians (ray-finned fishes). This suggests that crossopterygians evolved in warm shallow waters, using their simple lung when the oxygen level in the water became too low.

Fleshy lobe-fins supported on bones rather than ray-stiffened fins seems to have been an ancestral trait of all bony fishes (Osteichthyes). The lobe-finned ancestors of the tetrapods evolved them further, while the ancestors of the ray-finned fishes (Actinopterygii) evolved their fins in a different direction. The most primitive group of actinopterygians, the bichirs, still have fleshy frontal fins.

Fossil early tetrapods

Nine genera of Devonian tetrapods have been described, several known mainly or entirely from lower jaw material. All but one were from the European-North American supercontinent, which comprised Europe, North America and Greenland. The only exception is a single Gondwanan genus, *Metaxygnathus*, which has been found in Australia.

The first Devonian tetrapod identified from Asia was recognized from a fossil jawbone reported in 2002. The Chinese tetrapod *Sinostega pani* was discovered among fossilized tropical plants and lobe-finned fish in the red sandstone sediments of the Ningxia Hui Autonomous Region of northwest China. This finding substantially extended the geographical range of these animals and has raised new questions about the worldwide distribution and great taxonomic diversity they achieved within a relatively short time.

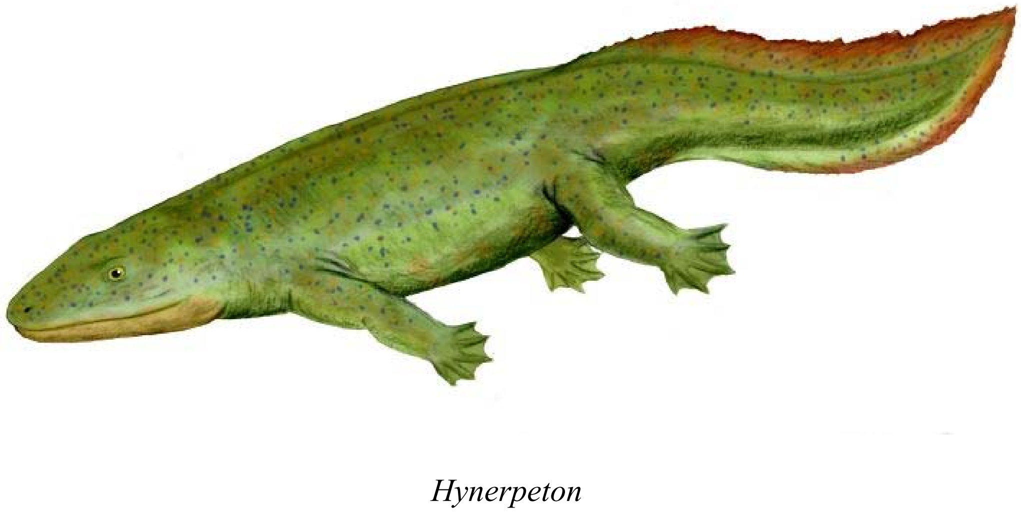
Eusthenopteron

Panderichthys

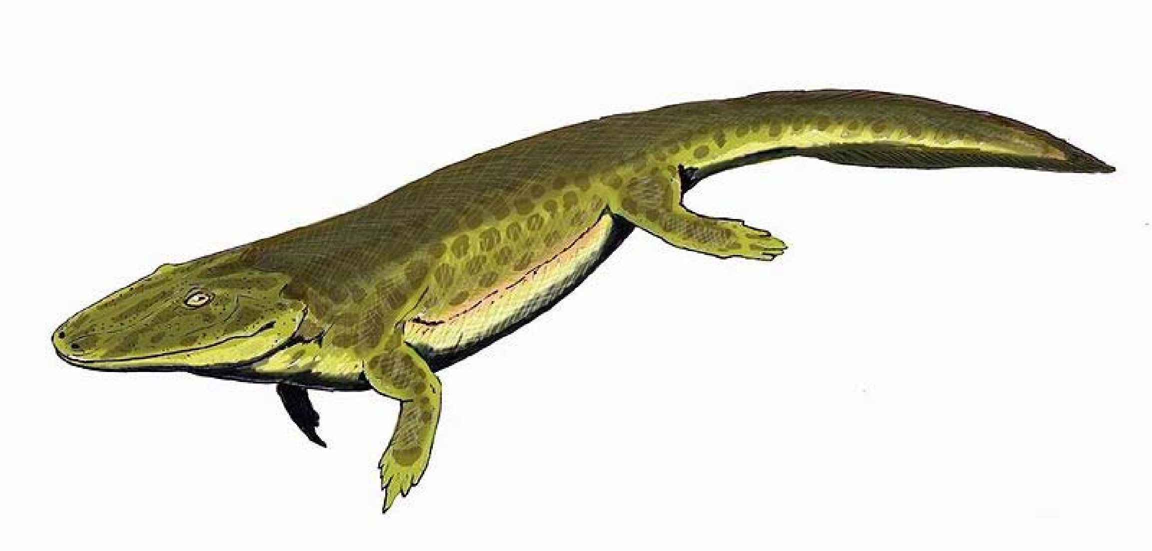
Tiktaalik

Acanthostega

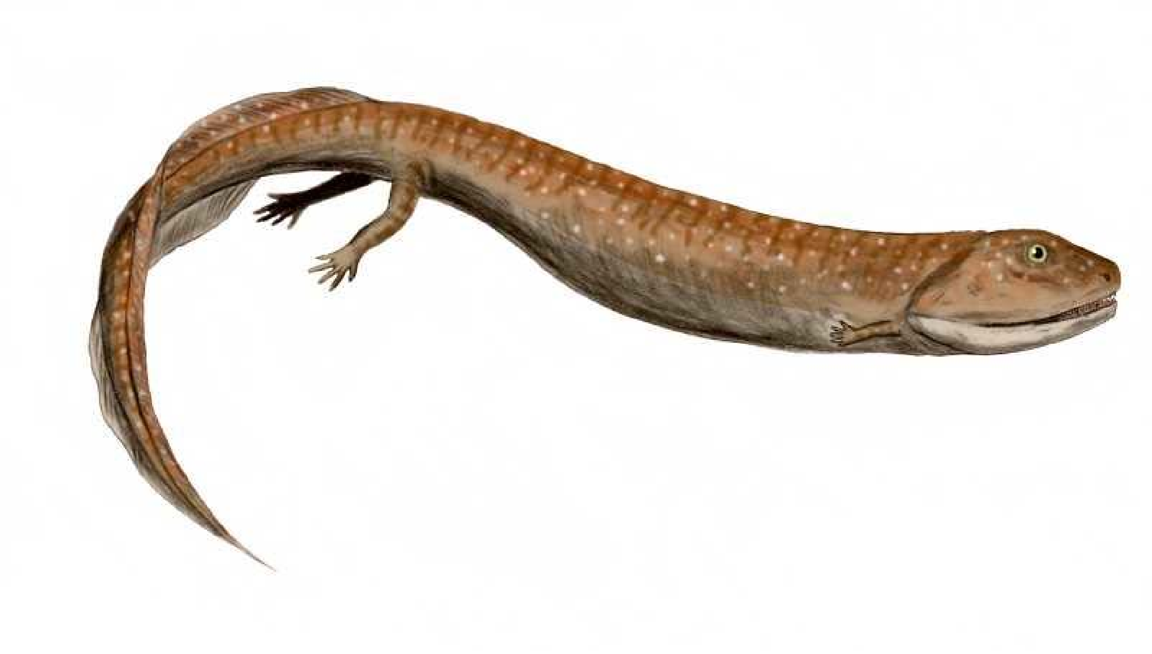
Ichthyostega



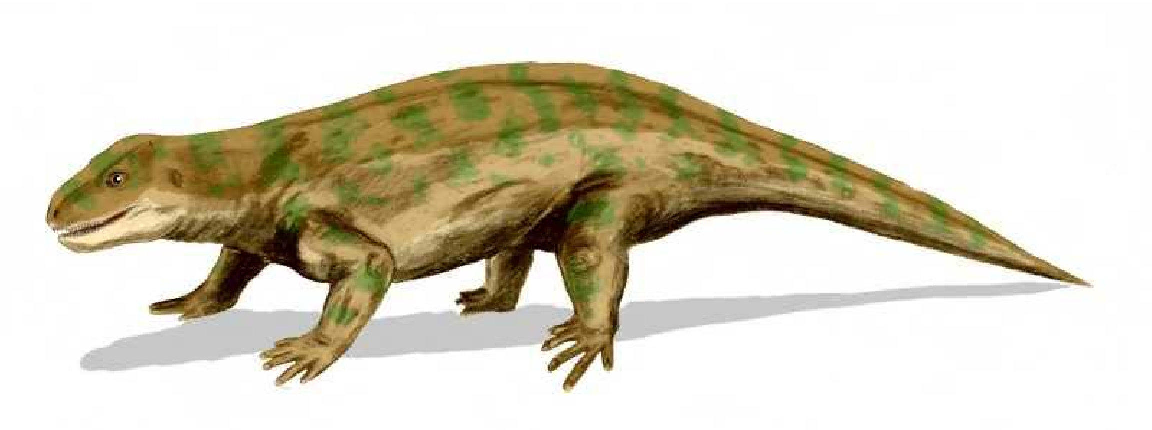
Hynerpeton



Tulerpeton



Crassigyrinus



Diadectes

These earliest tetrapods were not terrestrial. The earliest confirmed terrestrial forms are known from the early Carboniferous deposits, some 20 million years later. Still, they may have spent very brief periods out of water and would have used their legs to paw their way through the mud.

Why they went to land in the first place is still debated. One reason could be that the small juveniles who had completed their metamorphosis had what it took to make use of what land had to offer. Already adapted to breathe air and move around in shallow waters near land as a protection (just as modern fish (and amphibians) often spent the first part of their life in the comparative safety of shallow waters like mangrove forests), two very different niches partially overlapped each other, with the young juveniles in the diffuse line between. One of them was overcrowded and dangerous while the other was much safer and much less crowded, offering less competition over resources. The terrestrial niche was also a much more challenging place for primary aquatic animals, but because of the way evolution and the selection pressure works, those juveniles who could take advantage of this would be rewarded. Once they gained a small foothold on land, thanks to their preadaptations and being at the right place at the right time, favourable variations in their descendants would gradually result in continuing evolution and diversification.

At this time the abundance of invertebrates crawling around on land and near water, in moist soil and wet litter, offered a food supply. Some were even big enough to eat small tetrapods, but the land was free from dangers common in the water.

It is plausible that at first adults would be too heavy and slow and have greater needs for large prey. Small juveniles would be much lighter, faster and could subsist on relatively small invertebrates. Modern mudskippers are said to be able to snap insects in flight while on land, and the early juvenile tetrapods might also have shown formidable abilities.

From water to land

Initially making only tentative forays onto land, tetrapods adapted to terrestrial environments over time and spent longer periods away from the water, while also spending a longer part of their juvenile stage on land before returning to the water for the rest of their life. It is also possible that the adults started to spend some time on land (as the skeletal modifications in early tetrapods such as *Ichthyostega* suggests) but only to bask in the sun close to the water's edge, not to hunt or move around. The first true tetrapods that were adapted to terrestrial locomotion were small. Only later did they increase in size.

The fully grown kept most of the anatomical adaptations from their juvenile stage, giving them modified limbs and other traits associated with a terrestrial lifestyle. To be successful adults they first had to be successful juveniles. The adults of some of the smaller species were in that case probably able to move on land too when sufficiently evolved.

If some sort of neoteny or dwarfism occurred, making the animals sexually mature and fully grown while still living on land, they would only need to visit water to drink and reproduce.

Carboniferous tetrapods

Until the 1990s, there was a 30 million year gap in the fossil record between the late Devonian tetrapods and the reappearance of tetrapod fossils in recognizable mid-Carboniferous amphibian lineages. It was referred to as "Romer's Gap", after the palaeontologist who recognized it.

During the "gap", tetrapod backbones developed, as did limbs with digits and other adaptations for terrestrial life. Ears, skulls and vertebral columns all underwent changes too. The number of digits on hands and feet became standardized at five, as lineages with more digits died out. The very few tetrapod fossils found in the "gap" are all the more precious.

The transition from an aquatic lobe-finned fish to an air-breathing amphibian was a momentous occasion in the evolutionary history of the vertebrates. For an animal to live in a gravity-neutral, aqueous environment and then invade one that is entirely different required major changes to the overall body plan, both in form and in function. *Eryops* is an example of an animal that made such adaptations. It retained and refined most of the traits found in its fish ancestors. Sturdy limbs supported and transported its body while out of water. A thicker, stronger backbone prevented its body from sagging under its own weight. Also, by utilizing vestigial fish jaw bones, a rudimentary ear was developed, allowing *Eryops* to hear airborne sound.

By the Visean age of mid-Carboniferous times the early tetrapods had radiated into at least three main branches. Recognizable basal-group tetrapods are representative of the temnospondyls (e.g. *Eryops*) lepospondyls (e.g. *Diplocaulus*) and anthracosaurs, which were the relatives and ancestors of the Amniota. Depending on whichever authorities one follows, modern amphibians (frogs, salamanders and caecilians) are derived from either temnospondyls or lepospondyls (or possibly both, although this is now a minority position). The first amniotes are known from the early part of the Late Carboniferous, and during the Triassic counted among their number the earliest mammals, turtles, and crocodiles (lizards and birds appeared in the Jurassic, and snakes in the Cretaceous). As living members of the tetrapod clan — that is of the tetrapod "crown-group" — these varied tetrapods represent the phylogenetic end-points of these two divergent lineages. A fourth Carboniferous group, the baphetids, which are thought to be related to temnospondyls, left no modern survivors.

Permian tetrapods

In the Permian period, as the separate tetrapod lineages each developed in their own way, the term "tetrapoda" becomes less useful. In addition to temnospondyl and anthracosaur clades among the early "amphibia" (labyrinthodonts), there were two important divergent clades of amniotes, the Sauropsida and the Synapsida, of which the latter were the most important and successful Permian animals. Each of these lineages, however, remains grouped with the tetrapoda, just as *Homo sapiens* could be considered a very highly-specialized kind of *lobe-finned fish*.

Mesozoic

The beginning of the Mesozoic saw a major turnover in fauna following the Permian–Triassic extinction event. Many of the once large and diverse groups died out or were greatly reduced. Life on Earth seemed to recover quickly after the Permian extinctions, but this was mostly in the form of disaster taxa, such as the hardy *Lystrosaurus*. The most recent research indicates that the specialized animals that formed complex ecosystems, with high biodiversity, complex food webs and a variety of niches, took much longer to recover. It is thought that this long recovery was due to the successive waves of extinction which inhibited recovery, as well as to prolonged environmental stress to organisms which continued into the Early Triassic. Recent research indicates that recovery did not begin until the start of the mid-Triassic, 4M to 6M years after the extinction; and some writers estimate that the recovery was not complete until 30M years after the P-Tr extinction, i.e. in the late Triassic.

A small group of reptiles, the diapsids, began to diversify during the Triassic, notably the dinosaurs. By the late Mesozoic, the large Laborynthodont groups that first appeared during the Paleozoic such as temnospondyls and reptile-like amphibians had gone extinct. All current major groups of sauropsids evolved during the Mesozoic, with birds first appearing in the Jurassic as a derived clade of theropod dinosaurs. Many groups of synapsids such as anomodontians and therocephalians that once comprised the dominant terrestrial fauna of the Permian also became extinct during this time, but during the Triassic, one group (Cynodontia) gave rise to the descendant taxon Mammalia, which survived through the Mesozoic to later diversify into the dominant terrestrial fauna during the Cenozoic.

Extant (Living) tetrapods

Following the great faunal turnover at the end of the Mesozoic, only three categories of living crown group tetrapods were left, all of which also include many extinct groups:

- Lissamphibia : Modern frogs and toads, newts and salamanders, and caecilians
- Sauropsida : Turtles, lepidosaurians (tuataras, lizards, amphisbaenians and snakes), birds, and crocodilians
- Synapsida : Mammals

Classification

Tetrapods were originally classified by means of Linnean taxonomy, but currently their taxonomy is more frequently being evaluated cladistically.

Linnaean classification

Traditional classification has the tetrapods classed into four classes based on gross anatomical and physiological traits. Note that snakes and other legless reptiles are considered tetrapods because they are descended from ancestors who had a full complement of limbs. Similar considerations apply to caecilians and aquatic mammals:

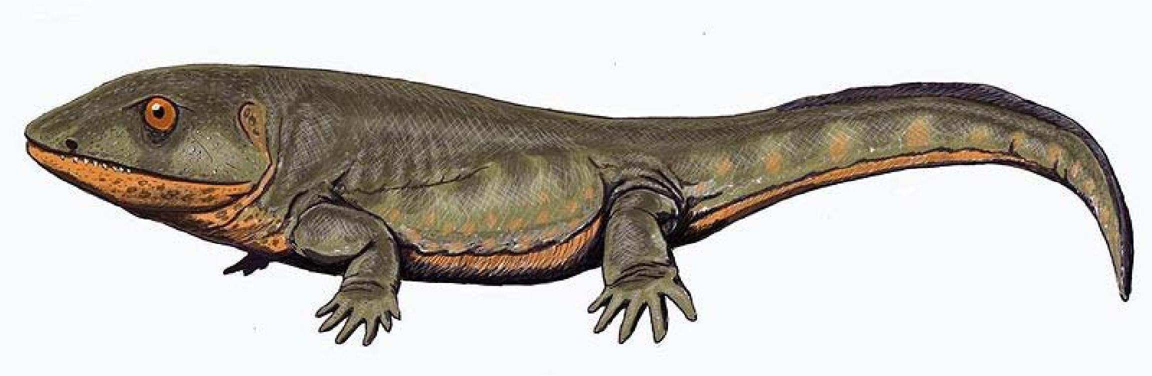
- Class Amphibia (Amphibians)
- Class Reptilia (Reptiles)
- Class Aves (Birds)
- Class Mammalia (Mammals)

This classification is the one most commonly encountered in school textbooks and popular works. While orderly and easy to use, has come under critique from cladistics. The earliest tetrapods are grouped under Class Amphibia, despite several of the groups would have been more closely related to Amniotes than to modern day amphibians. Reptiles too form a paraphyletic group, as they have given rise to (birds that are traditionally not considered to be a type of reptile. basal non-mammalian synapsids ("mammal-like reptiles") traditionally also sort under Class Reptilia as a separate subclass. They are however not among in the crown group reptiles, and while the early groups may have been reptile-like in biology, the later ones was decidedly not reptile-like, nor were they true mammals. Thus some authors have argued for a new classification based purely on phylogeny, disregarding the anatomy and physiology (see below).

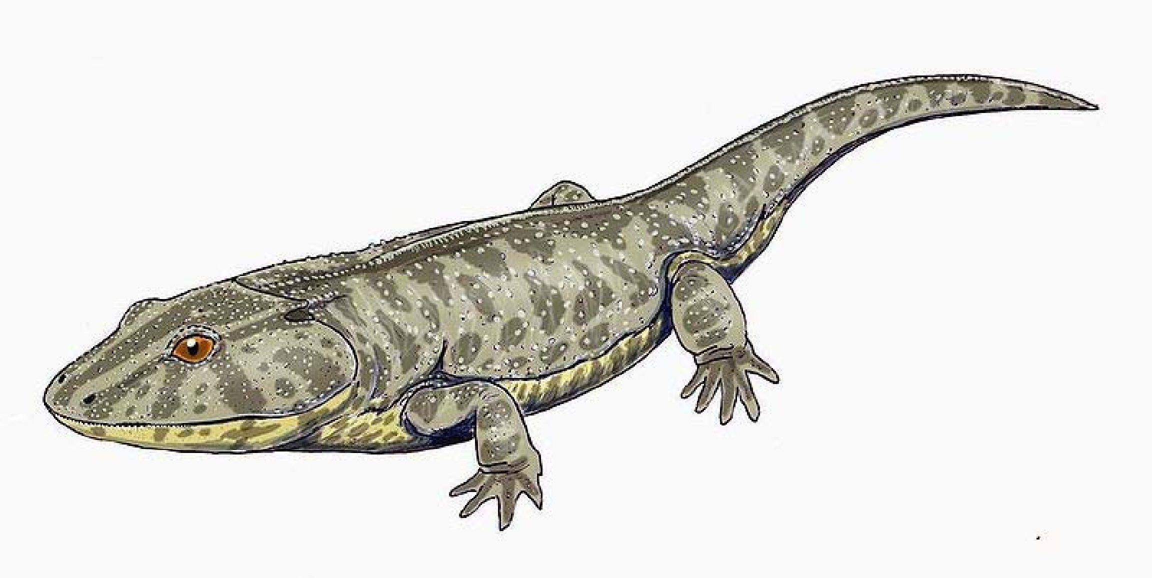
Phylogenetic classification

All early tetrapods and tetrapodomorphs that were not amphibians in the strict phylogenetic sense, nor amniotes, were once placed together in the paraphyletic group Labyrinthodontia. Labyrinthodonts were distinguished mainly by their complex dentine infolding tooth structure, a feature shared with crossopterygian fish. The labyrinthodonts were divided into the Ichthyostegalia (another paraphyletic assemblage of primitive tetrapods and kin, such as *Ichthyostega*), the Temnospondyli (possibly members of Amphibia), and the Anthracosauria (close relatives of amniotes). The main difference between the three groups was based on their respective vertebral structures. The Anthracosauria had small pleurocentra, which grew and fused, becoming the true centrum in later vertebrates. In contrast, the Temnospondyli had a conservative vertebral column in which the pleurocentra remained small in primitive forms, vanishing entirely in the more advanced ones. The intercentra are large and form a complete ring. Temnospondyli is thought to have been the sister group of Anthracosauria, which would eventually give rise to amniotes.

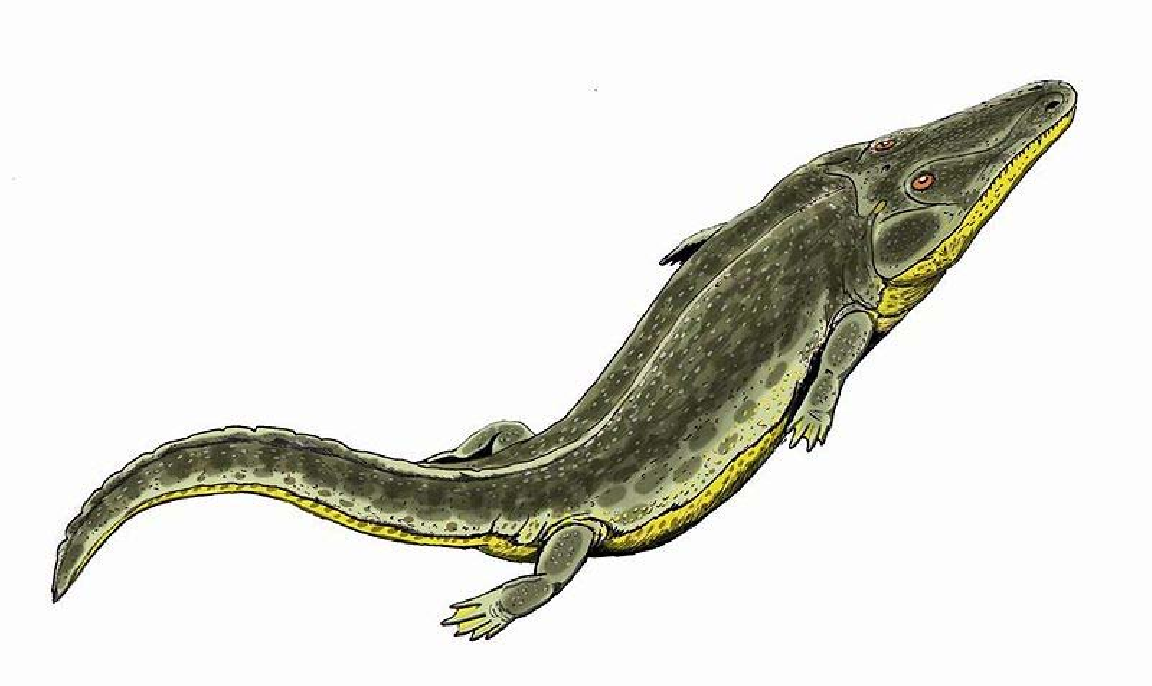
Tetrapod groups



Pederpes finneyae



Lyddekerina huxleyi



Benthosuchus sushkini

A partial taxonomy of the tetrapods:

- Phylum Chordata
    -
    - Class **Sarcopterygii**
      - **Subclass Tetrapodomorpha**
        - *Eusthenopteron*
        - *Panderichthys*
        - *Tiktaalik*
        - *Ventastega*
  - **Superclass Tetrapoda**
      -
        -
        - Family Elginerpetontidae
        - Family Acanthostegidae
        - Family Ichthyostegidae
        - *Hynerpeton*
        - Family Tulerpeton
        - Family Crassigyrinidae
        - Family Loxommatidae
        - Family Colosteidae
        - Family Whatcheeriidae
        - Family Diadectidae
    - Batrachomorpha (directly above, below, or redundant to Amphibia)

- **Class Amphibia** — Amphibians
    - Subclass Lepospondyli
    - Subclass Temnospondyli
    - Subclass Lissamphibia — frogs, salamanders
- **Superorder Reptiliomorpha** contains among others:
    - Series Amniota, which contains among others:
        - Class Reptilia — Reptiles
        - Class Aves — Birds
        - Class Synapsida — Mammal-like reptiles
        - Class Mammalia — Mammals

Anatomical features of early tetrapods

The tetrapod's ancestral fish must have possessed similar traits to those inherited by the early tetrapods, including internal nostrils (to separate the breathing and feeding passages) and a large fleshy fin built on bones that could give rise to the tetrapod limb. The rhipidistian crossopterygians fulfill every requirement for this ancestry. Their palatal and jaw structures were identical to those of early tetrapods, and their dentition was identical too, with labyrinthine teeth fitting in a pit-and-tooth arrangement on the palate. The crossopterygian paired fins were smaller than tetrapod limbs, but the skeletal structure was very similar in that the crossopterygian had a single proximal bone (analogous to the humerus or femur), two bones in the next segment (forearm or lower leg), and an irregular subdivision of the fin, roughly comparable to the structure of the carpus / tarsus and phalanges of a hand.

The major difference between crossopterygians and early tetrapods was in relative development of front and back skull portions; the snout is much less developed than in most early tetrapods and the post-orbital skull is exceptionally longer than an amphibian's.

A great many kinds of early tetrapods lived during the Carboniferous period. Therefore, their ancestor would have lived earlier, during the Devonian period. Devonian Ichthyostega were the earliest of true tetrapods, with a skeleton that is directly comparable to that of rhipidistian ancestors. Early temnospondyls (Late Devonian to Early Mississippian) still had some ichthyostegid features such as similar skull bone patterns, labyrinthine tooth structure, the fish skull-hinge, pieces of gill structure between the cheek and shoulder, and the vertebral column. They had, however, lost several other fish features such as the fin rays in the tail.

In order to propagate in the terrestrial environment, certain challenges had to be overcome. The animal's body needed additional support, because buoyancy was no longer a factor. A new method of respiration was required in order to extract atmospheric oxygen, instead of oxygen dissolved in water. A means of locomotion would need to be developed to traverse distances between waterholes. Water retention was now important since it was no longer the living matrix, and it could be lost easily to the environment.

Finally, new sensory input systems were required if the animal was to have any ability to function reasonably while on land.

Skull

The most notable characteristics that make a tetrapod's skull different from a fish's are the relative frontal and rear portion lengths. The fish had a long rear portion while the front was short; the orbital vacuities were thus located towards the anterior end. In the tetrapod, the front of the skull lengthened, positioning the orbits farther back on the skull. The lacrimal bone was not in contact with the frontal anymore, having been separated from it by the prefrontal bone. Also of importance is that the skull was now free to rotate from side to side, independent of the spine, on the newly forming neck.

A diagnostic character of temnospondyls is that the tabular bones (which formed the posterior corners of the skull-table) were separated from the respective left and right parietals by a sutural junction between the postparietals and supratemporals. Also at the rear of the skull, all bones dorsal to the cleithrum were lost.

The lower jaw of, for example, *Eryops* resembled its crossopterygian ancestors in that on the outer surface lay a long dentary that bore teeth. There were also bones below the dentary on the jaw: two splenials, the angulary and the surangular. On the inside were usually three coronoids that bore teeth and lay close to the dentary. On the upper jaw was a row of marginal labyrinthine teeth, located on the maxilla and premaxilla. In *Eryops*, as in all early amphibians, the teeth were replaced in waves that traveled from the front of the jaw to the back in such a way that every other tooth was mature, and the ones in between were young.

Dentition

The "labyrinthodonts" had a peculiar tooth structure from which their name was derived and, although not exclusive to the group, the labyrinthine dentition is a useful indicator as to proper classification. The important feature of the tooth is that the enamel and dentine were folded in such a way as to form a complicated corrugated pattern when viewed in cross section. This infolding resulted in strengthening of the tooth and increased wear resistance. Such teeth survived for 100 Ma, first among crossopterygian fish, then stem reptiles. Modern amphibians no longer have this type of dentition but rather pleurodont teeth, in fewer numbers of the whole group.

Sensory organs

The difference in density between air and water causes smells (certain chemical compounds detectable by chemoreceptors) to behave differently. An animal first venturing out onto land would have difficulty in locating such chemical signals if its sensory apparatus was designed for aquatic detection.

Fish have a lateral line system that detects pressure fluctuations in the water. Such pressure is non-detectable in air, but grooves for the lateral line sense organs were found on the skull of labyrinthodonts, suggesting a partially aquatic habitat. Modern amphibians, which are semi-aquatic, exhibit this feature whereas it has been retired by the higher vertebrates. The olfactory epithelium would also have to be modified in order to detect airborne odors.

In addition to the lateral line organ system, the eye had to change as well. This change came about because the refractive index of light differs between air and water, so the focal length of the lens was altered in order to properly function. The eye was now exposed to a relatively dry environment rather than being bathed by water, so eyelids developed and tear ducts evolved to produce a liquid, moistening the eyeball.

Hearing

The balancing function of the middle ear was retained from the fish ancestry, but delicate air vibrations could not set up pulsations through the skull in order for it to function a proper auditory organ. Typical of most labyrinthodonts, the spiracular gill pouch was retained as the otic notch, closed in by the tympanum, a thin, tight membrane.

The hyomandibula of fish migrated upwards from its jaw supporting position, and was reduced in size to form the stapes. Situated between the tympanum and braincase in an air-filled cavity, the stapes was now capable of transmitting vibrations from the exterior of the head to the interior. Thus the stapes became an important element in an impedance matching system, coupling airborne sound waves to the receptor system of the inner ear. This system had evolved independently within several different amphibian lineages.

In order for the impedance matching ear to work, certain conditions had to be met. The stapes must have been perpendicular to the tympanum, small and light enough to reduce its inertia and suspended in an air-filled cavity. In modern species that are sensitive to over 1 kHz frequencies, the footplate of the stapes is 1/20th the area of the tympanum. However, in early amphibians the stapes was too large, making the footplate area oversized, preventing the hearing of high frequencies. So it appears that only high intensity, low frequency sounds could be detected, with the stapes more probably being used to support the braincase against the cheek.

Girdles

The pectoral girdle of early tetrapods such as *Eryops* was highly developed, with a larger size for both increased muscle attachment to it and to the limbs. Most notably, the shoulder girdle was disconnected from the skull, resulting in improved terrestrial locomotion. The crossopterygian cleithrum was retained as the clavicle, and the interclavicle was well-developed, lying on the underside of the chest. In primitive forms, the two clavicles and the interclavical could have grown ventrally in such a way as to form a broad chest plate, although such was not the case in *Eryops*. The upper portion of the girdle had a flat, scapular blade, with the glenoid cavity situated below performing as the articulation surface for the humerus, while ventrally there was a large, flat coracoid plate turning in toward the midline.

The pelvic girdle also was much larger than the simple plate found in fishes, accommodating more muscles. It extended far dorsally and was joined to the backbone by one or more specialized sacral ribs. The hind legs were somewhat specialized in that they not only supported weight, but also provided propulsion. The dorsal extension of the pelvis was the ilium, while the broad ventral plate was composed of the pubis in front and the ischium in behind. The three bones met at a single point in the center of the pelvic triangle called the acetabulum, providing a surface of articulation for the femur.

The main strength of the ilio-sacral attachment of *Eryops* was by ligaments, a condition structurally, but not phylogenetically, intermediate between that of the most primitive embolomerous amphibians and early reptiles. The condition that is more usually found in higher vertebrates is that cartilage and fusion of the sacral ribs to the blade of the ilium are utilized in addition to ligamentous attachments.

Limbs

The humerus was the largest bone of the arm, its head articulating with the glenoid cavity of the pectoral girdle, distally with the radius and ulna. The radius resided on the inner side of the forearm and rested directly under the humerus, supporting much of the weight, while the ulna was located to the outside of the humerus. The ulna had a head, which muscles pulled on to extend the limb, called the olecranon that extended above the edge of the humerus.

The radius and the ulna articulated with the carpus, which was a proximal row of three elements: the radiale underlying the radius, the ulnare underneath the ulna and an intermedium between the two. A large central element was beneath the last and may have articulated with the radius. There were also three smaller centralia lying to the radial side. Opposite the head of each toe lay a series of five distal carpals. Each digit had a first segment, the metacarpal, lying in the palm region.

The pelvic limb bones were essentially the same as in the pectoral limb, but with different names. The analogue to the humerus was the femur, which was longer and slimmer. The two lower arm bones corresponded to the tibia and fibula of the hind leg, the former being the innermost and the latter the outermost bones. The tarsus is the hind version of the carpus and its bones correspond as well.

Feeding

Early tetrapods had a wide gaping jaw with weak muscles to open and close it. In the jaw were fang-like palatal teeth that, when coupled with the gape, suggests an inertial feeding habit. This is when the amphibian would grasp the prey and, lacking any chewing mechanism, toss the head up and backwards, throwing the prey farther back into the mouth. Such feeding is seen today in the crocodile and alligator.

The tongue of modern adult amphibians is quite fleshy and attached to the front of the lower jaw, so it is reasonable to speculate that it was fastened in a similar fashion in primitive forms, although it was probably not specialized like it is in a frog.

It is taken that early tetrapods were not very active, suggesting that they were not predatory. It is more likely that it fed on fish either in the water or on those that became stranded at the margins of lakes and swamps. Also abundant at the time was a large supply of terrestrial invertebrates, which may have provided a fairly adequate food supply.

Respiration

Modern amphibians breathe by inhaling air into lungs, where oxygen is absorbed. They also breathe through the moist lining of the mouth and skin, known as cutaneous respiration. *Eryops* also inhaled, but its ribs were too closely spaced to suggest that it did this by expanding the rib cage. More likely, it breathed by buccal pumping in which it opened its mouth and nostrils, depressed the hyoid apparatus to expand the oral cavity, closed its mouth and nostrils finally and elevated the floor of the mouth to force air back into the lungs — in other words, it gulped, then swallowed. It probably exhaled by contraction of the elastic tissue in the lung walls. Other special respiratory methods probably existed.

Circulation

Early tetrapods most likely had a three-chambered heart, as do modern amphibians and reptiles, in which oxygenated blood from the lungs and de-oxygenated blood from the respiring tissues enters by separate atria, and is directed via a spiral valve to the appropriate vessel — aorta for oxygenated blood and pulmonary vein for deoxygenated blood. The spiral valve is essential to keeping the mixing of the two types of blood to a minimum, enabling the animal to have higher metabolic rates, and be more active than otherwise.

Locomotion

In typical early tetrapod posture the upper arm and upper leg extended nearly straight horizontal from its body, and the forearm and the lower leg extended downward from the upper segment at a near right angle. The body weight was not centered over the limbs, but was rather transferred 90 degrees outward and down through the lower limbs, which touched the ground. Most of the animal's strength was used to just lift its body off the ground for walking, which was probably slow and difficult. With this sort of posture, it could only make short broad strides. This has been confirmed by fossilized footprints found in Carboniferous rocks.

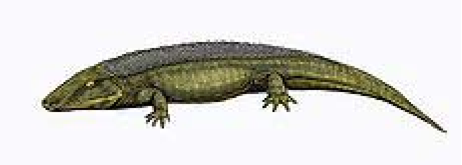
Ligamentous attachments within the limbs were present in *Eryops*, being important because they were the precursor to bony and cartilaginous variations seen in modern terrestrial animals that use their limbs for locomotion.

Of all body parts, the spine was the most affected by the move from water to land. It now had to resist the bending caused by body weight and had to provide mobility where needed. Previously, it could bend along its entire length. Likewise, the paired appendages had not been formerly connected to the spine, but the slowly strengthening limbs now transmitted their support to the axis of the body.

Chapter 2

Reptiliomorpha

Reptiliomorpha
Temporal range: Early Carboniferous–Middle Triassic
Descendant taxon Amniota survives to present



Chroniosuchus, a reptiliomorph

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Amphibia *sensu lato*
Subclass:	Labyrinthodontia
Superorder:	**Reptiliomorpha**

Major Sub-Groups

Order Anthracosauria
Order Chroniosuchia
Order Embolomeri
Order Seymouriamorpha
Order Diadectomorpha
Amniota

Reptiliomorpha refers to an order or subclass reptile-like amphibians, who gave rise to the amniotes in the Carboniferous. Under phylogenetic nomenclature, the Reptiliomorpha includes their amniote descendants though, even in phylogenetic nomenclature, the name is mostly used when referring to the non-amniote reptile-like labyrinthodont grade. An alternative name, **Anthracosauria** is commonly used for the group, but is confusingly also used for the "lower" grade of reptiliomorphs by Benton.

Characteristics

Basal reptiliomorphs were land-based, reptile-like amphibians, in anatomy falling between the mainly aquatic Devonian labyrinthodonts and the first reptiles. University of Bristol paleontologist Professor Michael J. Benton gives the following characteristics for the Reptiliomorpha:

- narrow premaxillae (less than half the skull width)
- vomers taper forward
- phalangeal formulae (number of joints in each toe) of foot 2.3.4.5.4–5

Cranium morphology

The group differ from the contemporary non-reptiliomorph labyrinthodonts by having a deeper, more domed skull, but retained the primitive kinesis (loose attachment) between skull roof and cheek. The skulls of the group are usually found with fine radiating grooves. The back of the skull held a deep otic notch in quadrate bone, likely holding a spiracle rather than a tympanum.

Postcranial skeleton

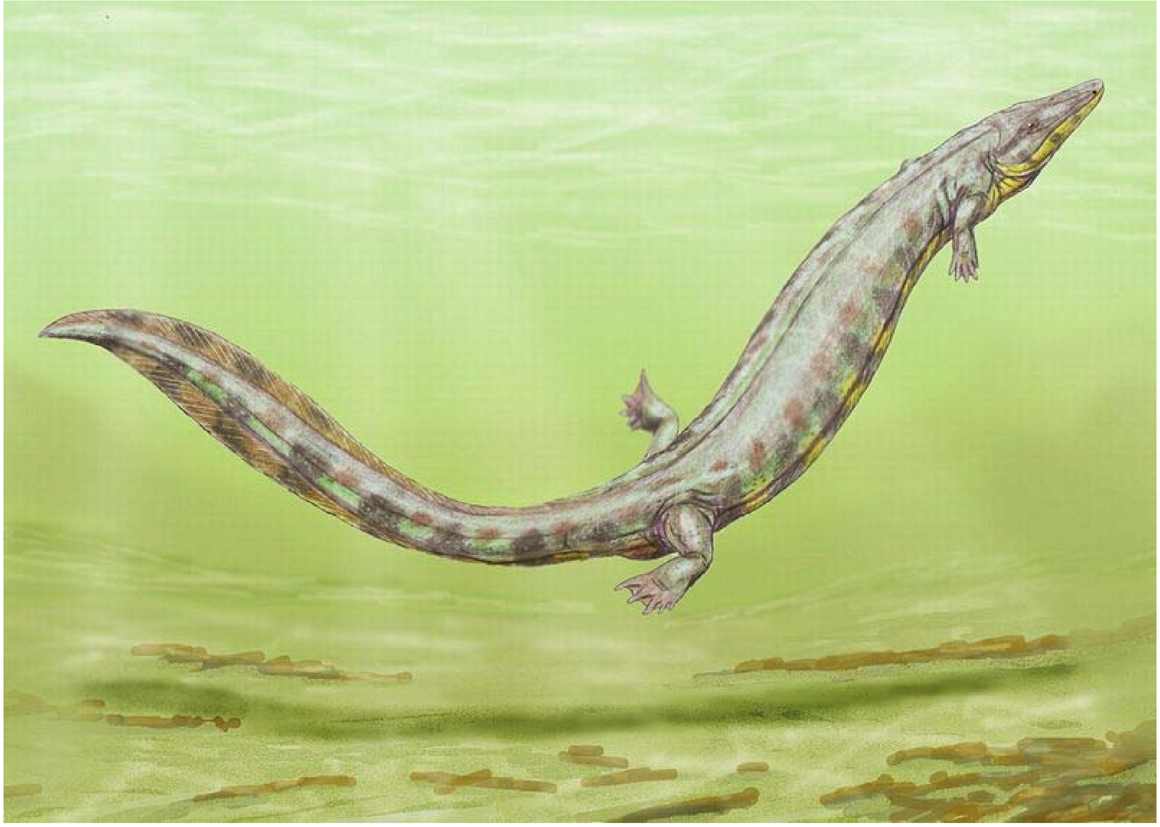
The vertebrae showed the typical multi-element construction as seen in labyrinthodonts, but with pleurocentrum being the dominant element. Unlike most labyrinthonts, the limbs was well-developed and ossified, indicating a predominately terrestrial lifestyle except in secondarily aquatic groups. Each foot held 5 digits, the pattern seen in their amniote descendants. They did however lack the reptilian type of ankle bone that would have allowed the use of the feet as levers for propulsion rather than as holdfasts.

Physiology

The general build was heavy in all forms, though otherwise very similar to that of early reptiles. The skin, at least in the more advanced forms probably had a water-tight epidermal horny overlay, like seen in todays reptiles, though they lacked horny claws. In chroniosuchians and some seymouriamorphans, like *Discosauriscus*, dermal scales are found in post-metamorphic specimens, indicating they may have had a "knobbly" if not scaly appearance.

Their reproduced in amphibian fashion with aquatic eggs that hatched into larvae (tadpoles) with external gills.

Evolutionary history



Archeria, a representant for the aquatic reptiliomorphs

Two *Seymouria* in dry environment.

Diadectes, an advanced reptiliiomorph, variously classified as a reptile or amphibian

During the Carboniferous and Permian periods, tetrapods evolved along a number of parallel lines towards a reptilian condition. Some of these tetrapods (e.g. *Archeria*, *Eogyrinus*) were elongate, eel-like aquatic forms with diminutive limbs, while others (e.g. *Seymouria*, *Solenodonsaurus*, *Diadectes*, *Limnoscelis*) were so reptile-like that until quite recently they actually had been considered true reptiles, and it is likely that to a modern observer they would have appeared as small to medium-sized, heavy-set lizards. Several groups however remained aquatic or semiaquatic. The chroniosuchians show the build and presumably habit similar to modern crocodiles as river-side predators, while the Chroniosuchia was either crocodile like or with elongated newt- or eel-like proportions.

With their terrestrial life style combined with the need to return to the water to lay eggs hatching to larvae (tadpoles) lead to a drive to abandon the larval stage and aquatic eggs. A possible reason may have been competition for breeding ponds, to exploit drier environments with less access to open water, or to avoid predation on tadpoles by fish, a problem still plaguing modern amphibians. Whatever the reason, the drive led to internal fertilization and direct development (completing the tadpole stage within the egg). A striking parallel can be seen in the frog family Leptodactylidae, which has a very diverse reproductive system, including foam nests, non-feeding terrestrial tadpoles and direct development.

True terrestrial life was achieved with the development of the amniote egg, where a number of membranous sacks protect the embryo. The first to evolve was probably the allantois, a sack that develops from the gut/yolk-sack. This sack contains the embryo's nitrogenous waste (urea) during development, stopping it from poisoning the embryo. A very small allantois is found in modern amphibians. Later came the amnion surrounding the fetus proper, and the chorion, encompassing the amnion, allantois, and yolk-sack.

Exactly where the border between reptile-like amphibians (non-amniote reptiliomorphs) and amniotes lies will probably never be known, as the reproductive structures involved fossilize poorly, but various small, advanced reptiliomorphs have been suggested as the first true amniotes, including *Casineria* and *Westlothiana*. Although the first amniote probably appeared as early as the latest Mississippian period (Middle Carboniferous), non-amniote (or amphibian) reptiliomorphs continued to flourish alongside their amniote descendants for many millions of years. By the middle Permian the non-amniote terrestrial forms had died out, but several aquatic non-amniote groups continued to the end of the Permain, and in the case of the Chroniosuchids survived the end Permian mass extinction, only to die out at the end of the Early Triassic. Meanwhile, the single most successful daughter-clade of the reptiliomorphs, the amniotes, continued to flourish and to inherit the Earth.

Changing Definitions

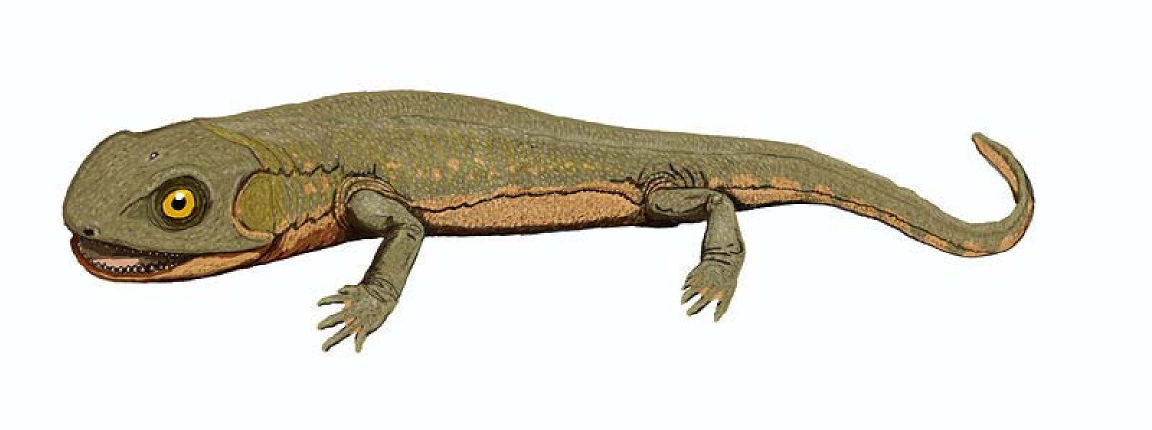
The name Reptiliomorpha was coined by Professor Gunnar Säve-Söderbergh in 1934 to designate various types of late Paleozoic reptile-like labyrinthodont "amphibians." However Alfred Sherwood Romer used the name Anthracosauria instead. In 1970, the German paleontologist Panchen reverted to Säve-Söderberghs definition, but Romer's terminology is still in use, e.g. Carroll 1988 and 2002, and Hildebrand & Goslow 2001.

In 1956 Friedrich von Huene included both amphibians and anapsid reptiles in the Reptiliomorpha. This included the following orders: 1. Anthracosauria, 2. Seymouriamorpha, 3. Microsauria, 4. Diadectomorpha, 5. Procolophonia, 6. Pareiasauria, 7. Captorhinidia, 8. Testudinata.

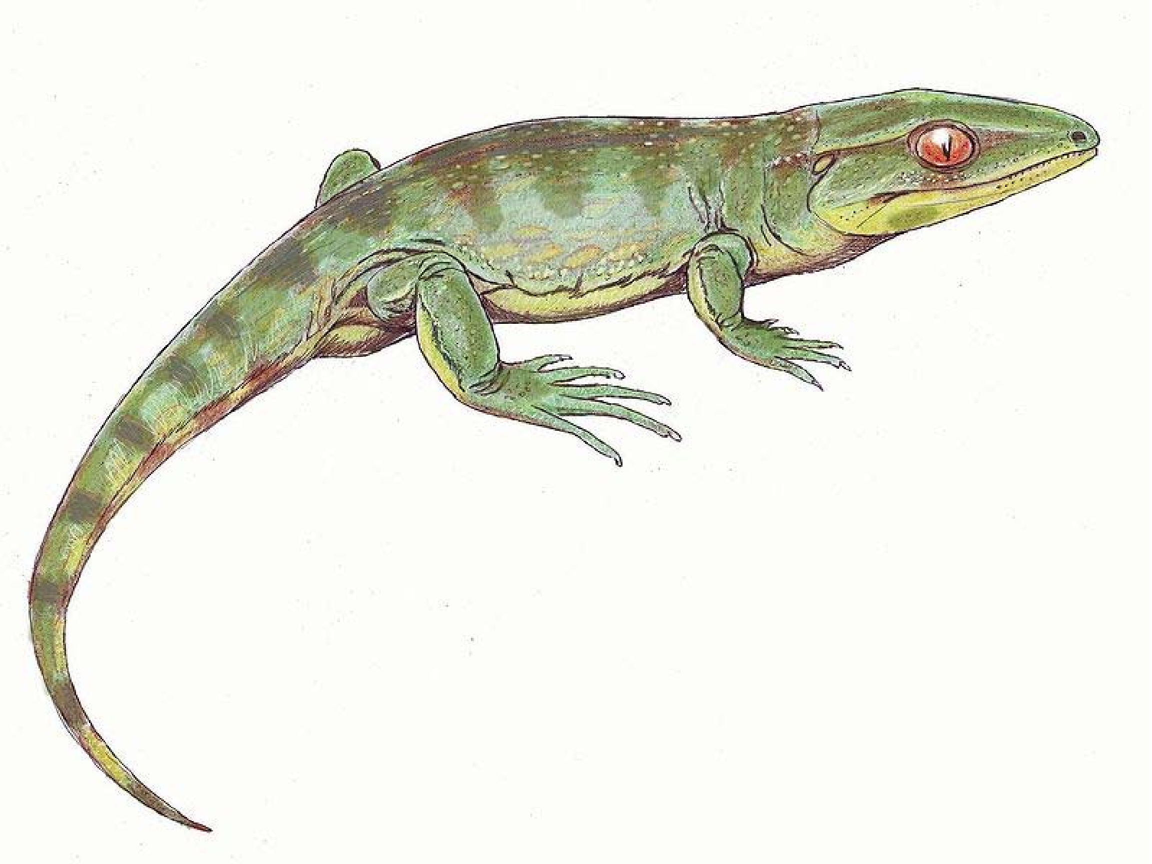
In 1997 Michel Laurin and Robert Reisz (1997) adapted the term in a cladistic sense. Michael Benton (2000, 2004) made it the sister-clade to Batrachomorpha. However, when considered a linnean ranking, Reptiliomorpha is given the rank of superorder and only includes reptile-like tetrapods. More recently Reptiliomorpha has been adopted as the term for the largest clade that includes – according to the technical definitions of the phylocode which only refers to species or genus level organisms – *Homo sapiens* but not *Ascaphus truei* (a primitive frog) (International Phylogenetic Nomenclature Meeting 2003); or is, as Toby White (Palaeos website) puts it, more like dogs than frogs (i.e. mammals but not amphibians). However, given the lack of consensus of the phylogeny of the labyrinthodonts in general, the actual content of the Reptiliomorpha under the latter definition is uncertain.

Taxonomy

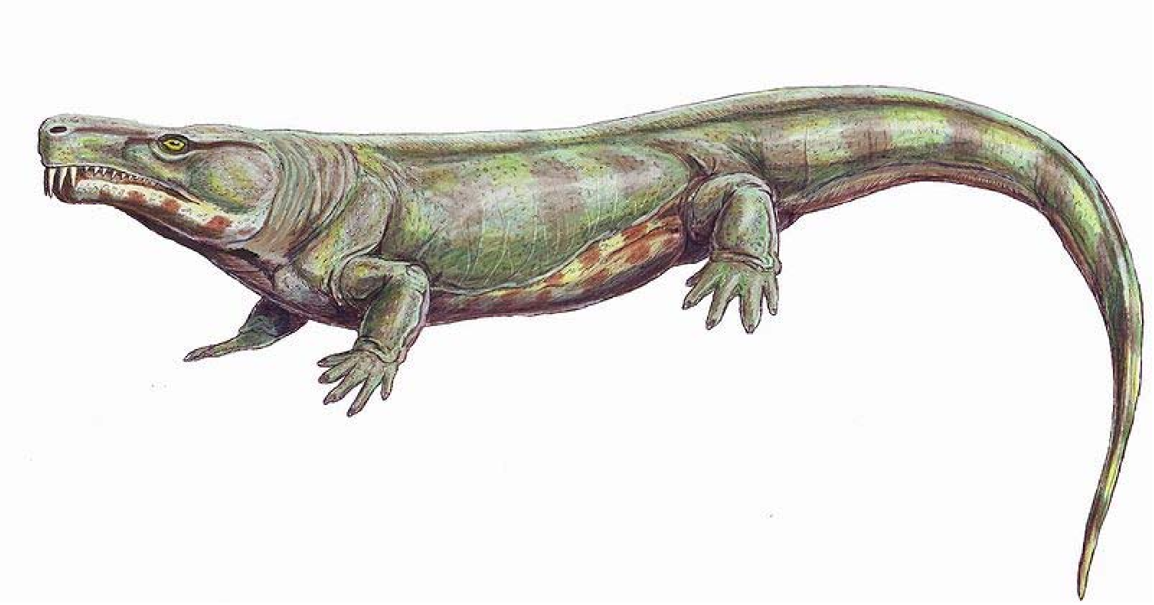
Classification after Benton (1997):



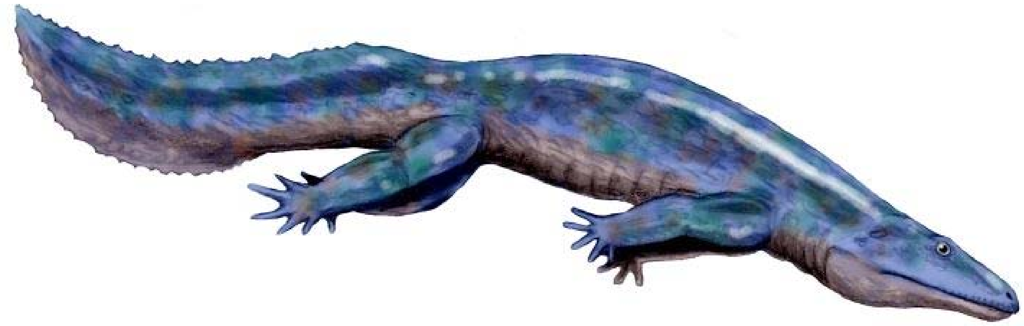
Discosauriscus.



Gefyrostegus.



Limnoscelis.



Diplovertebron.

- **Superclass Tetrapoda**
  - **Superorder Reptiliomorpha**
    - Family Caerorhachidae
    - Family Tokosauridae
    - **Order Chroniosuchia**
      - Family Bystrowianidae
      - Family Chroniosuchidae
    - **Order Embolomeri**
      - Family Eoherpetontidae
      - Family Anthracosauridae
      - Family Proterogyrinidae
      - Family Eogyrinidae

  - Family Archeriidae
- **Order Seymouriamorpha**
  - Family Kotlassiidae
  - Family Discosauriscidae
  - Family Seymouriidae
- (unranked) **Captorhinidae/Cotylosauria**
  - **Order Diadectomorpha**
    - Family Limnoscelidae
    - Family Diadectidae
  - **Series Amniota**

Chapter 3

Ventastega and Hynerpeton

Ventastega

Ventastega **Temporal range: 365 Ma** **Famennian (Late Devonian)**	

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Sarcopterygii
Genus:	***Ventastega***

Species

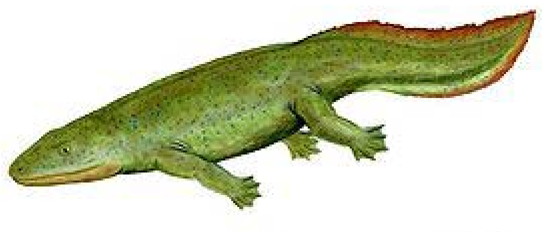
- *Ventastega curonica*

Ventastega was a basal tetrapod that lived during the Famennian subdivision of the Late Devonian period approximately 374.5 to 359.2 million years ago, though Ventastega origins as a tetrapod lineage are probably seated in the preceding Frasnian period of the Late Devonian (385.3 to 374.5 million years ago) when a surge of morphological diversification of tetrapods began. Ventastega is one of the earliest Devonian tetrapods yet discovered. Given two preferred orientations of the bones and the geological context in which Ventastega was found suggests a tidal-sea influence. However, like *Tiktaalik*, *Ventastega* was probably more aquatic than terrestrial.

Per Ahlberg, a professor of evolutionary biology at Uppsala University in Sweden reported in *Nature* that limbs, not fins were attached to *Ventastega*; this inference is based on the anatomy of key parts of its pelvis and its shoulders. The fossils reported were found in Latvia. They are 365 million years old. A skull, shoulders, and part of the pelvis of the *Ventastega curonica* were found. They indicate it was more tetrapod than fish and looked similar to a small alligator. The discovery contributes to the understanding of the evolutionary transition from fish to tetrapods, the animals with four limbs, whose descendents include amphibians, reptiles, dinosaurs and birds, and mammals).

Hynerpeton

Hynerpeton
Temporal range: 360 Ma
Late Devonian



Hynerpeton reconstruction

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Ichthyostegalia
Family:	Ichthyostegidae
Genus:	†***Hynerpeton***

Binomial name

Hynerpeton bassetti
Daeschler *et al.*, 1994

Hynerpeton was a basal carnivorous tetrapod that lived in the lakes and estuaries of the Late Devonian period around 360 million years ago. Like many primitive tetrapods, it is sometimes referred to as an "amphibian", though it is not a true member of the modern Lissamphibia. The Late Devonian saw the evolution of plants into trees and growing into vast forests pumping oxygen into the air, possibly giving *Hynerpeton* an edge because it evolved complex lungs to exploit it. Its lungs probably consisted of sacs like modern terrestrial vertebrates. In 1993, the paleontologists Ted Daeschler and Neil Shubin found the first *Hynerpeton* fossil, a shoulder bone, near Hyner, Pennsylvania. They were surveying the Devonian rocks of Pennsylvania in search of fossil evidence for the origin of animal limbs. The animal had a very robust shoulder, which indicated that it had powerful appendages. Only a few bones have been found from *Hynerpeton*, in Red Hill, Pennsylvania, U.S.A.. The known fossils include two shoulder girdles, two lower jaws, a jugal bone and some gastralia.

The structure of the shoulder girdle indicates this animal may have been one of the earlier, more primitive tetrapods to evolve during the Devonian. Information on the relationship of the known fossils of *Hynerpeton* to other Devonian tetrapods can be found in *Gaining Ground The Origin and Evolution of Tetrapods* by Jennifer A. Clack.

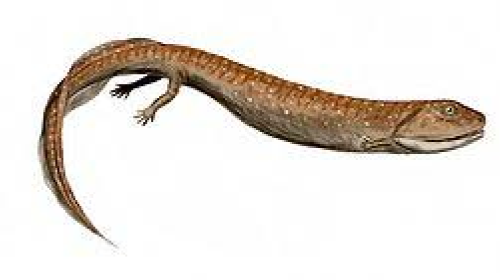
It is thought that that these early amphibians are descended from lobe-finned fish, such as *Hyneria*, whose stout fins evolved into legs and their swim bladder into lungs. It is still not known whether *Hynerpeton* is the direct ancestor to all later backboned land animals (including humans), but the fact that it had eight fingers, not five, suggests that it is simply our evolutionary cousin.

Chapter 4

Crassigyrinus and Baphetidae

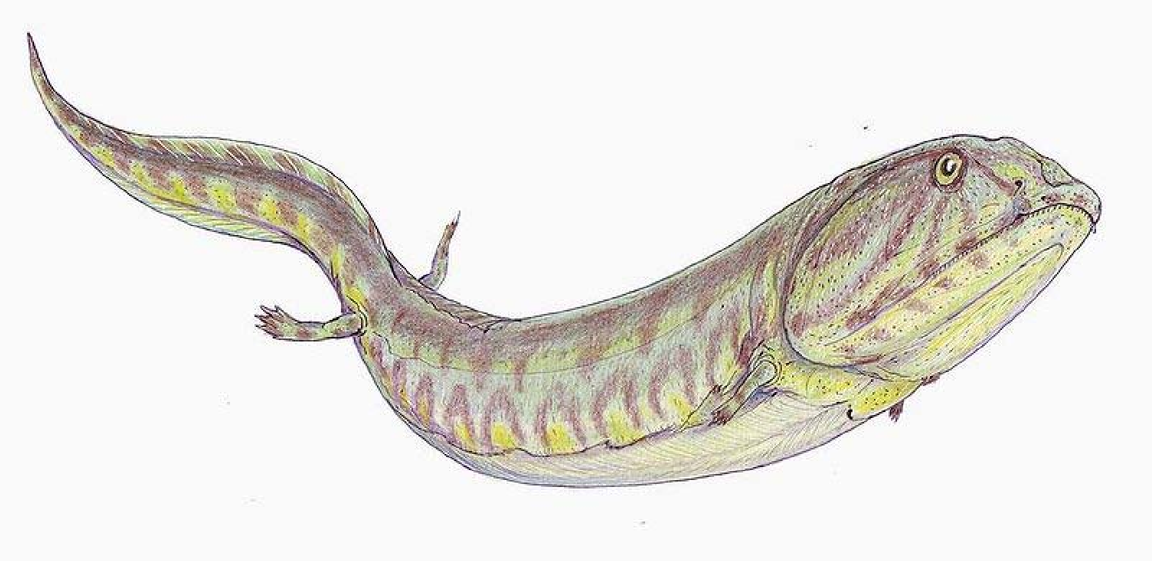
Crassigyrinus

Crassigyrinus **Temporal range: Early Carboniferous**	



restoration of *Crassigyrinus scoticus*

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Order:	Ichthyostegalia
Genus:	†***Crassigyrinus***
Species:	***C. scoticus***



Crassigyrinus

Crassigyrinus (meaning "thick tadpole") is an extinct genus of carnivorous Labyrinthodont amphibian from the Early Carboniferous of Scotland and a possible specimen from Greer, West Virginia. The type specimen was originally described as *Macromerium scoticum* and lacked a complete skull. With subsequent discoveries, *Crassigyrinus* is now known from three skulls, one of which is in articulation with a fairly complete skeleton, and a couple of incomplete lower jaws. *Crassigyrinus* grew up to 1.5 meters in length, coupled with tiny limbs and unusually large jaws. *Crassigyrinus* is taxonomically enigmatic, having confused paleontologists for decades with its apparent fish-like and tetrapod features. Some paleontologists have even considered it as the most basal Crown group tetrapod, while others hesitate to even place it within the Tetrapoda superclass. *Crassigyrinus* had unusually large jaws, enabling it to eat other animals it could catch and swallow. It had two rows of sharp teeth in its jaws, the second row having a pair of fangs. *Crassigyrinus* had large eyes, suggesting that it was either nocturnal, or lived in very murky water.

Description

Crassigyrinus had a streamlined body up to 1.5 meters in length. Its limbs were tiny and virtually useless, implying that the animal was almost completely aquatic. *Crassigyrinus* had unusually large jaws, equipped with two rows of sharp teeth, the second row having a pair of palatal fangs. Studies have shown that *Crassigyrinus* may have been able to open its mouth as wide as 60 degrees, which further suggest that it was a powerful predator with a strong bite. This strongly suggests that it was ideally suited for catching fish, and the animal was probably a fast-moving predator. Several thickened bony ridges ran along the dorsal midline of the snout and between the eyes, and several paleontologists have suggested that they helped the skull to withstand stress when the animal bit prey. *Crassigyrinus* had large eyes, suggesting that it was either nocturnal, or lived in very murky water. It possessed large otic (spiracular) notches, probably accommodating a spiracle rather than a tympanic membrane.

Its peculiar stunted forelimbs were tiny and the humerus was only 35 mm long (the whole animal was about 1.5 m long). Various foramina on the humeral surfaces are very similar to those seen in *Ichthyostega*, *Acanthostega*, and lobe-finned fishes like *Eusthenopteron*. The hindlimbs were much larger than the forelimbs, and in the pelvis the ilium lacked a bony connection to the vertebral column (a classic feature of aquatic tetrapods). The tail is unknown but is assumed to have been long and laterally compressed.

Baphetidae

Baphetids
Temporal range: 326–307 Ma
Early to Late Carboniferous

Life restoration of *Loxomma*

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Superfamily:	†Baphetoidea
Family:	†**Baphetidae** Cope, 1865

Subfamilies

- †Baphetinae
- †Loxommatinae

Synonyms

- Loxommatidae

Baphetidae is an extinct family of early tetrapods. Baphetids were large labyrinthodont predators of the Late Carboniferous period (Namurian through Westphalian) of Europe. Fragmentary remains from the Early Carboniferous of Canada have been tentatively assigned to the group. The phylogenetic relationships of baphetids is uncertain; while many studies have placed the group as a close relative of Amniota, other analyses have found Baphetidae to be a more basal clade of early stem tetrapods. Baphetids were among the first of the Carboniferous fossil tetrapods to be found and were originally described in 1850 by William Dawson. The baphetids have been referred to the family **Loxommatidae**, but this group was later shown to be a junior synonym of Baphetidae, which was named earlier in 1865. Baphetids are known mainly from skulls; very little skeletal material has been found.

Palaeobiology

The presence of lateral lines and the long rows of needle-like teeth show that most were fish-eaters. Their development were likely amphibian, though no larval fossils are known. Their best-known characteristic was a curious, keyhole-shaped orbit formed by excavation of the lacrimal and prefrontal bones in front of the eye. It has been suggested that this space accommodated a salt gland or some kind of electrosensory organ. Perhaps the better hypothesis is that the space allowed room for the contraction of an enlarged pterygoideus muscle. In that case, this skull modification would represent an early form of skull fenestration for jaw muscles.

The skull is shallow. Unlike the better-known embolomeres, the baphetid cheek and skull roof are sutured together. There is a strongly embayed spiracular ("otic") notch, but the stapes is distally broad, which seems to rule out a sensitive hearing apparatus. The palate is closed -- a primitive character, but very different from the temnospondyls. The coronoids bear no teeth or denticles, while the dentary has a double tooth row.

Since the taxon is based almost exclusively on skulls, the body is very poorly known. It is often said that the body was crocodile-like, but this appears to be largely supposition.

Megalocephalus

It is not clear whether all of the genera assigned to this group are really closely related. The traditional four genera of baphetids (*Loxomma*, *Baphetes*, *Megalocephalus*, and *Spathicephalus*) have recently been supplemented by *Eucritta*, a somewhat different form. It has also been suggested that *Crassigyrinus* may be closely related.

Taxonomy

Baphetids were first described by Edward Drinker Cope when he erected the family Baphetidae in 1865 for *Baphetes*. Richard Lydekker named Loxomatinae in 1889 for *Loxomma*, which later became known as Loxommatidae. D. M. S. Watson described the group as Loxommidae in 1917. Later studies have shown *Baphetes* and *Loxomma* to be close relatives within the same family, and because Baphetidae was named before Loxommatidae, it has seniority and is the valid name of the group.

Phylogeny

Baphetids have been previously considered primitive temnospondyls and more recently batrachosaurs (reptile-like amphibia). It is likely, however, that they represent one more of a number of early Carboniferous tetrapodomorph radiations. Computer-assisted phylogenetic analyses of a data matrix using characteristics of most of the major groups of terrestrial vertebrates place the Baphetids close to the ancestry of amniotes.

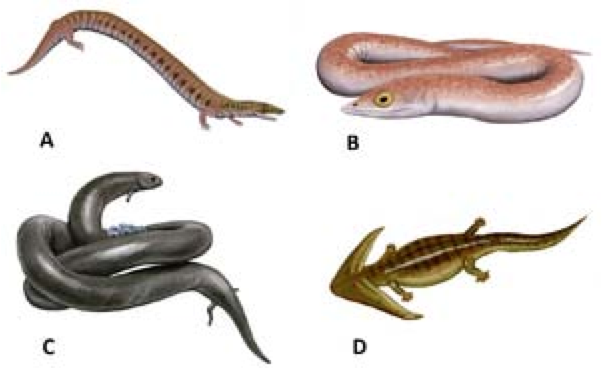
With the reinterpretation of *Ichthyostega* and its relatives as aquatic forms, baphetids are good candidates for the spot of first tetrapodomorph group to actually spend substantial time on land. If so, baphetids may be a rather important taxon.

Chapter 5

Lepospondyli and Lissamphibia

Lepospondyli

Lepospondyls
Temporal range: Carboniferous - Permian



Lepospondyli diversity. (*Rhynchonkos* (A), *Phlegethontia* (B), *Lysorophus* (C) & *Diplocaulus* (D))

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Amphibia
Subclass:	**Lepospondyli** Zittel, 1888

Lepospondyli are a group of small but diverse Carboniferous to early Permian tetrapods. Six different groups are known, the Acherontiscidae, Adelospondyli, Aïstopoda, Lysorophia, Microsauria and Nectridea, and between them they include newt-like, eel- or snake-like, and lizard-like forms, along with species that don't fit any current category. Various species were aquatic, semi-aquatic, or terrestrial. None were large (the biggest genus, the keraterpetontid *Diplocaulus*, reached a meter in length, but most were much smaller), and it can be assumed that they lived in specialised ecological niches not taken by their more numerous Temnospondyl contemporaries.

Classification

All lepospondyls are characterised by having simple, spool-shaped vertebra, which were not preformed as cartilage, but rather grew as bony cylinders around the notochord. In addition, the upper portion of the vertebra, the neural arch, is usually fused to the centra (the main body of the vertebra) (Colbert 1969).

No clear common ancestors are known, since each of the known clades are already highly specialised when they first appear in the fossil record. It is not known whether the lepospondyls are an artificial (polyphyletic) group which independently evolved similar characteristics of the vertebra, or whether they descended from a single common ancestor.

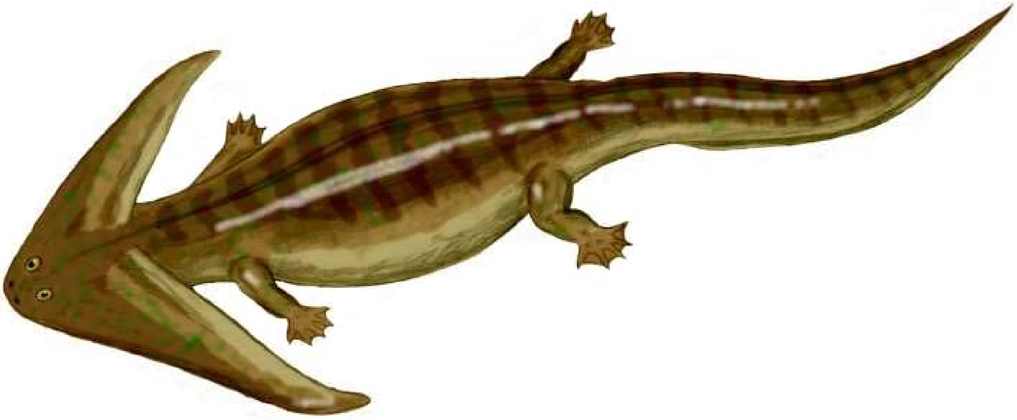
At one time it was thought that some lepospondyls are related or perhaps ancestral to modern Urodela, but not the other modern amphibians, although this view is no longer held. For a long time they were considered one of the three subclasses of amphibians (Romer 1966, Colbert 1969, Carroll 1988). More recently, it has been suggested that the lepospondyls may be related or ancestral to modern amphibians as well as to amniotes (reptiles etc) (Laurin 1996), that they are an artificial grouping with some members related to both extinct and living amphibians (Batrachomorpha) but not amniotes (Benton 2000), or alternatively are a monophyletic group closely related to the ancestry of amniotes but not to recent amphibians (Benton 2004).

Apart from the Nectridea, lepospondyls are limited in distribution to Europe and North America (Carroll 1988).

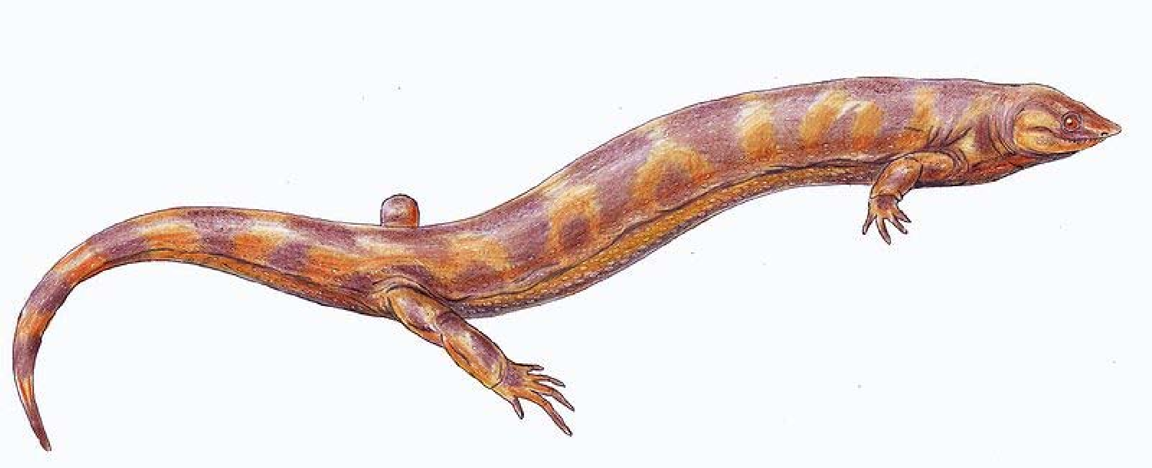
Taxonomy

Adelospondylus, an adelospondyl.

Ophiderpeton, an aïstopod.



Diplocaulus, a nectridean.



Pelodosotis, a microsaur.

Class Amphibia

- **Subclass LEPOSPONDYLI**
  - **Order Adelospondyli**
  - Family Acherontiscidae
  - **Order Aïstopoda**
    - Family Lethiscidae
    - Family Ophiderpetontidae
    - Family Oestocephalidae
    - Family Pseudophlegethontiidae
    - Family Phlegethontiidae
  - **Order Nectridea**
    - *Arizonerpeton*

    - Family Scincosauridae
    - Family Keraterpetontidae
    - Family Urocordylidae
  - **Superorder Microsauria**
    - Family Odonterpentontidae
    - **Tuditanomorpha**
      - Family Pantylidae
      - Family Tuditanidae
      - Family Hapsidopareiontidae
      - Family Gymnarthridae
      - Family Ostodolepidae
      - Family Trihecatontidae
      - Family Goniorhynchidae
    - Family Brachystelechidae
    - **Order Lysorophia**
      - Family Lysorophidae

Lissamphibia

Lissamphibia
Temporal range: Early Triassic–present

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Amphibia
Subclass:	**Lissamphibia** Haeckel, 1866

Orders

Anura
Caudata
Gymnophiona
†Allocaudata

The subclass **Lissamphibia** includes all recent amphibians and means *smooth amphibia*.

Extant amphibians fall into one of three orders — the Anura (frogs and toads), the Caudata or Urodela (salamanders and newts), and the Gymnophiona or Apoda (the limbless caecilians).

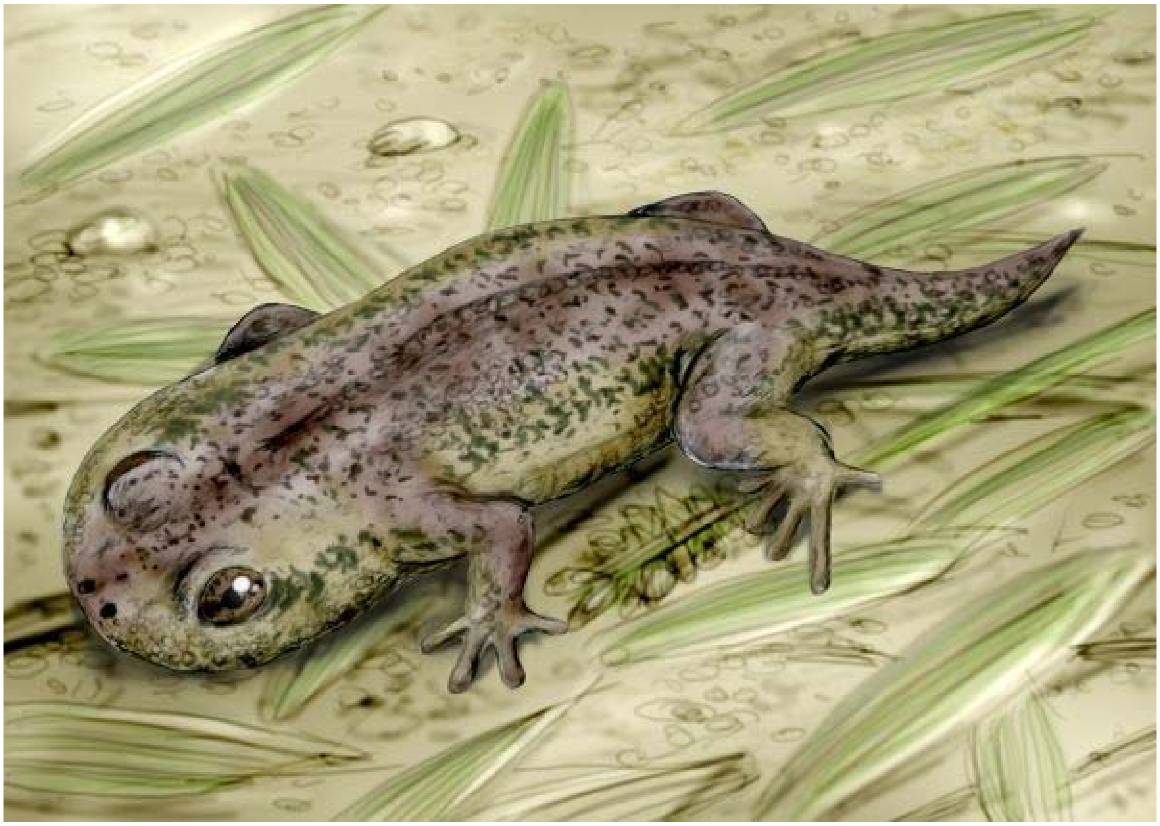
Although the ancestry of each group is still unclear, all share certain common characteristics, which indicates they evolved from a common ancestor and so form a clade. The publication of a Permian-period stem form *Gerobatrachus hottoni* showed the frogs and salamanders had a common ancestor more recently (ca 290 Ma) than had been thought by using the molecular clock alone.

Characteristics

The following characteristics are shared by some, most, or all Lissamphibia. Some of these apply to the soft body parts and hence not present in fossils. However, those which refer to the skeleton are also known from several types of Palaeozoic amphibians:

- Double or paired occipital condyle
- Two types of skin glands (mucous & granular)
- Fat bodies associated with gonads
- Double-channeled sensory papillae in the inner ear
- Green rods (a special type of visual cell, unknown in caecilians)
- Ribs do not encircle body
- Ability to elevate the eye (with levetator bulbi muscle)
- Forced pump respiratory mechanism
- Cylindrical centra (the main body of the vertebra; cylindrical centra are also found in several groups of early tetrapods)
- Pedicellate teeth (the crown of the teeth is separated from the root by a zone of fibrous tissue; also found in some Dissorophoidea; the teeth of some fossil salamanders are not pedicellate)
- Bicuspid teeth (two cusps per tooth, also found in juvenile dissorophoids)
- Operculum (small bone in the skull, linked to shoulder girdle by the opercularis muscle; perhaps involved in hearing and balance; absent in caecilians and some salamanders, fused to the stapes (ear bones) in most anurans)
- Loss of posterior skull bones (also in Microsauria and Dissorophoidea)
- Small, widely separated pterygoids (also found in Temnospondyli and Nectridea)
- Wide cultriform process of the parasphenoid (also found in some Microsauria (*Rhynchonchos*) and Lysorophia)

Relationships and definition



Reconstruction of *Gerobatrachus*, possible ancestor of salamanders and frogs

The features unition the Lissamphibia was first noted by Ernst Haeckel. In the early to mid 20th cetury, a bipyletic origin of amphibians (and thus of tetrapods in general) was favoured. In the late 20th century, a flood of new fossil evidence mapped out in some detail the nature of the transition between the elpistostegalid fish and the early amphibians, most paleontologists no longer accept the diphyletic view. Whilst the monophyly of the Lissamphibia is accepted by most herpetologists and paleontologists, the origin and relationships of the various Lissamphibian groups both with each other and among other early tetrapods remains controversial. Not all paleontologists are convinced that the lissamphibia are indeed a natural group, as the various characteristics are also shared with some Palaeozoic amphibians, and it is still possible that these characteristics evolved independently.

Currently there are three prevailing theories of Lissamphibian origin:

- Monophyletic within the temnospondyli
- Monophyletic within lepospondyli
- Diphyletic (two separate ancestries) with apodans within the lepospondyls and salamanders and frogs within the temnospondyli.

Chapter 6

Amniote

Amniotes
Temporal range: Mississippian–Recent, 340–0 Ma

A baby tortoise emerges from an amniotic egg

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
(unranked):	Reptiliomorpha
(unranked):	**Amniota** Haeckel, 1866

Clades

- Synapsida
- Sauropsida

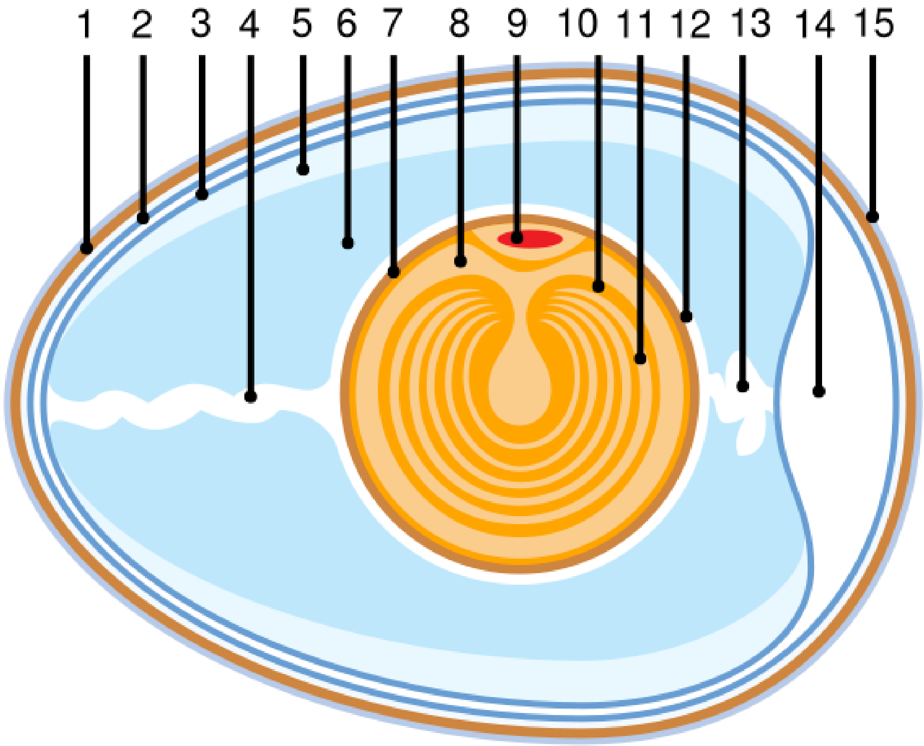
The **amniotes** are a group of tetrapod vertebrates (four-limbed animals with backbones or spinal columns) that have a terrestrially adapted egg. They include mammals (synapsids) and sauropsids (reptiles and birds), as well as their fossil ancestors. Amniote embryos, whether laid as eggs or carried by the female, are protected and aided by several extensive membranes. In eutherian mammals (such as humans), these membranes include the amniotic sac that surrounds the fetus. These embryonic membranes, and the lack of a larval stage, distinguish amniotes from tetrapod amphibians.

The first amniotes (referred to as "basal amniotes" or "stem amniotes"), such as *Casineria*, resembled small lizards and had evolved within reptiliomorphs which were amphibian about 340 million years ago, in the Carboniferous geologic period. Their eggs could survive out of the water, allowing amniotes to branch out into drier environments. The eggs could also "breathe" and cope with waste, allowing the eggs and the amniotes themselves to evolve into larger forms. The amniotes spread across the globe and became the dominant land vertebrates.

Very early in the evolutionary history of amniotes, basal amniotes evolved into two main lines of amniotes, the **synapsids** and the **sauropsids**, both of which persist into the modern era. The oldest known fossil synapsid is Protoclepsydrops from about 320 million years ago, while the oldest known sauropsid is probably *Paleothyris*, in the order Captorhinida, from the Middle Pennsylvanian epoch (ca. 306-312 million years ago).

Description

Amniotes can be characterized in part by embryonic development that includes the formation of several extensive membranes, the amnion, chorion, and allantois. Amniotes develop directly into a (typically) terrestrial form with limbs and a thick stratified epithelium, rather than first entering a feeding larval tadpole stage followed by metamorphosis as in amphibians. In amniotes the transition from a two-layered periderm to cornified epithelium is triggered by thyroid hormone during embryonic development, rather than metamorphosis. The unique embryonic features of amniotes may reflect specializations of eggs to survive drier environments, or the massive size and yolk content of eggs evolved for direct development to a larger size.



Anatomy of an amniotic egg
1. Eggshell
2. Outer membrane
3. Inner membrane
4. Chalaza
5. Exterior albumen (outer thin albumen)
6. Middle albumen (inner thick albumen)
7. Vitelline membrane
8. Nucleus of Pander
9. Germinal disk (blastoderm)
10. Yellow yolk
11. White yolk
12. Internal albumen
13. Chalaza
14. Air cell
15. Cuticula

Features of amniotes evolved for survival on land include a sturdy but porous leathery or hard eggshell and an allantois evolved to facilitate respiration while providing a reservoir for disposal of wastes. Their kidneys and large intestines are also well-suited to water retention. Most mammals do not lay eggs, but corresponding structures may be found inside the placenta.

The first amniotes, such as *Casineria kiddi*, which lived about 340 million years ago, evolved from amphibian reptiliomorphs and resembled small lizards. Their eggs were small and covered with a membrane, not a hard shell like most modern amniote eggs. Although some modern amphibians lay eggs on land, with or without significant protection, they all lack advanced traits like an amnion. This kind of egg only became possible with internal fertilization. The outer membrane, a soft shell, evolved as a protection against the harsher environments on land, as species evolved to lay their eggs on land where they were safer than in the water. One can assume the ancestors of the amniotes laid their eggs in moist places, as such modest-sized animals would not have difficulty finding depressions under fallen logs or other suitable places in the ancient forests, and dry conditions were probably not the main reason why the soft shell emerged.

In fish and amphibians there is only one inner membrane, also called an embryonic membrane. In amniotes the inner anatomy of the egg has evolved further and new structures have developed to take care of the gas exchanges between the embryo and the atmosphere, as well as dealing with the waste problems. To grow a thicker and tougher shell required new ways to supply the embryo with oxygen, as diffusion alone was not enough. After the egg developed these structures, further sophistication allowed amniotes to lay much bigger eggs in much drier habitats. Bigger eggs allowed for bigger offspring, and bigger adults could produce bigger eggs, so amniotes grew bigger than their ancestors. Real growth was not possible, however, until they stopped relying on small invertebrates as their main food source and started to eat plants or other vertebrates, or returned to the water. New habits and heavier bodies meant further evolution for the amniotes, both in behavior and anatomy.

There are three main lines of amniotes, which may be distinguished by the structure of the skull and in particular the number of temporal fenestrae (openings) behind the eye. In anapsids (turtles) there are none, in synapsids (mammals and their extinct relatives) there is one, and in most diapsids (non-anapsid reptiles, including dinosaurs and birds) there are two.

The skeletal remains of amniotes can be identified from their Labyrinthodont ancestors by their having at least two pairs of sacral ribs, a sternum in the pectoral girdle (some amniotes have lost it) and an astragalus bone in the ankle.

Definition and classification

Amniota was first formally described by embryologist Ernst Haeckel in 1866 on the presence of the amnion, hence the name. A problem with this definition is that the trait (apomorphy) in question does not fossilize, and the status of fossil forms has to be inferred from other traits. Thus Jacques Gauthier and colleagues forwarded a definition of Amniota in 1988 as "the most recent common ancestor of extant mammals and reptiles, and all its descendants". Gauthiers definition being a node-based crown group, his definition of the group has a slightly different content than the group defined as biological amniotes (apomorphy-based clade).

Traditional classification

Classifications of the amniotes have traditionally recognised three classes based on major traits and physiology:

- **Class Reptilia** (reptiles)
    - Subclass Anapsida ("proto-reptiles", possibly including turtles)
    - Subclass Diapsida (majority of reptiles, progenitors of birds)
    - Subclass Synapsida (mammal-like reptiles, progenitors of mammals)
- **Class Aves** (birds)
    - Subclass Neornithes (all modern birds, several extinct subclasses recognised)
- **Class Mammalia (mammals)**
    - Subclass Monotremata (egg-laying mammals)
    - Subclass Theria (marsupials and placental mammals)

This rather orderly scheme is the one most commonly found in popular and basic scientific works. It has come under critique from cladistics, as the class Reptilia is paraphyletic, that is, it has given rise to two other classes not included in Reptilia.

Phylogenetic classification

With the advent of cladistics, some researchers have attempted to establish new classes, based on phylogeny, but disregarding the physiological and anatomical unity of the groups. One such classification, by Michael Benton, is presented in simplified form below.

- **Clade Amniota** ("reptiles")
    - **Class Synapsida** - includes mammal-like reptiles
        - *Order Pelycosauria †
        - Order Therapsida
            - **Class Mammalia** - Mammals
    - **Class Sauropsida**
        - Subclass Anapsida
            - Order Testudines - Turtles
        - Subclass Diapsida
            - Order Araeoscelidia †
            - Order Younginiformes †
            - Infraclass Ichthyosauria †
            - Infraclass Lepidosauromorpha
                - Superorder Sauropterygia †
                    - Order Placodontia †
                    - Order Nothosauroidea †

- Order Plesiosauria †

- Superorder Lepidosauria
    - Order Sphenodontida - Tuatara
    - Order Squamata - Lizards & snakes

- Infraclass Archosauromorpha
    - Order Prolacertiformes †
    - Division Archosauria
        - Subdivision Crurotarsi
            - Order Crocodylia - Crocodilians
        - Subdivision Avemetatarsalia
            - Order Pterosauria †
            - Superorder Dinosauria
                - Order Ornithischia †
                - Order Saurischia
                    - **Class Aves** - Birds

Chapter 7

Synapsid

Synapsids

Temporal range: 320-100Ma. Descendant taxon Mammalia survives to present.

Dimetrodon grandis skeleton at the National Museum of Natural History of U.S.A.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
(unranked):	Reptiliomorpha
(unranked):	Amniota
Class:	**Synapsida** Osborn, 1903

Orders & Suborders

- Order **Pelycosauria** *
    - Suborder †**Caseasauria**
    - Suborder **Eupelycosauria** *
- Order **Therapsida** *
    - Suborder †**Biarmosuchia**
    - (unranked) **Eutherapsida**
        - Suborder †**Dinocephalia**

    - (unranked) **Neotherapsida**
        - Suborder †**Anomodontia**
    - (unranked) **Theriodontia**
        - Suborder †**Gorgonopsia**
    - (unranked) **Eutheriodontia**
    - Suborder **Cynodontia** *
    - Suborder †**Therocephalia**

Synonyms

- Theropsida

Synapsids ('fused arch') are a group of animals that includes mammals and everything more closely related to mammals than to other living amniotes. They are easily separated from other amniotes by having an opening low in the skull roof behind each eye, leaving a bony arch beneath each, accounting for their name. Primitive synapsids are usually called pelycosaurs; more advanced mammal-like ones, therapsids. The non-mammalian members are described as **mammal-like reptiles** in classical systematics, but are referred to as "**stem-mammals**" or "**proto-mammals**" under cladistic terminology. Synapsids evolved from basal amniotes and are one of the two major groups of the later amniotes, the other major group being the sauropsids (reptiles and birds). They are distinguished from other amniotes by having a single opening (temporal fenestra) in their skull behind each eye, which developed in the ancestral synapsid about 324 million years ago (mya) during the late Carboniferous Period.

Synapsids were the dominant terrestrial animals in the middle to late Permian period. As with almost all groups then extant, their numbers and variety were severely reduced by the Permian extinction. Some species survived into the Triassic period, but archosaurs quickly became the dominant animals and few of the non-mammalian synapsids outlasted the Triassic, although survivors persisted into the Cretaceous. However, as a phylogenetic unit they included the mammal descendants, and in this sense synapsids are still very much a living group of vertebrates. In the form of mammals, Synapsids (most recently and notably humans) again became the dominant land animals after they outcompeted birds following the K-T extinction event.

Linnaean and cladistic classifications

Synapsids as a reptilian subclass

Synapsids were originally defined at the turn of the 20th century, as one of the four main subclasses of reptiles, on the basis of their distinctive temporal openings. These openings in the cheek bones allowed attachment of larger jaw muscles, hence a more efficient bite. Synapsids were considered to be the reptilian lineage that led to mammals via gradually evolved, increasingly mammalian features, hence the name "mammal-like reptiles" which became a broad, traditional description for all non-mammalian synapsids.

The "mammal-like reptiles"

The traditional classification of synapsids as reptiles is continued by a number of palaeontologists (e.g. Carroll 1988, Colbert & Morales 2001) and in general biology. In the 1990s this approach was complemented by a cladistic one, according to which the only valid groups are those that include common ancestors and all of their descendants: these are known as monophyletic groups, or clades. Because mammals are directly descended from the synapsids, mammals are included under Synapsida as a clade, though in formal classification mammals are treated as a separate class that has evolved from the (paraphyletically-defined) Synapsida.

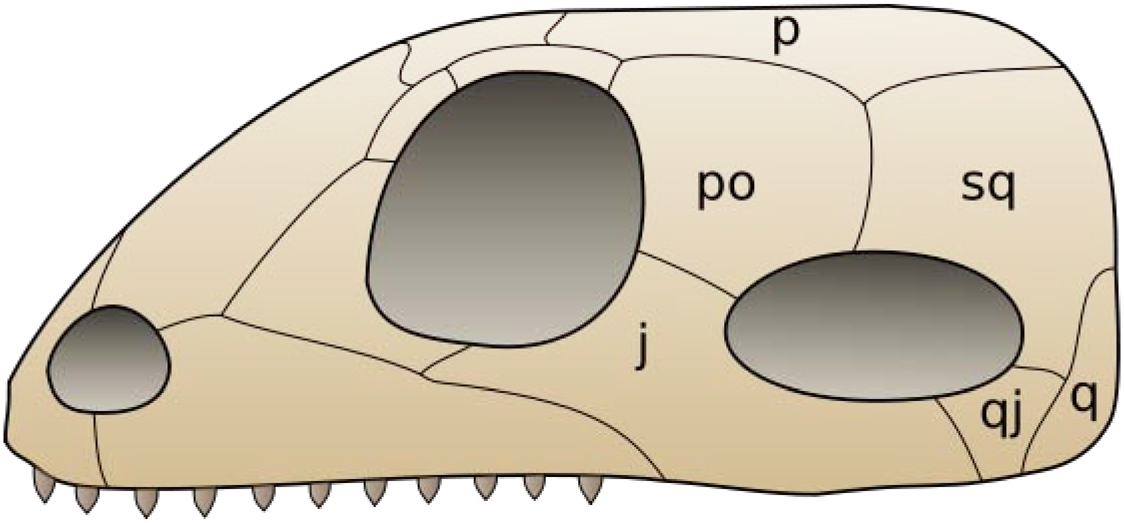
Phylogenetically synapsids are the entire synapsid/mammal branch of the tree of life, though practically the term is used when referring to the reptile-grade synapsids. The term "mammal-like reptiles" is considered obsolete under the cladistic approach, but remains common in general use as a reference to all non-mammalian synapsids. The actual phylogeny of the synapsids are not in doubt though, and whether the term "synapsids contain the mammals" or "synapsids gave rise to the mammals" is used, remains a matter of individual preference, as they both express the same phylogeny.

Primitive and advanced synapsids

The mammal-like reptiles are traditionally divided into a primitive group and an advanced group, known respectively as 'pelycosaurs' and therapsids. 'Pelycosaurs' make up a paraphyletic grouping of the six most primitive families of synapsids. They were all rather lizard-like with sprawling gait and possibly horny scutes. The therapsids contain the more advanced synapsids, having a more erect pose and possibly hair, at least in some forms. The latter are the ancestors of mammals. Thus both of the two synapsid groups represent evolutionary grades: the pelycosaurs have given rise to the therapsids, who in their turn have given rise to the mammals. In traditional Linnaean systematics, the Pelycosauria and Therapsida are considered orders of the subclass Synapsida. In Bentons systematics, the two groups constitute a separate class.

Characteristics

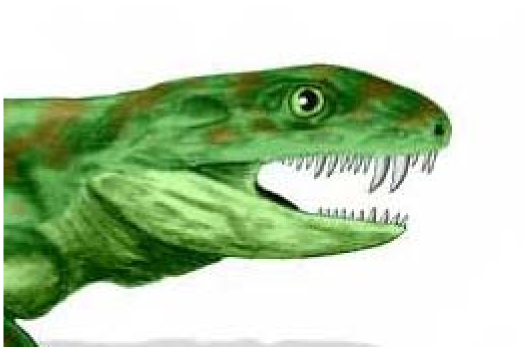
Temporal openings



The synapsids are distinguished by a single hole behind each eye.

Synapsids evolved a temporal fenestra behind each eye orbit on the lateral surface of the skull. It may have evolved to provide new attachment sites for jaw muscles. A similar development took place in the Diapsids, who evolved two rather than one opening behind each eye. Originally, the opening in the skull left the inner cranium only covered by the jaw muscles, but in higher therapsids and mammals the sphenoid bone has expanded to close the opening. This has left the lower margin of the opening as an arch extending from the lower edges of the braincase.

Teeth



Eothyris, an early synapsid with multiple canines.

Synapsids are characterized by having differentiated teeth. These include the canines, molars, and incisors. The trend towards differentiation is found in some labyrinthodonts and early anapsid reptilians in the form of enlargement of the first teeth on the maxilla, forming a form of proto-canines. This trait was subsequently lost in the Sauropsid line, but developed further in the synapsids. Early synapsids could have 2 or even 3 enlarged "canines", but in the therapsids, the pattern had settled to one canine in each upper jaw half. The lower canines developed later.

Jaw

Most paleontologists hold fossilized jaw remains to be the distinguishing feature used to classify synapsids and reptiles. The jaw transition is a good classification tool as most other fossilized features that make a chronological progression from a reptile-like to a mammalian condition follow the progression of the jaw transition. The mandible, or lower jaw, consists of a single, tooth-bearing bone in mammals (the dentary), whereas the lower jaw of modern and prehistoric reptiles consists of a conglomeration of smaller bones (including the dentary, articular, and others). As they evolved, these jaw bones were reduced in size and either lost or, in the case of the articular, gradually moved into the ear, forming one of the middle ear bones: while mammals possess the malleus, incus and stapes, mammal-like reptiles (like all other tetrapods) possess only a stapes. The malleus is derived from the articular (a lower jaw bone) while the incus is derived from the quadrate, (a skull bone).

Mammalian jaw structures are also set apart by the dentary-squamosal jaw joint. In this form of jaw joint, the dentary forms a connection with a depression in the squamosal known as the glenoid cavity. In contrast, all other jawed vertebrates, including reptiles and nonmammalian synapsids, possess a jaw joint in which one of the smaller bones of the lower jaw, the articular, makes a connection with a bone of the skull called the quadrate bone to form the articular-quadrate jaw joint. In forms transitional to mammals, the jaw joint is composed of a large, lower jaw bone (similar to the dentary found in mammals) that does not connect to the squamosal but connects to the quadrate with a receding articular bone.

Palate

Over time, as synapsids became more mammalian and less 'reptilian', they began to develop a secondary palate, separating the mouth and nasal cavity. In early synapsids, a secondary palate began to form on the sides of the maxilla, still leaving the mouth and nostril connected.

Eventually, the two sides of the palate began to curve together, forming a U-shape instead of a C-shape. The palate also began to extend back toward the throat, securing the entire mouth and creating a full palatine bone. The maxilla is also closed completely. In fossils of one of the first eutheriodonts, the beginnings of a palate are clearly visible. The later *Thrinaxodon* has a full and completely closed palate, forming a clear progression.

Skin

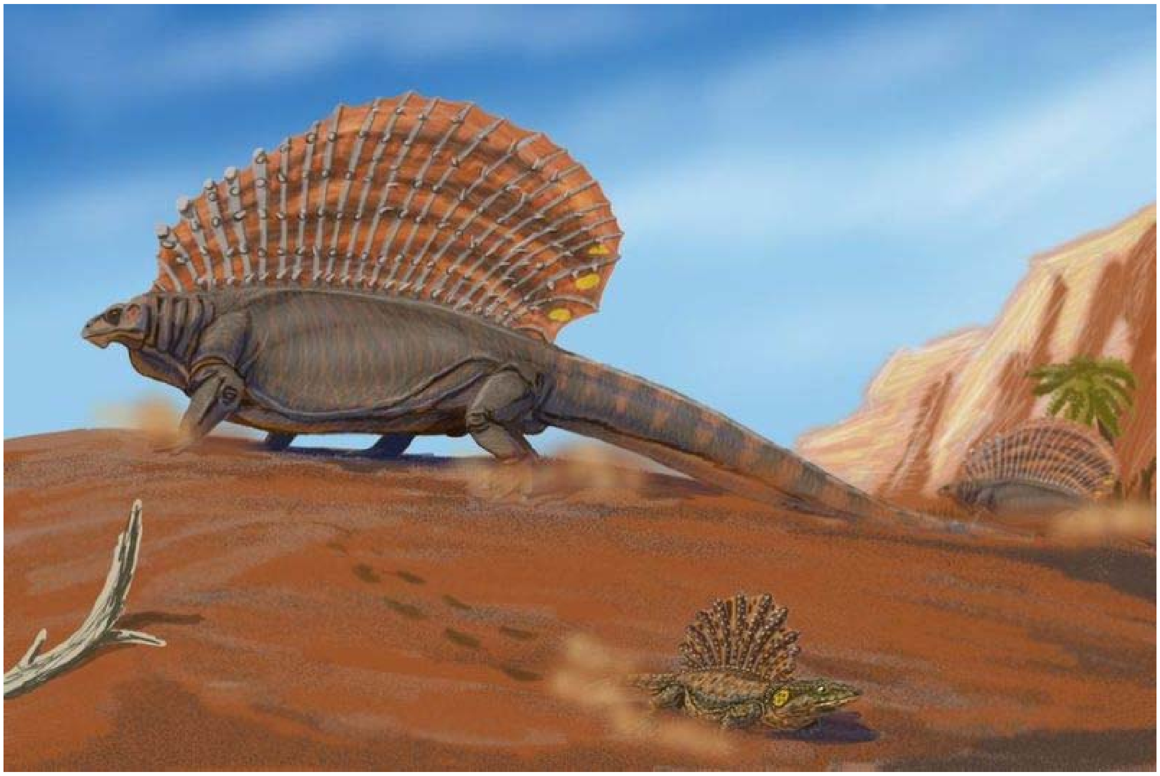
Synapsid combination of hair and scutes, detail of a rat's tail.

The actual skin of the synapsids has been subject to some discussion. Basal reptilian skin is rather thin, and lack the thick dermal layer that produces leather in mammals. Exposed parts of reptiles are protected by horny scales or scutes. Mammal hide has a thick, fibrous dermis and rarely exhibits scutes. A hallmark of mammals is the presence of copious glands and hair follicles.

When the change from reptilian to mammalian type skin took place is not known, though fossilized skin impressions indicate that at least the pelycosaurs retained the scutes of more primitive tetrapods on their undersides. The pelycosaur scutes probably were non-overlapping dermal structures with a horny overlay, like those found in modern crocodiles and turtles. These differed in structure from the scales of lizards and snakes, which are an epidermal feature (like mammalian hair or avian feathers). The upper surface of the pelycosaurs may have borne scutes too, or may have been glandular and leathery like that of a mammal. If so, they may perhaps be visualized as being "naked lizards", both furless and scaleless, as their overall anatomy was more like a modern lizard than a modern mammal.

It is currently unknown at what stage the synapsids acquired mammalian characteristics such as body hair and mammary glands, as the fossils only rarely provide direct evidence for soft tissues. An exceptionally well preserved skull of *Estemmenosuchus*, a therapsid from the Upper Permian show smooth hairless skin with what appears to be glandular depressions. The oldest known fossil showing unambiguous imprints of hair is the Callovian (late middle Jurassic) *Castorocauda*, an early mammal. Much, however, can be inferred from differences in skeletal structure. The more advanced therapsids could have had a combination of naked skin, scutes and hair, a combination still found in some modern mammals like rodents and the opossum.

Metabolism

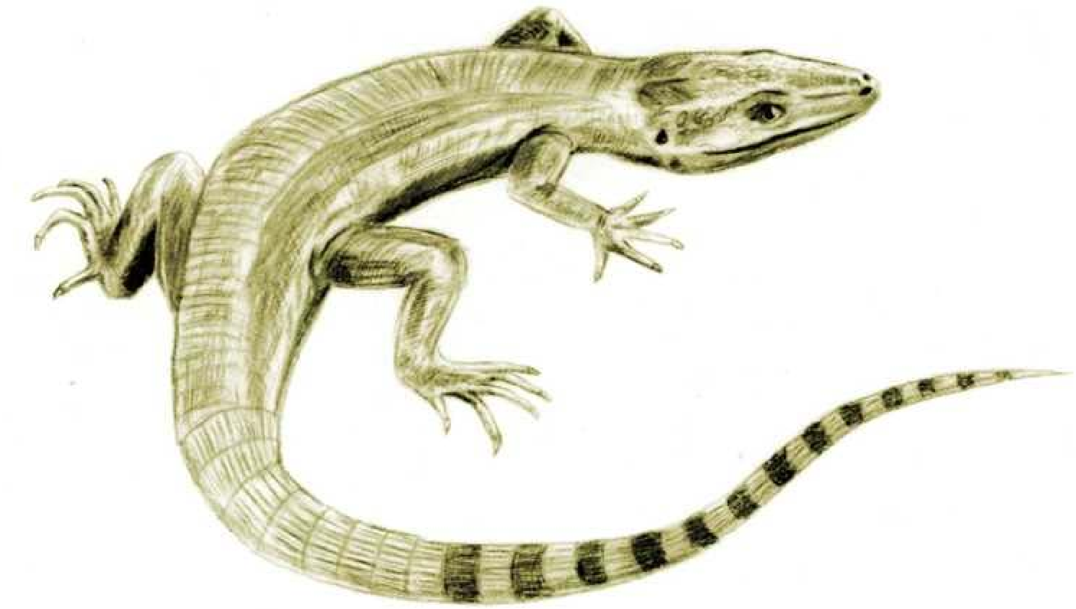


Sail-back pelycosaurs like *Edaphosaurus* indicate an early trend toward temperature regulation in synapsids.

The first pelycosaurs had the usual reptilian cold-blooded metabolism by all indications, including sprawling gait and a low slung body. However, there appears to have been an early trend towards a form of temperature regulation in several Pelycosaur lines, as indicated by the large "sails" in both edaphosaurids and sphenacodontids (e.g. *Dimetrodon*).

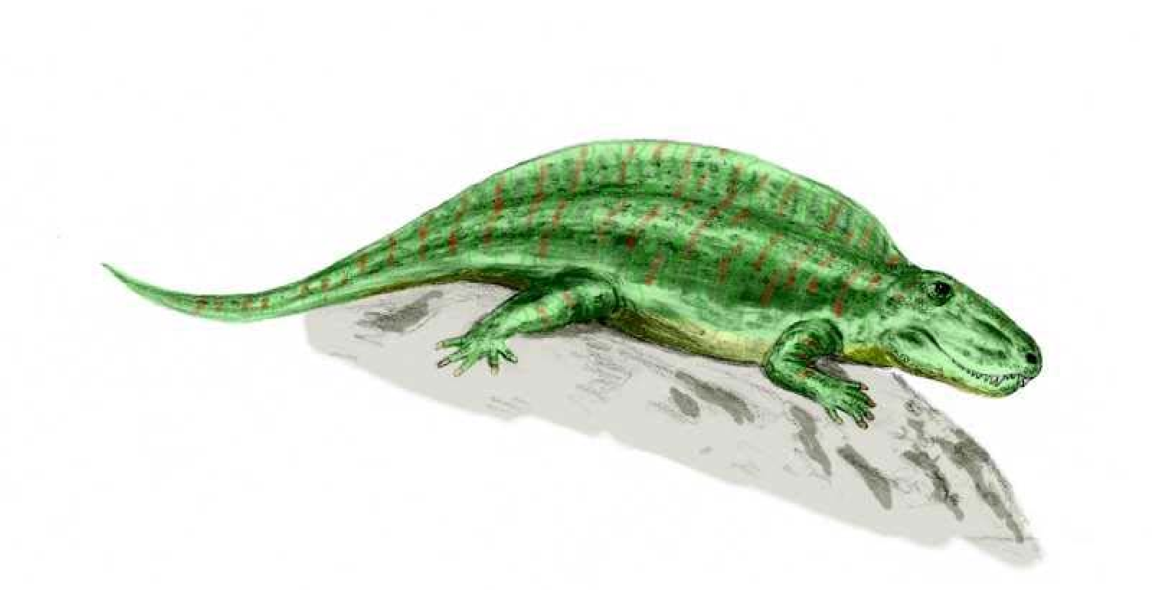
The sphenacodontids gave rise to the therapsids, who may have inherited the temperature regulation. The legs and feet of the early therapsid groups point to a more erect posture, traditionally interpreted as a sign of more efficient metabolism. None of them show any sign of a sail, indicating any temperature regulation would have relied on the creatures own metabolism rather than external heat. In the later cynodonts, the presence of a secondary palate, erect posture and other indicators of high metabolic rate suggests that many mammalian features, including an effective insulating layer of body hair, had evolved by this stage. This is now confirmed by impressions of fur in rocks directly underlying some fossil therapsids.

Evolutionary history



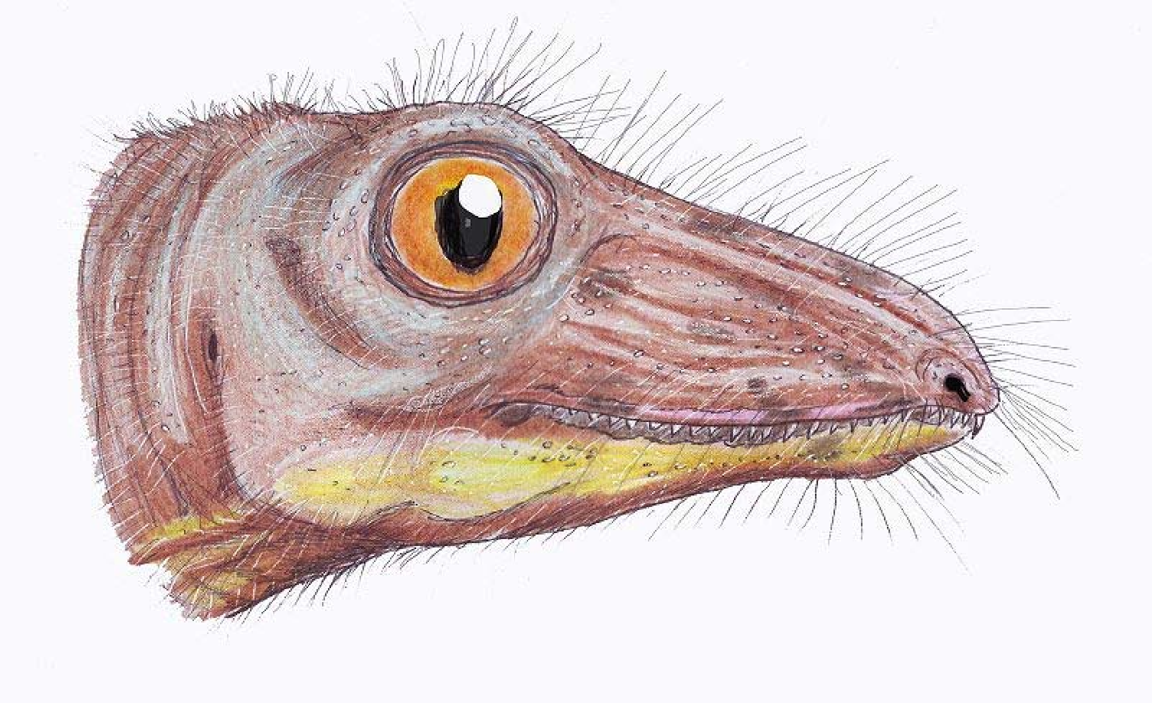
Archaeothyris, one of the oldest synapsids found.

Archaeothyris and *Clepsydrops* are the earliest known synapsids. They lived in the Pennsylvanian subperiod of the Carboniferous Period and belonged to the series of primitive synapsids which are conventionally grouped as pelycosaurs. The pelycosaurs were the first successful group of amniotes, spreading and diversifying until they became the dominant large terrestrial animals in the latest Carboniferous and Early Permian Periods. They were sprawling, bulky, cold-blooded and had small brains. They were the largest land animals of their time, ranging up to 3 m (10 ft) in length. Many, like *Dimetrodon*, had large sails that may have helped raise their body temperature. A few relict groups lasted into the later Permian, but most of the pelycosaurs became extinct before the end of Permian.

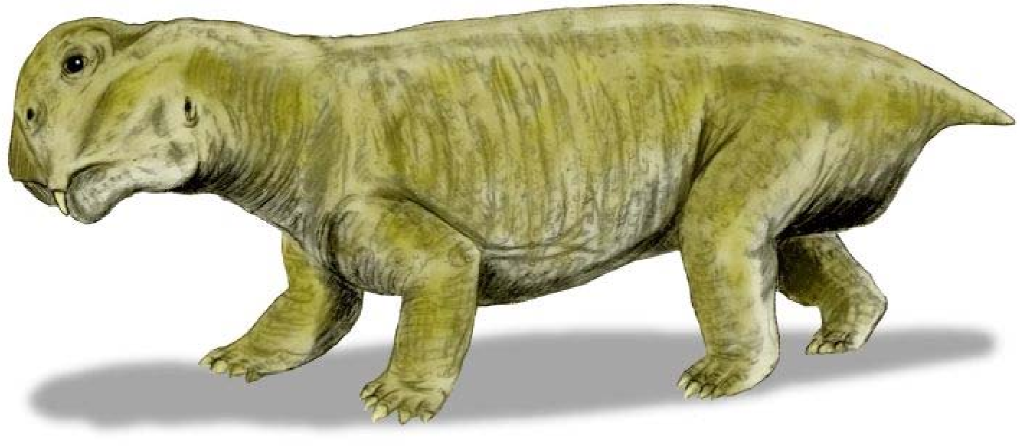


Sphenacodon was a carnivorous pelycosaur that was closely related to *Dimetrodon* and the therapsids.

The therapsids, a more advanced group of synapsids, appeared during the first half of the Permian and went on to become the dominant large terrestrial animals during the latter half. They have dominated the world twice: once in the Permian and once in the Cenozoic, the current era. They were by far the most diverse and abundant animals of the Middle and Late Permian and included herbivores and carnivores, ranging from small animals the size of a rat (e.g.: *Robertia*), to large bulky herbivores a ton or more in weight (e.g.: *Moschops*). After flourishing for many millions of years, these successful animals were all but wiped out by the Permian-Triassic mass extinction about 250 Mya, the largest extinction in Earth's history, which may have been related to the Siberian Traps volcanic event.



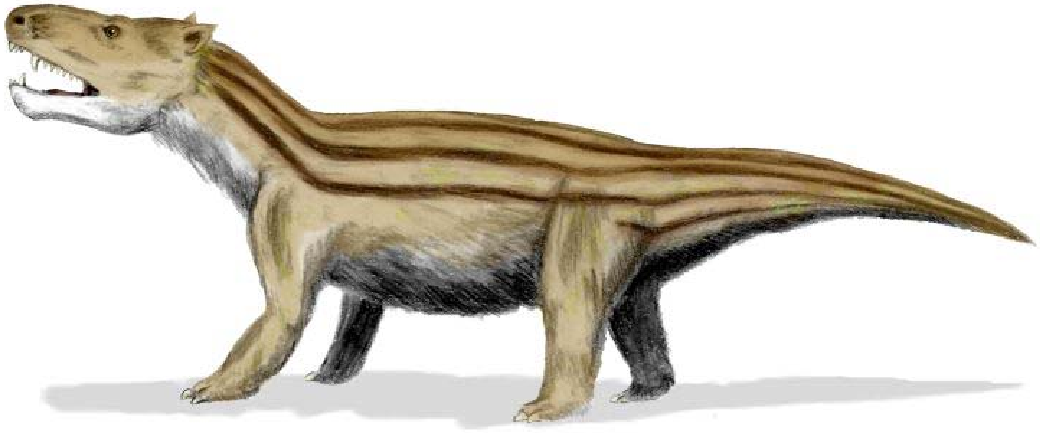
Nikkasaurus - an enigmatic synapsid from the Middle Permian of Russia.



Lystrosaurus was the most common synapsid shortly after the Permian-Triassic extinction event.

Only a few therapsids (and some relict 'pelycosaur' taxa) survived the Permian extinction and went on to be successful in the new early Triassic landscape; they include *Lystrosaurus* and *Cynognathus*, the latter of which appeared later in the early Triassic. Now, however, they were accompanied by the early archosaurs (soon to give rise to the dinosaurs). Some of these, like *Euparkeria*, were small and lightly built, while others, like *Erythrosuchus*, were as big as or bigger than the largest therapsids.

Triassic therapsids included three groups. Specialised, beaked herbivores known as dicynodonts (such as *Lystrosaurus* and its descendants, the Kannemeyeriidae), contained some members which reached large size (up to a tonne or more). The increasingly mammal-like carnivorous, herbivorous, and insectivorous cynodonts included the eucynodonts from the Olenekian age, an early representative of which was *Cynognathus*. Finally, there were the therocephalians, which only lasted into the early part of the Triassic.



Cynognathus was the largest predatory cynodont of the Triassic.

Unlike the dicynodonts, which remained large, the cynodonts became progressively smaller and more mammal-like as the Triassic progressed. From the most advanced and tiny cynodonts, which were only the size of a shrew, came the first mammal precursors, during the Carnian age of the Late Triassic, about 220 Mya.

During the evolutionary succession from early therapsid to cynodont to eucynodont to mammal, the main lower jaw bone, the dentary, replaced the adjacent bones. Thus, the lower jaw gradually became just one large bone, with several of the smaller jaw bones migrating into the inner ear and allowing sophisticated hearing.

Whether through climate change, vegetation change, ecological competition, or a combination of factors, most of the remaining large cynodonts (belonging to the Traversodontidae) and dicynodonts (of the family Kannemeyeriidae) had disappeared by the Norian age, even before the Triassic-Jurassic extinction event that killed off most of the large non-dinosaurian archosaurs. The remaining Mesozoic synapsids were small, ranging from the size of a shrew to the badger-like mammal *Repenomamus*.

During the Jurassic and Cretaceous, the remaining non-mammalian cynodonts were small, such as *Tritylodon*. No cynodont grew larger than a cat. Most Jurassic and Cretaceous cynodonts were herbivorous, though some were carnivorous. The family Trithelodontidae first appeared near the end of the Triassic. They were carnivorous and persisted well into the Middle Jurassic. The other, Tritylodontidae, first appeared at the same time as the trithelodonts, but they were herbivorous. This group became extinct at the end of the Early Cretaceous epoch. Dicynodonts are thought to have become extinct near the end of the Triassic period, but there is evidence that this group survived. New fossil finds have been found in the Cretaceous rocks of Gondwana.

Today, there are 5,400 species of living synapsids known as the mammals, including both aquatic (whales) and flying (bats) species, and the largest animal ever known to have existed (the blue whale). Humans are synapsids as well. Uniquely among the synapsids, however, most mammals are viviparous and give birth to live young rather than laying eggs, the exception being the monotremes.

Synapsids' evolution into mammals is believed to have been triggered by moving to a nocturnal niche. Proto-mammals with higher metabolic rates were able to keep their bodies warm at night, and were more likely to survive. This meant consuming food (generally thought to be insects) in much greater quantity. To facilitate rapid digestion, proto-mammals evolved mastication (chewing) and specialized teeth that aided chewing. Limbs also evolved to move under the body instead of to the side, allowing proto-mammals to breathe more efficiently during locomotion and also to be able to change direction more quickly in order to catch small prey at a faster rate. This helped make it possible to support their higher metabolic demands. It is believed that, rather than out-running predators, proto-mammals adapted the strategy of outmaneuvering predators using their improved locomotor capabilities.

Taxonomy

Classification

- Series **Amniota**
  - CLASS **SYNAPSIDA** *
    - Order **Pelycosauria** *
      - Suborder **Caseasauria**
        - Family **Caseaidae**
        - Family **Eothyrididae**
      - Suborder **Eupelycosauria** *
        - Family **Edaphosauridae**
        - Family **Lupeosauridae**
        - Family **Ophiacodontidae**
        - Family **Sphenacodontidae**
        - Family **Varanopsidae**
    - Order **Therapsida** *
      - Suborder **Biarmosuchia**

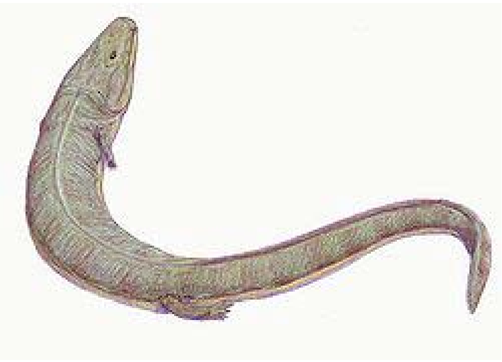
        - (unranked) **Eutherapsida**
            - Suborder **Dinocephalia**
                - Infraorder **Anteosauria**
                - ?Infraorder **Tapinocephalia**
        - (unranked) **Neotherapsida**
            - Suborder **Anomodontia**
            - Superfamily **Venyukoviamorpha**
                - Family **Venyukoviidae**
            - ?Infraorder **Dicynodonta**
        - (unranked) **Theriodontia**
            - Suborder **Gorgonopsia**
        - (unranked) **Eutheriodontia**
        - Suborder **Therocephalia**
        - Suborder **Cynodontia** *
    - CLASS **MAMMALIA**

Chapter 8

Greererpeton , Kyrinion and Madygenerpeton

Greererpeton

Greererpeton
Temporal range: Early Carboniferous



Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia *sensu lato*
Order:	Ichthyostegalia
Family:	Colosteidae
Genus:	***Greererpeton*** Romer, 1969
Species:	***G. burkemorani***

Greererpeton is an extinct genus of tetrapods from the Early Carboniferous period (late Visean) of North America.

Greererpeton had an elongated body adapted for swimming, reaching up to 1.5 metres (4.9 ft) in length, including the tail. Its body had 40 vertebrae, twice the usual amount, and a flattened skull about 18 centimetres (7.1 in) long. The limbs were short, and mainly used for steering, with the long tail providing the main propulsive force while swimming.

Some marks on the side of the skull indicate that *Greererpeton* had a lateral line, a sensory organ commonly found only in fish. Its ears were also poorly developed. Taken together, these are indications that *Greererpeton* was a primitive amphibian that had returned to an almost wholly aquatic existence, rarely, if ever, venturing onto dry land.

Greererpeton was a carnivore and probably lived in rivers and swamps.

Greererpeton burkemorani.

Kyrinion

Kyrinion **Temporal range: Late Carboniferous**	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Family:	†Baphetidae
Subfamily:	†Loxommatinae
Genus:	†***Kyrinion*** Clack, 2003

Species

- †***K. martilli*** Clack, 2003 (type)

Kyrinion is an extinct genus of baphetid tetrapod from the Late Carboniferous of England. It is known from a skull that was found in Tyne and Wear county dating back to the Westphalian stage. Along with the skull is part of the lower jaw, an arch of the atlas bone (the vertebra that connects to the skull) and a rib possibly belonging to a cervical (neck) vertebra. The type species *K. martilli* was named from this material in 2003.

Description

The holotype skull of *Kyrinion* is well preserved with the back of the skull and both stapes, or ear bones, intact. The orbits, or eye sockets, are somewhat triangular in shape. Areas connecting the palate with the jaws and braincase make the skull inflexible. Lateral lines, used for sensory perception in aquatic environments, are present on the quadratojugal bone behind the eyes. The lower jaw lacks the distinctive features of some other baphetids, such as teeth on the parasymphysial plate, a piece of bone that overlies the dentary symphysis.

Classification

Kyrinion is a member of the family Baphetidae, a group of large aquatic tetrapods that somewhat resembled salamanders. Among baphetids, *Kyrinion* is most closely related to *Loxomma* and *Megalocephalus*. In 2009, all three genera were placed within the newly erected subfamily Loxommatinae.

Discovery

The holotype skull of *Kyrinion* was found embedded in a piece of ironstone by paleontologist David Martill in 1993. Martill found the rock on a beach at Whitley Bay and noticed part of an exposed bone. In 2003, after extensive preparation of the holotype, paleontologist Jennifer A. Clack described the specimen and named the species after Martill. It is now housed in the Hancock Museum in Newcastle upon Tyne.

Madygenerpeton

Madygenerpeton **Temporal range: Middle/Upper Triassic**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Order:	Chroniosuchia
Family:	Chroniosuchidae
Genus:	***Madygenerpeton*** Schoch, Voigt & Buchwitz, 2010
Species	
• *M. pustulatus* Schoch, Voigt & Buchwitz, 2010 (type)	

Madygenerpeton is an extinct genus of chroniosuchid reptiliomorph from middle and upper Triassic deposits of Madygen Formation of Kyrgyzstan. It was first named by paleontologists Rainer R. Schoch, Sebastian Voigt and Michael Buchwitz in 2010 from a nearly complete skull and associated osteoderms. The type species is *M. pustulatus*.

Description

Madygenerpeton, like other chroniosuchids, has osteoderms, or bony plates, overlying its spine. These osteoderms interlock with each other and connect to their associated vertebrae on the spinal column. They are wide and have curved or peaked surfaces. On the upper surface of the front end and the lower surface of the back end of each osteoderm there are facets covered in concentric ridges and furrows. These facets allow the plates to interlock with each other. The relatively narrow width of the osteoderms in *Madygenerpeton* allow for more lateral flexion in the trunk of than other chroniosuchids, up to 7.5°.

The skull has a parabolic outline and its surface is covered with pustular ornamentation. This distinctive ornamentation gives the type species its name, *M. pustulatus*. Unlike other chroniosuchids, *Madygenerpeton* lacks an antorbital fontanelle in front of the eyes.The postparietal or posterior area of the skull is concave.

Paleobiology

The tightly interlocking osteoderms along the back of Permian chroniosuchians were likely an adaptation to terrestrial locomotion. The plates made the vertebral column more rigid, allowing it to better cope with stresses from shearing, torsion, compression, and tension. However, the increased stability of the vertebral column resulted in less flexibility. In *Madygenerpeton*, the increased flexibility of the trunk may have been an adaptation to a secondarily aquatic lifestyle. Greater lateral flexion would have enabled lateral undulation useful for swimming.

Chapter 9

Pederpes and Sauropsida

Pederpes

Pederpes **Temporal range: Middle Mississippian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Class:	Amphibia *sensu lato*
Family:	Whatcheeriidae
Genus:	***Pederpes*** Clack, 2002
Species	
P. finneyae Clack, 2002 (type)	

Pederpes is an extinct genus of early Carboniferous tetrapod, dating from the Tournaisian age (lower Mississippian, 359 - 345 Ma). *Pederpes* contains one species, *P. finneyae*, 1 m long.

This most basal Carboniferous tetrapod had a large, somewhat triangular head, similar to that of later American sister-genus *Whatcheeria*, from which it is distinguished by various skeletal features, such as a spike-like latissimus dorsi (an arm muscle) attachment on the humerus and several minor skull features. The feet had characteristics that distinguished it from the paddle-like feet of the Devonian Ichthyostegalia and resembled the feet of later, more terrestrially adapted Carboniferous forms. *Pederpes* is the earliest-known tetrapod to show the beginnings of terrestrial locomotion and despite the probable presence of a sixth digit on the forelimbs it was at least functionally pentadactyl.

Discovery and Classification

Pederpes was discovered in 1971 in central Scotland and classified as a lobe-finned fish. Its fossils were found in the Ballagan Formation. The type specimen was a nearly complete, articulated skeleton. Only the tail and some bones of the skull and limbs were missing. It was not until 2002 that Jennifer Clack named and reclassified the fossil as a primitive tetrapod.

Pederpes is placed in the family Whatcheeriidae, of uncertain relationships to other tetrapod families. While undoubtedly amphibian in life and reproductive mode, under cladistic taxonomy, *Pederpes* is not considered an amphibian in the meaning of modern amphibians. As a very basal (primitive) tetrapod, it falls under the traditional class Amphibia in Linnaean taxonomy.

Pederpes is an important fossil because it comes from the period of time known as Romer's Gap and provides biologists with rare information about the development of tetrapods in a time where terrestrial life was rare.

Anatomy and Lifestyle.

Pederpes was 1 m long, making it average-sized for an early tetrapod.

The shape of the skull and the fact that the feet face forward rather than outward indicate that *Pederpes* was well adapted to land life. It is currently the earliest known fully terrestrial animal, although the structure of the ear shows that its hearing was still much more functional underwater than on land, and may have spent much of its time in the water and could have hunted there.

The narrow skull suggests that *Pederpes* breathed by inhaling with a muscular action like most modern tetrapods, rather than by pumping air into the lungs with a throat pouch the way many modern amphibians do.

Sauropsida

Sauropsids
Temporal range: 320–0 Ma
Carboniferous – Recent

"Reptile-faced": A red eared slider and a mallard; both are sauropsids

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
(unranked):	Amniota
(unranked):	**Sauropsida** Goodrich, 1916

Clades

- Reptilia *
    - Anapsida
    - Diapsida
        - †Araeoscelidia
        - †Avicephala
        - Neodiapsida
            - †Younginiformes
            - †Ichthyopterygia
            - Sauria

Sauropsida ("lizard faces") is a group of amniotes that includes all existing reptiles and birds and their fossil forefathers, including the dinosaurs, the immediate ancestors of birds. Sauropsida is distinguished from Theropsida ("beast faces"), more commonly called Synapsida, which includes mammals and their fossil ancestors.

History of classification

Huxley and the fossil gaps

The term *Sauropsida* ("lizard faces") has a long history, and hails back to Thomas Henry Huxley, and his opinion that birds had risen from the dinosaurs. He based this chiefly on the fossils of *Hesperornis* and *Archaeopteryx*, that were starting to become known at the time. In the Hunterian lectures delivered at the Royal College of Surgeons in 1863, Huxley grouped the vertebrate classes informally into mammals, sauroids, and ichthyoids (the latter containing the anamniotes), based on the gaps in physiological traits and lack of transitional fossils that seem to exist between the three groups. He subsequently proposed the names of Sauropsida and Ichthyopsida for the two latter. It is worth noting that mammal-like reptiles like *Dicynodon*, described as a reptile by Richard Owen as early as 1845, were beginning to become known at the time Huxley gave his systematic lecture. His Sauropsida differs from later usage of the word, in that it contained the cynodonts as well.

Sauropsids redefined

By the early 20th century, the fossils of Permian synapsids from South Africa had become well known, allowing palaeontologists to trace synapsid evolution in much greater detail. The term Sauropsida was taken up by E.S. Goodrich in 1916 much like Huxley's, to include lizards, birds and their relatives. He distinguished them from mammals and their extinct relatives, which he included in the sister group Theropsida (now usually replaced with the name Synapsida). Goodrich's classification thus differs somewhat from Huxley's, in which the synapsids (or at least the Pelycosaurs) would quite possibly have fallen under the sauropsids. Goodrich supported this division by the nature of the hearts and blood vessels in each group, and other features such as the structure of the forebrain. According to Goodrich, both lineages evolved from an earlier stem group, the Protosauria ("first lizards"), which included some Paleozoic amphibians as well as early reptiles predating the sauropsid/synapsid split (and thus not true sauropsids).

Mammal-like reptiles and other reptiles

In 1956, D.M.S. Watson observed that sauropsids and synapsids diverged very early in their history, and so he divided Goodrich's Protosauria between the two groups. He also reinterpreted the Sauropsida and Theropsida to exclude birds and mammals respectively, making them paraphyletic, unlike Goodrich's definition. Thus his Sauropsida included Procolophonia, Eosuchia, Millerosauria, Chelonia (turtles), Squamata (lizards and snakes), Rhynchocephalia, Crocodilia, "thecodonts" (paraphyletic basal Archosauria), non-avian dinosaurs, pterosaurs, ichthyosaurs, and sauropyterygians.

This classification supplemented, but was never as popular as, the classification of the reptiles (according to Romer's classic *Vertebrate Paleontology*) into four subclasses according to the positioning of *temporal fenestrae*, openings in the sides of the skull behind the eyes. Since the advent of phylogenetic nomenclature, the term Reptilia has fallen out of favor with many taxonomists, who have used Sauropsida in its place to include a monophyletic group containing the traditional reptiles and the birds.

Cladistics and the Sauropsida

The class Reptilia has been known to be an evolutionary grade rather than a clade for as long as evolution has been recognised. Reclassifying reptiles has been among the key aims of phylogenetic nomenclature. The term Sauropsida was originally used to denote all species not on the synapsid side after the synapsid/sauropsid split, a branch-based clade. This group encompasses all now-living reptiles as well as birds, and as such is comparable to Goodrich's classification, the difference being that better resolution of the early amniote tree has split up most of the Goodrich's "Protosauria". Later cladistic work has used Sauropsida more restrictively, to signify the crown group, i.e. all descendants of the last common ancestor of extant reptiles and birds. A number of phylogenetic stem, node and crown definitions has been published, anchored in a variety of fissil and extant organisms, thus there is currently no consensus of the actual definition (and thus content) of Sauropsida as a phylogenetic unit.

Some taxonomists, such as Benton (2004), have co-opted the term to fit into traditional rank-based classifications, making Sauropsida and Synapsida class-level taxa to replace the traditional Class Reptilia, while Modesto and Anderson (2004), using the PhyloCode standard, have suggested replacing the name Sauropsida with their redefinition of Reptilia, arguing that the latter is by far better known and should have priority.

Chapter 10

Temnospondyli

Temnospondyls
Temporal range: Carboniferous–Early Cretaceous
Possible descendant taxon Lissamphibia survives to present.

Skeleton of *Eryops*, Galerie de Paléontologie, MNHN, Paris.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Subclass:	Labyrinthodontia
Order:	**†Temnospondyli** Zittel, 1888

Temnospondyli is an important and extremely diverse taxon of small to giant primitive amphibians that flourished worldwide during the Carboniferous, Permian, and Triassic periods. A few stragglers continued into the Cretaceous. During their evolutionary history they adapted to a very wide range of habitats, including fresh-water aquatic, semi-aquatic, amphibious, terrestrial, and in one group even near-shore marine, and their fossil remains have been found on every continent. Authorities disagree over whether some specialised forms were ancestral to some modern amphibians, or whether the whole group died out without leaving any descendants.

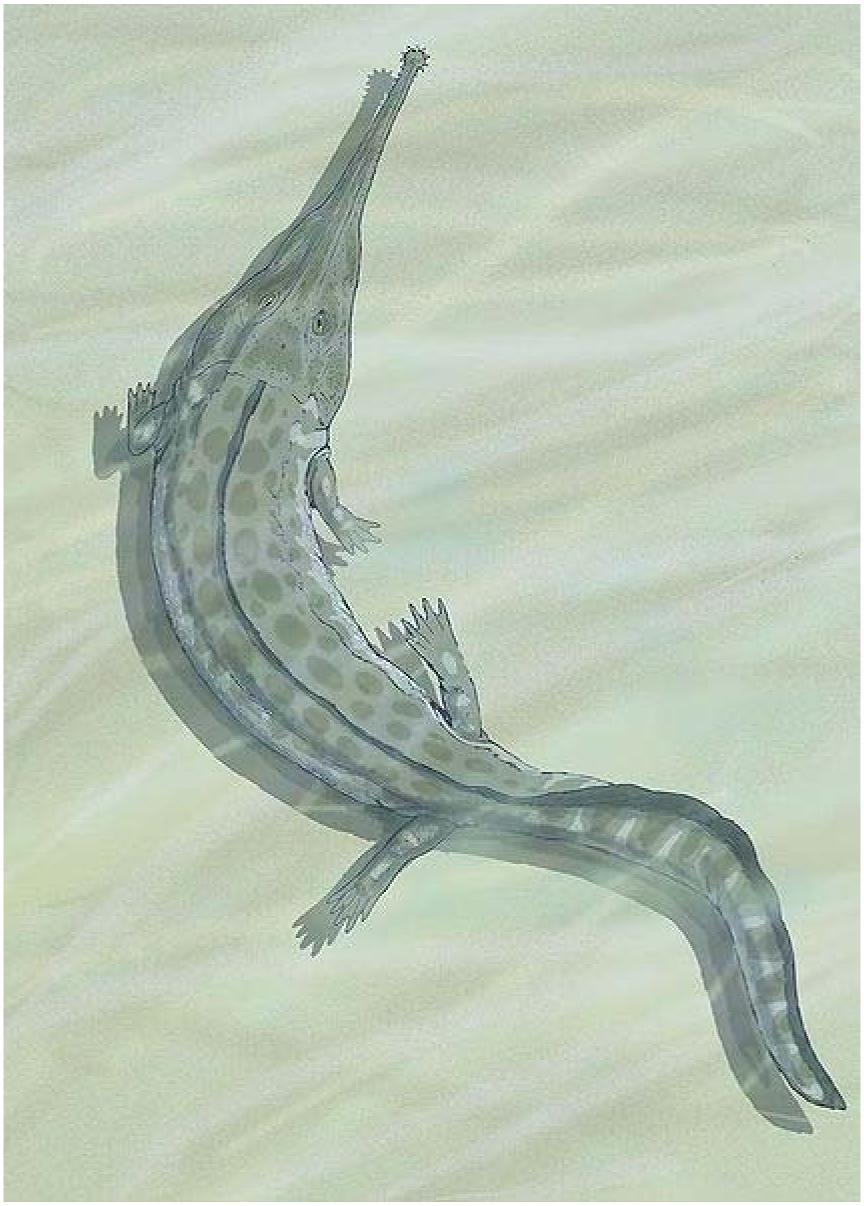
Evolutionary History

Carboniferous and early Permian Temnospondyli

Capetus, a basal temnospondyl.

During the Carboniferous, Temnospondyli included basal medium-sized (*Dendrerpeton*) or large (*Cochleosaurus*, about 1.5 metres (4.9 ft) long) semi-aquatic forms. Others such as the amphibamids were smaller and more derived, resembling newts or salamanders, and some taxa, such as the genus *Branchiosaurus*, even retained external gills like the modern-day axolotl. During the latest Carboniferous and early Permian (ca. 300 Ma), several groups such as the dissorophoids evolved strong, robust limbs and vertebrae and became adapted to life on land while others such as the eryopids and trematopids developed into large (c. 1.5 metres (4.9 ft) long) and heavy-bodied semi-aquatic predators.

Late Permian Temnospondyli

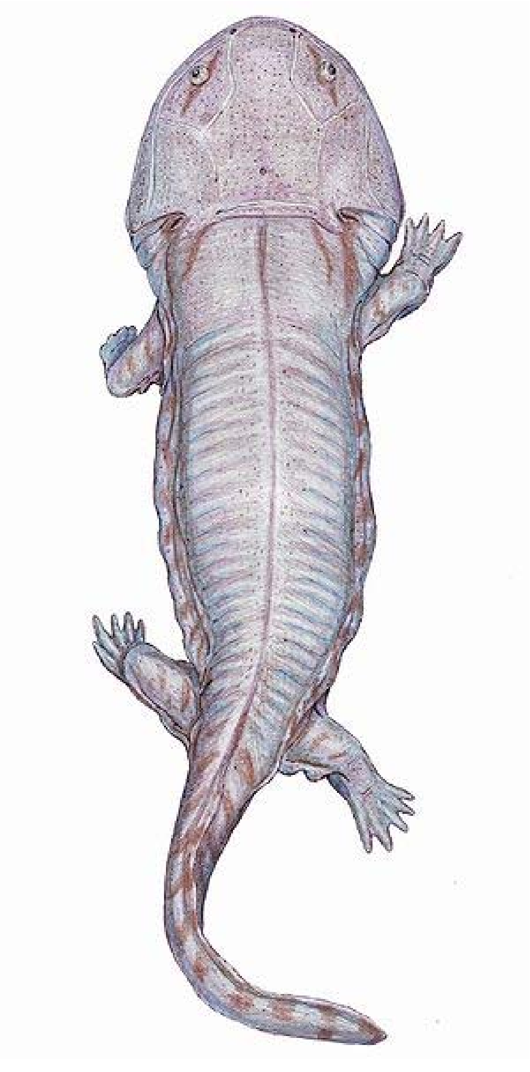


Prionosuchus from the Permian, the largest amphibian ever described.

During the later Permian, increasing aridity and more successful reptiles meant the end of the terrestrial temnospondyls, but semi- and fully aquatic animals continued to flourish, including the large *Melosaurus* of Eastern Europe. Other temnospondyls such as archegosaurids developed long snouts and an astonishing similarity to crocodiles, although they lacked the armour characteristic of the latter group. These temnospondyls included the largest known amphibian, the 9 metres (30 ft) long *Prionosuchus* of Brazil.

As these amphibians continued to flourish and diversify in the lakes and rivers of the late Permian (260.4 - 251.0 Ma), a number of groups became more dependent on life in the water. The vertebrae became weak, the limbs small and vestigal, and the heavy skull large and flat, with the eyes looking upwards. These include the classic Stereospondyli, and other related types. During the Triassic period these animals dominated the fresh-water ecosystems, evolving in a range of both small and large forms. During the Early Triassic (251.0 - 245.0 Ma) one group of successful long-snouted fish eaters, the trematosaurs, even adapted to a life in the sea, the only known amphibians to do so with the exception of the modern Crab-eating frog). Another group, the Capitosauroidea, included not only medium-sized but also many giant species, 2.3 to 4 metres (7.5 to 13 ft) or more in length (e.g. *Paracyclotosaurus*, *Cyclotosaurus*), with huge and extraordinarily flat skulls, over a meter long in the largest forms (*Mastodonsaurus*). These animals seem to have lived on the river bottom, perhaps spending most or all their entire lives in water, and catching their prey by a sudden opening of the upper jaw, sucking in fish or smaller tetrapods that happened to swim past.

Mesozoic survivors



Siderops, a Jurassic temnospondyl.

In the Carnian stage of the late Triassic (228.0 - 216.5 Ma) capitosauroids were joined by the superficially very similar Metoposauridae (1.5 metres (4.9 ft) long—and distinguished mainly by the different position of the eye-sockets), and the curious wide-headed plagiosaurs (about a meter in length), with external gills.

The Triassic-Jurassic extinction event (ca. 199.6 Ma) killed all the giant temnospondyls. Only the smaller Brachyopidae and Chigutisauridae survived. These grew to large size during the Jurassic, with the brachyopids flourishing in China, and the chigutisaurs in Gondwana.

The most recent known temnospondyl was the giant chigutisaur *Koolasuchus*, known from the Early Cretaceous of Australia where it seems to have survived in rift valleys that were too cold in the winter for crocodiles, co-existing with dinosaurs. At around 2.5 to 5 meters in length, this was one of the largest of its kind, as well as the last.

Relationship to modern amphibians

The Lissamphibia, the modern amphibians, appear to have risen in the Permian. The root of the group is controversial, but may be with the Temnospondyli. Skull morphology of some of the smaller later form has been compared to those of modern frogs and salamanders. The presence of bicuspid, pedicellate teeth in small, paedomorphic or immature temnospondyls like the genus *Doleserpeton* has been cited as the most convincing argument in favor of the temnospondyl origin of lissamphibians. Other analysis indicate that another fossil group, the Lepospondyli, are more likely candidates for lissamphibian origin, leaving the Temnospondyli an extinct group.

Systematics

Two types of vertebrae

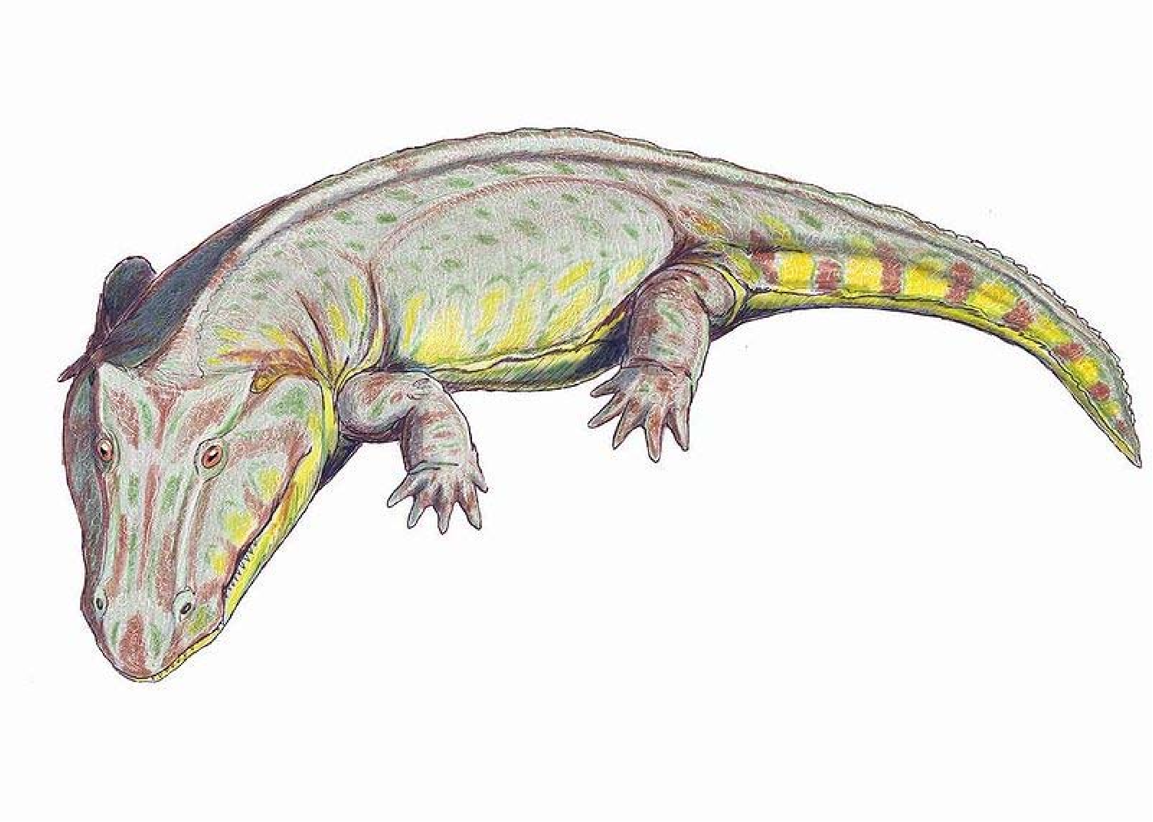
Originally, Temnospondyli were classified according to the structure of the vertebrae. Earlier forms, with complex vertebrae consisting of a number of separate elements, were called "Rachitomi", and large Triassic aquatic forms with simpler weaker vertebrae were called "Stereospondyli"; and these two types were considered suborders of the order Temnospondyli.

In the Rachitomous condition the intercentra were large and wedge-shaped, and the pleurocentra were relatively small blocks that fitted between them. Both elements supported the neural arch, and well-developed interlocking zygapophyses strengthened the connections between the vertebrae. The strong backbone and strong limbs let many ratchitomes be at least partially, and in some cases fully, terrestrial.

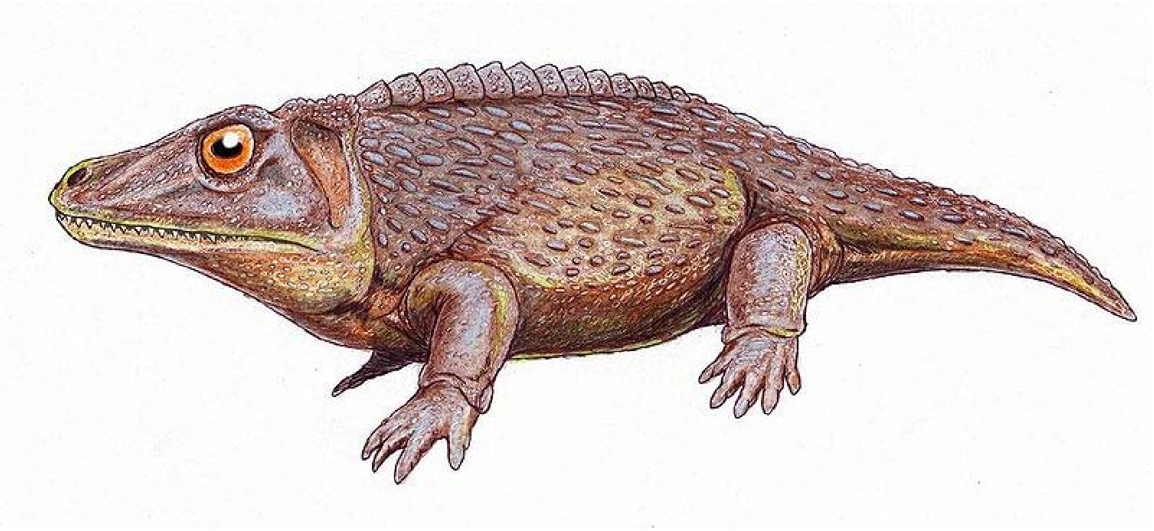
In the stereospondylous condition the pleurocentra have been lost, and the vertebral centra reduced to simple blocks made up of the intercentra only. This weaker type of backbone indicates a more fully aquatic existence.

More recent research has shown that this classification is no longer viable. The basic rachitomous condition is primitive for amphibians (tetrapods) in general. The pure stereospondyls seem to have arisen from different ancestors. Some temnospondyls have rachitomous, semi-rachitomous, and sterospondylous vertebrae at different points the vertebral column of the same individual. Other taxa have intermediate morphologies that do not fit into one or the other category. However, at least according to some analyses, the stereospondyls (minus some ambiguous taxa) can still be considered a clade.

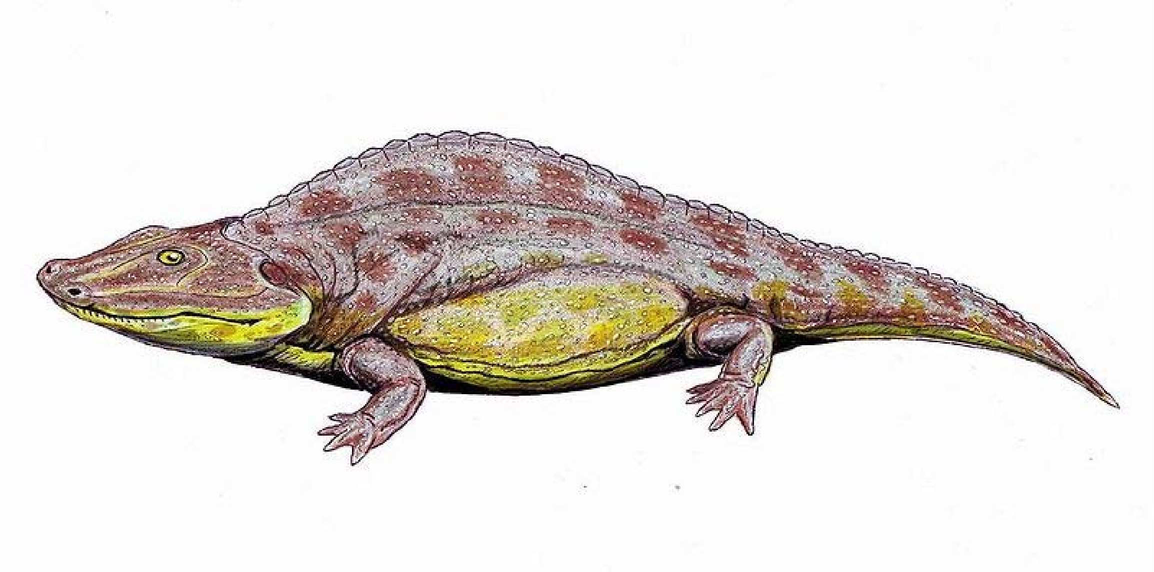
Taxonomy



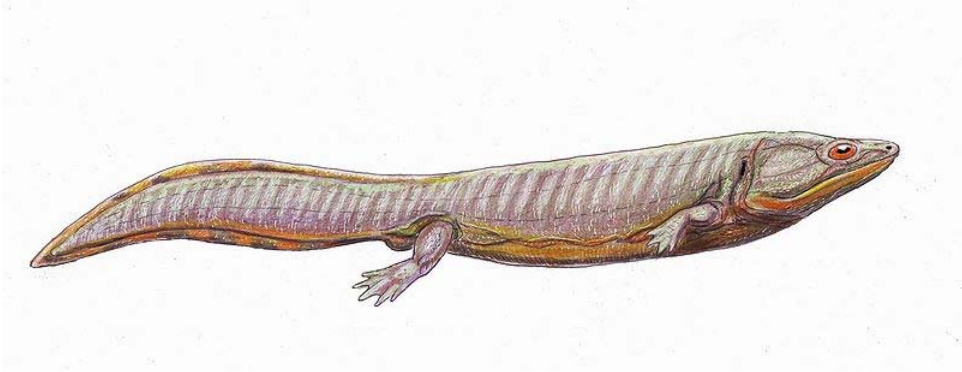
Edops, a basal edopoid.



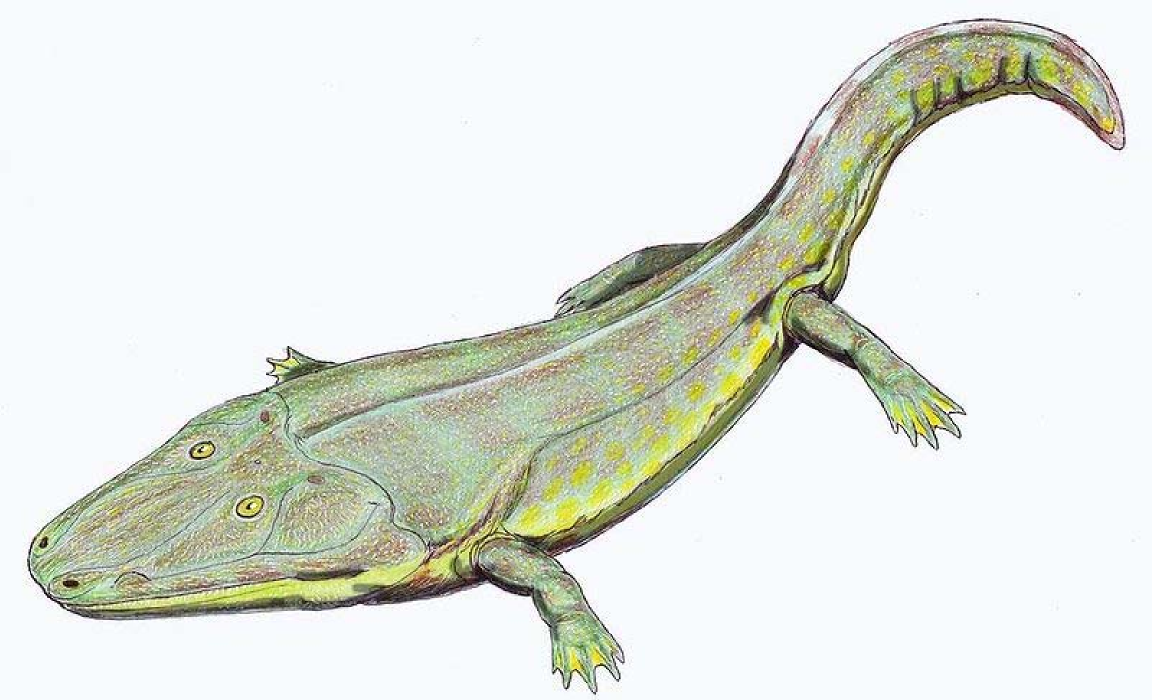
Zygosaurus, a dissorophid.



Sclerothorax, a basal limnarchian.



Dvinosaurus, a dvinosaurid.



Cyclotosaurus, a capitosaurid.

Class Amphibia

- **Order Temnospondyli**
    - *Saharastega*
    - Superfamily Edopoidea
        - Family Cochleosauridae (Chenoprosopidae)
        - Family Edopidae
    - *Capetus*
    - *Iberospondylus*
    - Family Dendrerpetontidae
    - **Suborder Euskelia**
    - **Clade Limnarchia**
        - Suborder Dvinosauria
        - Clade Stereospondylomorpha
            - Superfamily Archegosauroidea
                - Family Actinodontidae
                - Family Archegosauridae
                - Family Intasuchidae?
            - Suborder Stereospondyli
                - Family Peltobatrachidae
                - Family Lapillopsidae
                - Family Rhinesuchidae
                - Family Lydekkerinidae
                - Clade Capitosauria

        - Superfamily Mastodonsauroidea (Capitosauroidea)
            - Family Heylerosauridae
            - Family Mastodonsauridae
            - Family Sclerothoracidae
    - Infraorder Trematosauria
        - Superfamily Trematosauroidea
        - Superfamily Metoposauroidea
        - Superfamily Plagiosauroidea
        - Superfamily Brachyopoidea
        - Superfamily Rhytidosteoidea

Chapter 11

Diadectidae

Diadectidae
Temporal range: Late Carboniferous – Early Permian, 305–271 Ma
(possible Early Carboniferous occurrence)

Skeleton of *Diadectes sideropelicus* in the American Museum of Natural History

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Subclass:	Labyrinthodontia
(unranked):	Reptiliomorpha
Suborder:	†Diadectomorpha
Family:	†**Diadectidae** Cope 1880

Genera

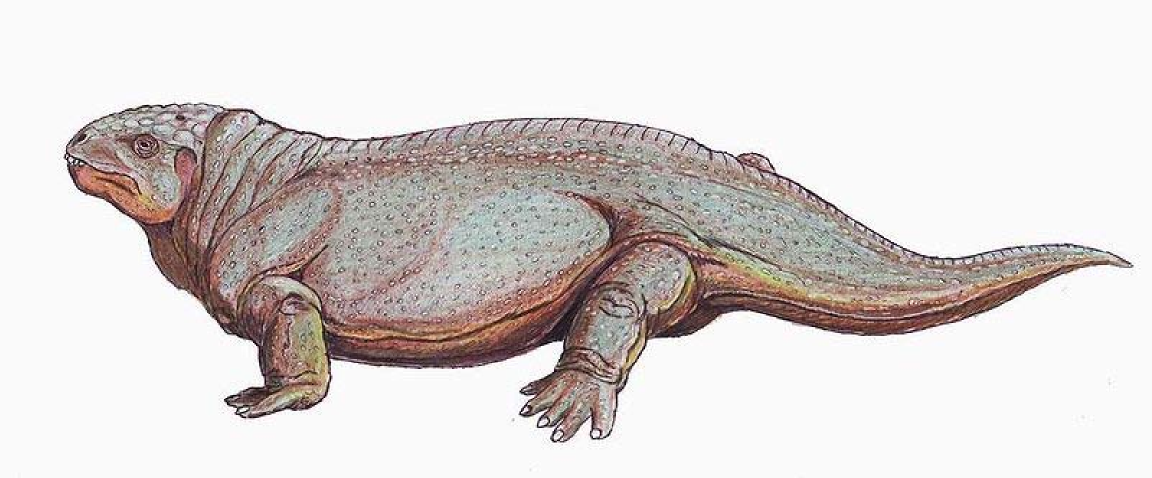
†*Ambedus*
†*Desmatodon*
†*Diadectes*
†*Diasparactus*
†*Oradectes*
†*Orobates*

†*Phanerosaurus*
†*Silvadectes*
†*Stephanospondylus*

Diadectidae is an extinct family of large diadectomorph reptiliomorphs. Diadectids lived in North America and Europe during the Late Carboniferous and Early Permian. They were the first herbivorous tetrapods, and also the first fully terrestrial animals to attain large sizes. Footprints indicate that diadectids walked with an erect posture. They were the first to exploit plant material in terrestrial food chains, making their appearance an important stage in both vertebrate evolution and terrestrial ecosystems.

The best known and largest representative of the family is *Diadectes*, a heavily built animal that attained a maximum length of several metres. Several other genera and various fragmentary fossil remains are also known. Although well known genera like *Diadectes* first appear in the Late Pennsylvanian, fragmentary remains of possible diadectids are known from much earlier deposits, including a piece of lower jaw found in Mississippian strata from Tennessee.

Description



Life restoration of *Diadectes*, a well-known Early Permian diadectid

Diadectids were some of the first tetrapods, or four-legged vertebrates, to attain large sizes. Diadectids first appear in the Late Carboniferous with the genus *Desmatodon*, although recently described bones from Tennessee suggest that they may have appeared even earlier in the Early Carboniferous. They have large bodies with relatively short limbs. The rib cage is barrel-shaped to accommodate a large digestive tract necessary for the digestion of cellulose in plants. The skulls of diadectids are wide and deep with blunt snouts. The internal nares are also short. Paleontologist E.C. Case compared diadectids to turtles in 1907, noting their large pectoral girdles, short, strong limbs, and robust skulls. Case described them as "lowly, sluggish, inoffensive herbivorous reptiles, clad in an armor of plate to protect them from the fiercely carnivorous pelycosaurs."

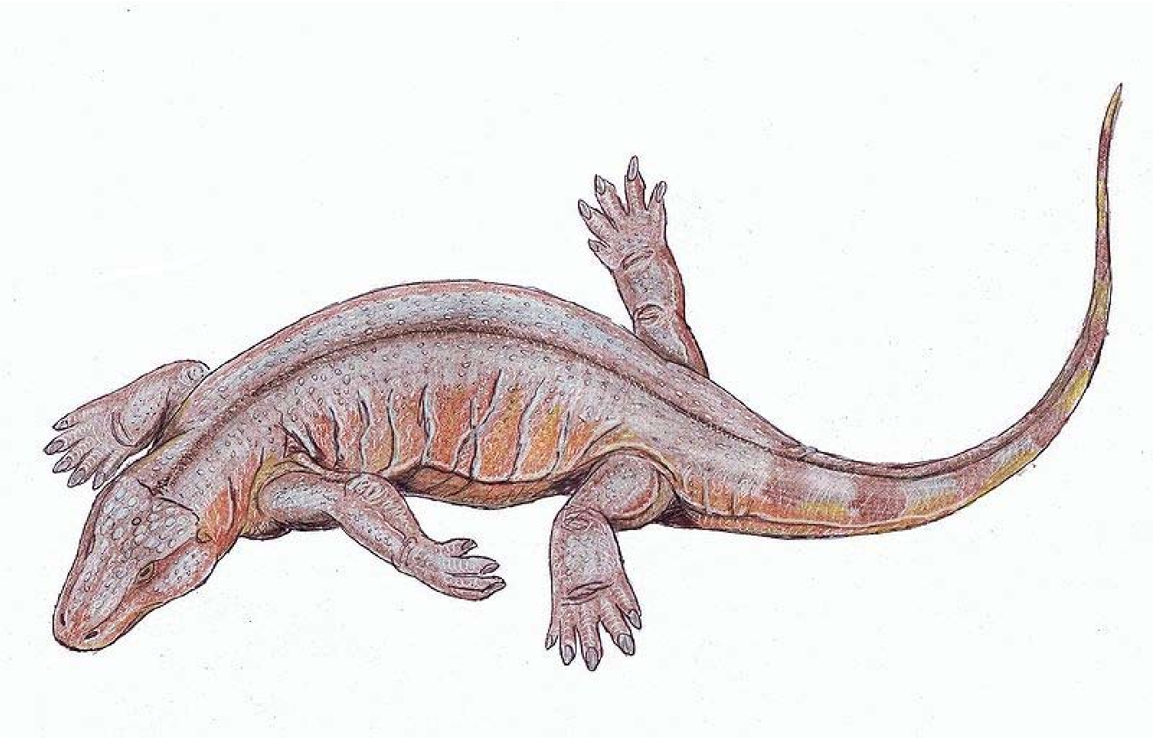
Diadectids have a hederodont dentition, meaning that their teeth vary in shape along the length of the jaws. The teeth are wide and bear many cusps or projections, an indication that diadectids ate tough plants. Some teeth are leaf-shaped and laterally compressed, another indication that diadectids were able to shred plant material. The procumbent front teeth of the lower jaw project forward. Diadectids likely had strong jaw muscles for processing plant material; the placement of the jaw joints above or below the level of the occlusal planes (the planes at which the teeth come together) would have given diadectid jaws mechanical advantage. The joints themselves give the jaws a complex range of movement suitable for consuming plants. Large holes and cavities in the skull called adductor chambers and temporal openings would have provided room for large jaw-closing muscles. A ridge on the dentary bone of the lower jaw may have provided a surface for chewing or even supported a beak.

History

The first diadectid to be described was *Diadectes*. American paleontologist Edward Drinker Cope named the genus in 1878 on the basis of several vertebrae and teeth from the Early Permian of Texas. Cope erected the family Diadectidae in 1880 to include *Diadectes* and *Empedocles*, a genus he named two years earlier. *Nothodon*, named by Cope's rival Othniel Charles Marsh in 1878, was soon placed in the family.

Cope named several other diadectids, including *Helodectes* in 1880, *Chilonyx* and *Empedias* in 1883, and *Bolbodon* in 1896. Paleontologist E.C. Case named four other diadectids: *Desmatodon* in 1908, *Diasparactus* in 1910, *Diadectoides* in 1911, and *Animasaurus* along with paleontologist Samuel Wendell Williston in 1912. Case and Williston considered Marsh's *Nothodon* and Cope's *Bolbodon* to be synonymous with *Diadectes*. Marsh named *Nothodon* in the *American Journal of Science* only five days before Cope described *Diadectes* in *Proceedings of the American Philosophical Society*. Under rules of the International Code of Zoological Nomenclature, the name *Nothodon* would have priority over *Diadectes*, but because the name *Diadectes* has been in use since Case and Williston first synonymized the genera, *Diadectes* remains the accepted name.

In North America, diadectids are known from Texas, Colorado, Utah, New Mexico, Oklahoma, Ohio, West Virginia, Pennsylvania, and Prince Edward Island. A possible diadectid has also been found from Tennessee. It is known from a broken lower jaw and several teeth found in Mississippian-age (Chesterian) strata that are likely part of the Bangor Formation. In a detailed review of Diadectidae, paleontologist E.C. Olson placed three North American genera within the family: *Diadectes*, *Diasparactus*, and *Desmatodon*. *Chilonyx*, *Empedias*, *Diadectoides*, and *Animasaurus* were synonymized with *Diadectes*, and four species of *Diadectes* (*D. sideropelicus*, *D. tenuitectes*, *D. lentus*, and *D. carinatus*) were recognized. A fourth genus, *Ambedus*, was named in 2004 from the Early Permian of Ohio.



Orobates, a diadectid from Germany

Diadectids are also known from Germany. *Phanerosaurus* was described from several vertebrae near Zwickau by German paleontologist Christian Erich Hermann von Meyer in 1860, but was not recognized as a diadectid until 1925. A second species of *Phanerosaurus* was identified from some vertebrae and a fragmentary skull in 1882, and was given its own genus, *Stephanospondylus*, in 1905. In 1998, a new species of *Diadectes*, *D. absitus*, was described from the Bromacker sandstone quarry of the Tambach Formation in the Thuringian Forest of central Germany. A new genus of diadectid called *Orobates* was also named from the Bromacker Quarry in 2004.

Classification

Diadectids have traditionally been considered close relatives of the amniotes, tetrapods that lay eggs on land. The family was placed in the larger group Diadectomorpha by paleontologist D.M.S. Watson in 1917. Diadectidae is closely related to another family of large diadectomorphs, the Limnoscelidae, as well as the monotypic diadectomorph family Tseajaiidae, represented by the genus *Tseajaia*. In some phylogenetic studies, Diadectomorpha is placed as the sister taxon of Amniota, and together the two groups form the larger clade Cotylosauria. While most studies place diadectids outside Amniota, some have considered them to be true amniotes.

Most phylogenetic studies of the three diadectomorph families – Diadectidae, Limnoscelidae, and Tseajaiidae – have found diadectids and limnoscelids to be more closely related to each other than either is to *Tseajaia*. In other words, Diadectidae and

Limnoscelidae form a clade within Diadectomorpha and *Tseajaia* is excluded from the clade. In a 2010 phylogenetic analysis, Diadectidae formed a clade that was characterized by wide cheek teeth with cusps on either side. Unlike previous studies, it was found to be more closely related to Tseajaiidae than Limnoscelidae. The family was defined as *Diadectes* and all taxa sharing a more recent common ancestor with *Diadectes* than with *Tseajaia*. Below is a cladogram modified from the 2010 analysis:

Diadectes is the best known diadectid with six species named since its initial description. In a 2005 phylogenetic analysis, most species of *Diadectes* formed a clade with *Diasparactus zenos*. Two species, *Diadectes absitus* and *Diadectes sanmiguelensis*, were placed in more basal positions. These species possess primitive characteristics found in non-diadectid forms such as *Limnoscelis* and *Tseajaia*. Because *D. absitus* and *D. sanmiguelensis* were placed far from other species of *Diadectes* in the analysis, their assignment to the genus was questioned. The same results were found in the 2010 analysis. Two new genera were erected in the study to include *D. abstus* and *D. sanmiguelensis*. *D. sanmiguelensis*, the more basal of the two forms, was placed in the new genus *Oradectes*. *D. abstus* was renamed *Silvadectes*.

Paleobiology

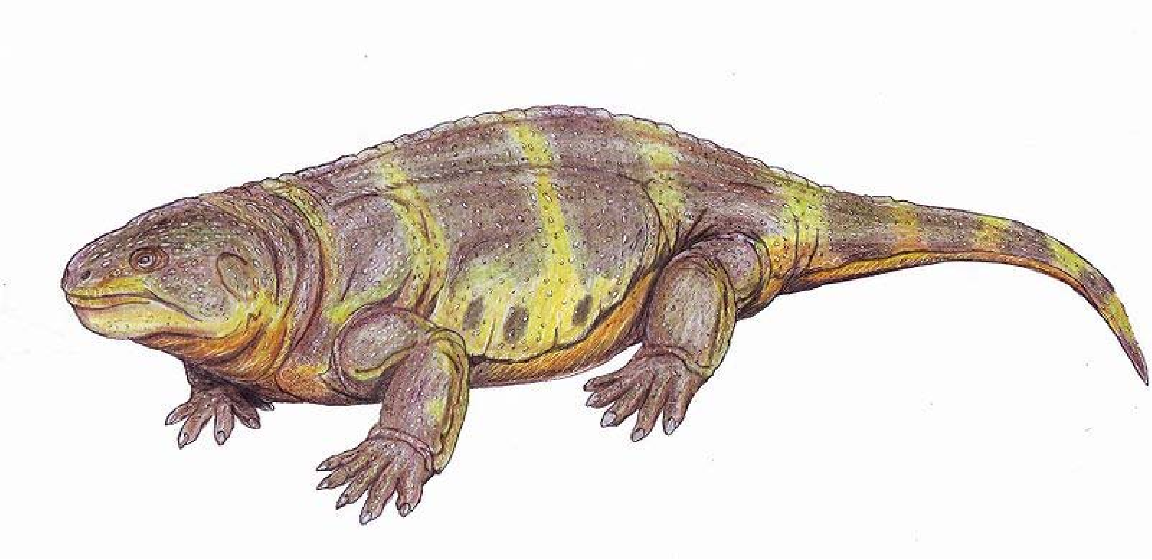
Locomotion

Diadectids were once thought to be sprawling animals with their short, robust legs positioned to the sides of their large bodies. Despite this, several lines of evidence including trackways and limb morphology suggest that diadectids moved in a more erect posture. While earlier tetrapods possess several simple tarsal bones in their ankles, diadectids have a more complex astragalus formed from the fusion of these bones. Astragali are present in terrestrial amniotes and are identical in structure to those of diadectids. Therefore, the ankle structure of diadectids bears a closer resemblance to those of advanced terrestrial vertebrates like mammals and reptiles than those of earlier tetrapods. Since diadectids are the only diadectomorphs with astragali, they likely developed the structure independent of amniotes.

Although they bear similarities to those of amniotes, the taral bones of diadectids are poorly ossified and loosely connected. The digits of the foot connect only to the fourth distal tarsal, providing a wide range of movement in the foot. This flexibility enabled diadectids to rotate their feet in a forward position while walking, providing greater force when pushing off. The feet could also be placed closer to the midline of the body to give diadectids an erect stance.

Evidence for an erect stance can be found in trackways attributed to diadectids. The most well-preserved of these trackways are present in the Tambach Formation in central Germany. A 2007 study identified two different ichnospecies, *Ichniotherium cottae* and *I. sphaerodactylum*, as footprints of the diadectids *Silvadectes absitus* and *Orobates pabsti*, respectively. This was the first species-level identification of trackmakers of Paleozoic-era trackways, making the footprints the oldest yet associated with specific animal species. The close positioning of the footprints suggests that the animals held their feet almost underneath their bodies, giving them a stance more like that of mammals than sprawling amphibians and reptiles.

Diet



Life restoration of *Diasparactus*

Diadectids were the first fully herbivorous tetrapods. Although several other groups of early tetrapods independently acquired herbivory, diadectids were the only Carboniferous tetrapods that were able to process high-fiber terrestrial plants. Diadectids were also the most diverse group of herbivores, representing the first radiation of plant-eating tetrapods. Both Cope and Marsh recognized that diadectids were herbivores in 1878 when they studied their distinctively broad, cusped teeth. In his description of *Diadectes*, Cope mentioned, "animals belonging to this genus were, in all probability, herbivorous."

Diadectids underwent an evolutionary radiation, diversifying into thirteen species in the Late Carboniferous and Early Permian, outnumbering other diadectomorphs such as the limnoscelids. This radiation was likely the result of diadectids' expansion into a new herbivorous ecological niche that was previously unfilled. While the distribution of limnoscelids is limited to parts of North America and *Tseajaia* is restricted to only the southwestern United States, diadectids are present in Europe and much of North America, occupying a much wider geographic range than other diadectids.

Chapter 12

Bird

Birds
Temporal range: Late Jurassic–Recent, 150–0 Ma

Representatives of 18 of the almost 30 living bird orders.

Scientific classification [e]	
Kingdom:	Animalia

Phylum:	Chordata
(unranked):	Reptiliomorpha
(unranked):	Amniota
(unranked):	Avialae
Class:	**Aves** Linnaeus, 1758

Subclasses & orders

- About two dozen modern orders and several extinct orders and subclasses

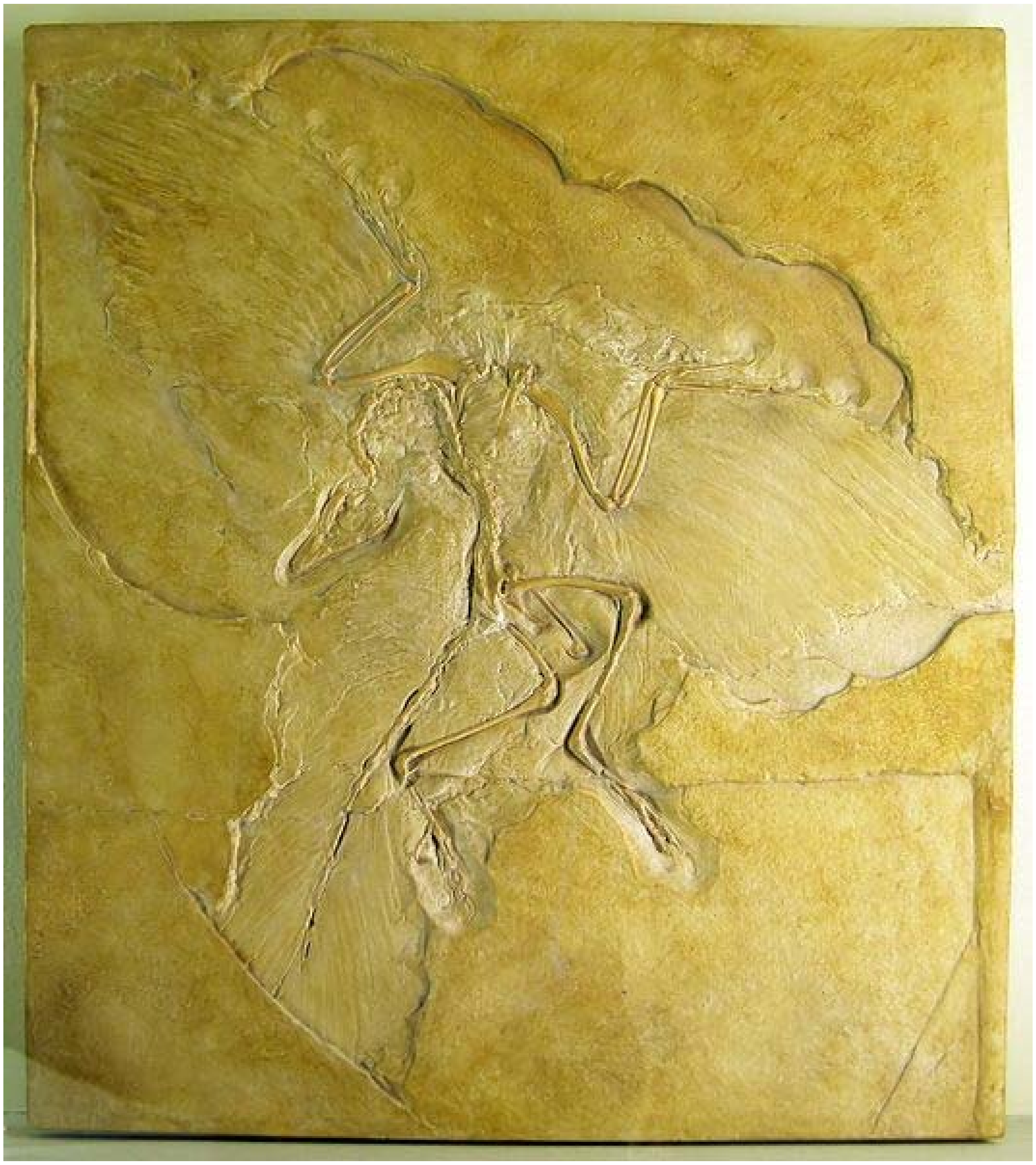
Birds (class **Aves**) are feathered, winged, bipedal, endothermic (warm-blooded), egg-laying, vertebrate animals. There are around 10,000 living species, making them the most speciose class of tetrapod vertebrates. They inhabit ecosystems across the globe, from the Arctic to the Antarctic. Extant birds range in size from the 5 cm (2 in) Bee Hummingbird to the 2.75 m (9 ft) Ostrich. The fossil record indicates that birds evolved from theropod dinosaurs during the Jurassic period, around 150–200 Ma (million years ago), and the earliest known bird is the Late Jurassic *Archaeopteryx*, *c* 150–145 Ma. Most paleontologists regard birds as the only clade of dinosaurs to have survived the Cretaceous–Tertiary extinction event approximately 65.5 Ma.

Modern birds are characterised by feathers, a beak with no teeth, the laying of hard-shelled eggs, a high metabolic rate, a four-chambered heart, and a lightweight but strong skeleton. All *living* species of birds have wings - the now extinct flightless Moa of New Zealand were the only exceptions. Wings are evolved forelimbs, and most bird species can fly, with some exceptions including ratites, penguins, and a number of diverse endemic island species. Birds also have unique digestive and respiratory systems that are highly adapted for flight. Some birds, especially corvids and parrots, are among the most intelligent animal species; a number of bird species have been observed manufacturing and using tools, and many social species exhibit cultural transmission of knowledge across generations.

Many species undertake long distance annual migrations, and many more perform shorter irregular movements. Birds are social; they communicate using visual signals and through calls and songs, and participate in social behaviours including cooperative breeding and hunting, flocking, and mobbing of predators. The vast majority of bird species are socially monogamous, usually for one breeding season at a time, sometimes for years, but rarely for life. Other species have breeding systems that are polygynous ("many females") or, rarely, polyandrous ("many males"). Eggs are usually laid in a nest and incubated by the parents. Most birds have an extended period of parental care after hatching.

Many species are of economic importance, mostly as sources of food acquired through hunting or farming. Some species, particularly songbirds and parrots, are popular as pets. Other uses include the harvesting of guano (droppings) for use as a fertiliser. Birds figure prominently in all aspects of human culture from religion to poetry to popular music. About 120–130 species have become extinct as a result of human activity since the 17th century, and hundreds more before then. Currently about 1,200 species of birds are threatened with extinction by human activities, though efforts are underway to protect them.

Evolution and taxonomy



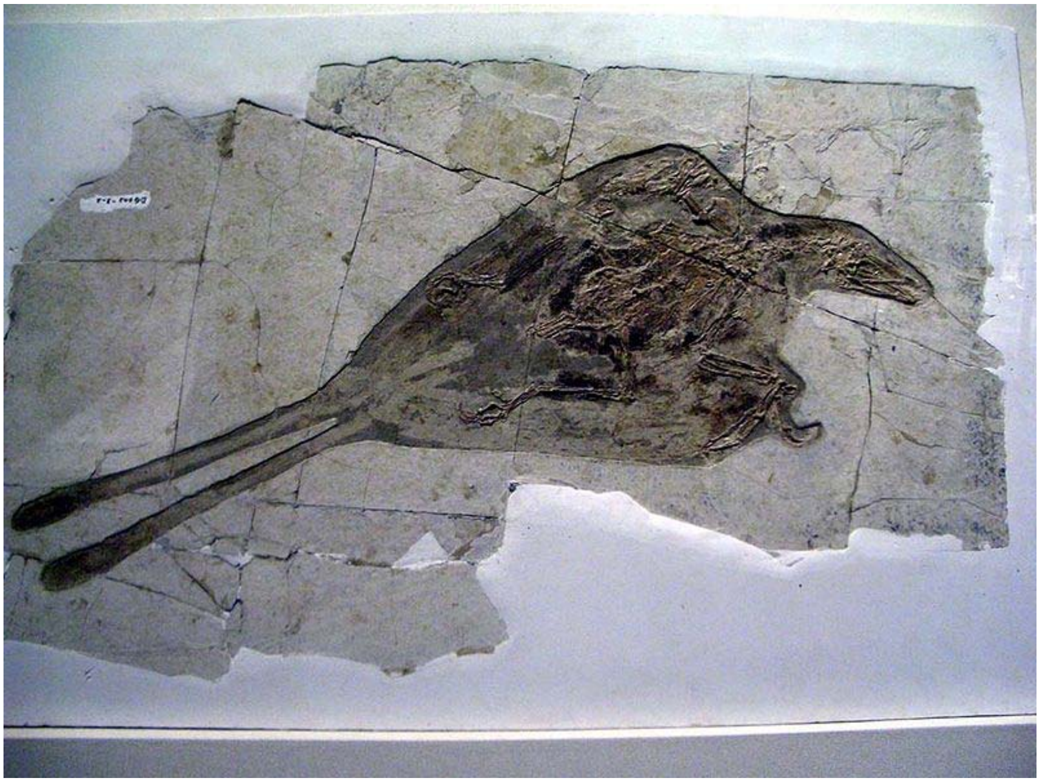
Archaeopteryx, the earliest known bird

The first classification of birds was developed by Francis Willughby and John Ray in their 1676 volume *Ornithologiae*. Carolus Linnaeus modified that work in 1758 to devise the taxonomic classification system currently in use. Birds are categorised as the biological class Aves in Linnaean taxonomy. Phylogenetic taxonomy places Aves in the dinosaur clade Theropoda. Aves and a sister group, the clade Crocodilia, contain the only living representatives of the reptile clade Archosauria. Phylogenetically, Aves is commonly defined as all descendants of the most recent common ancestor of modern birds and *Archaeopteryx lithographica*.

Archaeopteryx, from the Tithonian stage of the Late Jurassic (some 150–145 million years ago), is the earliest known bird under this definition. Others, including Jacques Gauthier and adherents of the Phylocode system, have defined Aves to include only the modern bird groups, the crown group. This has been done by excluding most groups known only from fossils, and assigning them, instead, to the Avialae in part to avoid the uncertainties about the placement of *Archaeopteryx* in relation to animals traditionally thought of as theropod dinosaurs.

All modern birds lie within the subclass Neornithes, which has two subdivisions: the Palaeognathae, containing birds that are flightless (like ostriches) or weak fliers, and the wildly diverse Neognathae, containing all other birds. These two subdivisions are often given the rank of superorder, although Livezey and Zusi assigned them "cohort" rank. Depending on the taxonomic viewpoint, the number of known living bird species varies anywhere from 9,800 to 10,050.

Dinosaurs and the origin of birds



Confuciusornis, a Cretaceous bird from China

Based on fossil and biological evidence, most scientists accept that birds are a specialized sub-group of theropod dinosaurs. More specifically, they are members of Maniraptora, a group of theropods which includes dromaeosaurs and oviraptorids, among others. As scientists discover more non-avian theropods that are closely related to birds, the previously clear distinction between non-birds and birds has become blurred. Recent discoveries in the Liaoning Province of northeast China, which demonstrate that many small theropod dinosaurs had feathers, contribute to this ambiguity.

The consensus view in contemporary paleontology is that the birds, Aves, are the closest relatives of the deinonychosaurs, which include dromaeosaurids and troodontids. Together, these three form a group called Paraves. The basal dromaeosaur *Microraptor* has features which may have enabled it to glide or fly. The most basal deinonychosaurs are very small. This evidence raises the possibility that the ancestor of all paravians may have been arboreal, may have been able to glide, or both.

The Late Jurassic *Archaeopteryx* is well-known as one of the first transitional fossils to be found and it provided support for the theory of evolution in the late 19th century. *Archaeopteryx* has clearly reptilian characteristics: teeth, clawed fingers, and a long, lizard-like tail, but it has finely preserved wings with flight feathers identical to those of modern birds. It is not considered a direct ancestor of modern birds, but is the oldest and most primitive known member of Aves or Avialae, and it is probably closely related to the real ancestor.

Alternative theories and controversies

There have been many controversies in the study of the origin of birds. Early disagreements included whether birds evolved from dinosaurs or more primitive archosaurs. Within the dinosaur camp there were disagreements as to whether ornithischian or theropod dinosaurs were the more likely ancestors. Although ornithischian (bird-hipped) dinosaurs share the hip structure of modern birds, birds are thought to have originated from the saurischian (lizard-hipped) dinosaurs, and therefore evolved their hip structure independently. In fact, a bird-like hip structure evolved a third time among a peculiar group of theropods known as the Therizinosauridae. A few scientists suggest that birds are not dinosaurs, but evolved from early archosaurs like *Longisquama*.

Early evolution of birds

Birds diversified into a wide variety of forms during the Cretaceous Period. Many groups retained primitive characteristics, such as clawed wings and teeth, though the latter were lost independently in a number of bird groups, including modern birds (Neornithes). While the earliest forms, such as *Archaeopteryx* and *Jeholornis*, retained the long bony tails of their ancestors, the tails of more advanced birds were shortened with the advent of the pygostyle bone in the clade Pygostylia.

The first large, diverse lineage of short-tailed birds to evolve were the Enantiornithes, or "opposite birds", so named because the construction of their shoulder bones was in reverse to that of modern birds. Enantiornithes occupied a wide array of ecological niches, from sand-probing shorebirds and fish-eaters to tree-dwelling forms and seed-eaters. More advanced lineages also specialised in eating fish, like the superficially gull-like subclass of Ichthyornithes ("fish birds").

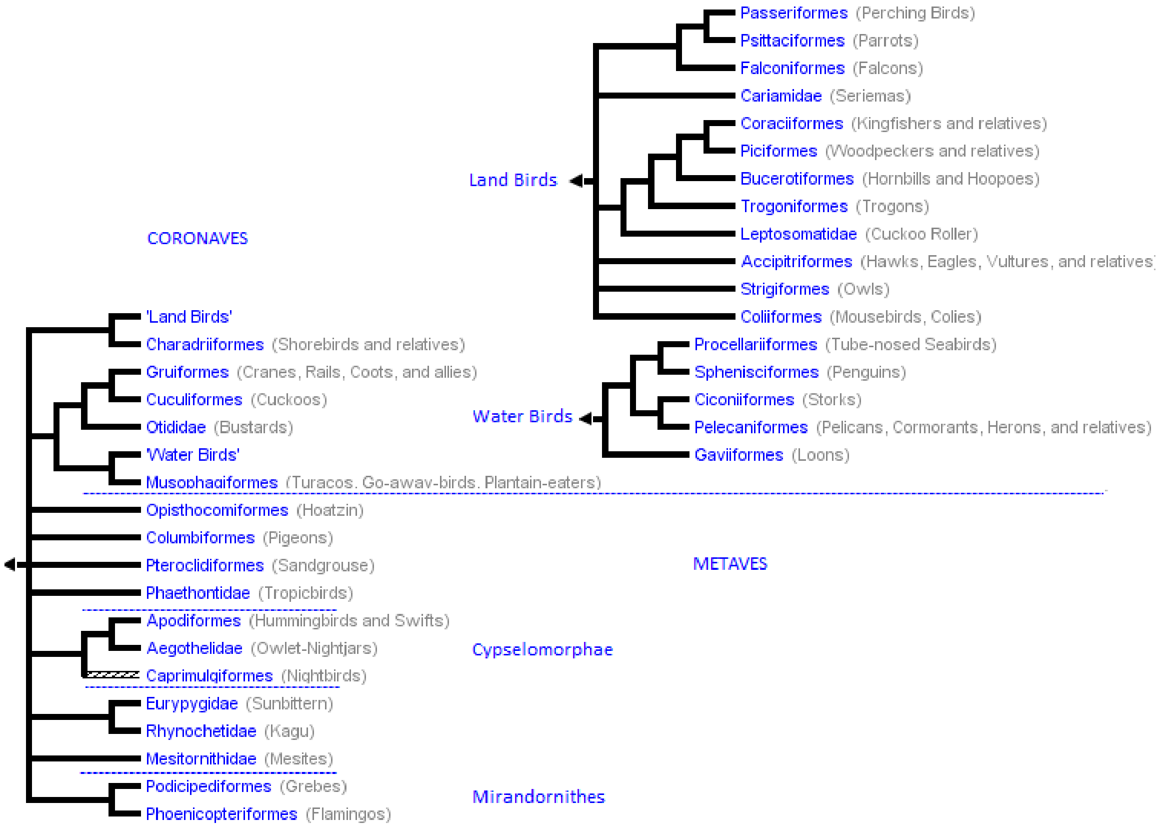
One order of Mesozoic seabirds, the Hesperornithiformes, became so well adapted to hunting fish in marine environments that they lost the ability to fly and became primarily aquatic. Despite their extreme specializations, the Hesperornithiformes represent some of the closest relatives of modern birds.

Diversification of modern birds

Containing all modern birds, the subclass Neornithes is, due to the discovery of *Vegavis*, now known to have evolved into some basic lineages by the end of the Cretaceous and is split into two superorders, the Palaeognathae and Neognathae. The paleognaths include the tinamous of Central and South America and the ratites. The basal divergence from the remaining Neognathes was that of the Galloanserae, the superorder containing the Anseriformes (ducks, geese, swans and screamers) and the Galliformes (the pheasants, grouse, and their allies, together with the mound builders and the guans and their allies). The dates for the splits are much debated by scientists. It is agreed that the Neornithes evolved in the Cretaceous, and that the split between the Galloanseri from other Neognathes occurred before the K–T extinction event, but there are different opinions about whether the radiation of the remaining Neognathes occurred before or after the extinction of the other dinosaurs. This disagreement is in part caused by a divergence in the evidence; molecular dating suggests a Cretaceous radiation, while fossil evidence supports a Tertiary radiation. Attempts to reconcile the molecular and fossil evidence have proved controversial.

The classification of birds is a contentious issue. Sibley and Ahlquist's *Phylogeny and Classification of Birds* (1990) is a landmark work on the classification of birds, although it is frequently debated and constantly revised. Most evidence seems to suggest that the assignment of orders is accurate, but scientists disagree about the relationships between the orders themselves; evidence from modern bird anatomy, fossils and DNA have all been brought to bear on the problem, but no strong consensus has emerged. More recently, new fossil and molecular evidence is providing an increasingly clear picture of the evolution of modern bird orders.

Modern bird orders: Classification



Cladogram showing the most recent classification of Neoaves, based on several phylogenetic studies.

This is a list of the taxonomic orders in the subclass Neornithes, or modern birds. This list uses the traditional classification (the so-called Clements order), revised by the Sibley-Monroe classification. The list of birds gives a more detailed summary of the orders, including families.

Subclass Neornithes
The subclass Neornithes has two superorders –

Superorder Palaeognathae:

The name of the superorder is derived from 'paleognath', the ancient Greek for "old jaws" in reference to the skeletal anatomy of the palate, which is described as more primitive and reptilian than that in other birds. The Palaeognathae consists of two orders which comprise 49 existing species.

- Struthioniformes—ostriches, emus, kiwis, and allies

- Tinamiformes—tinamous

Superorder Neognathae:

The superorder Neognathae comprises 27 orders which have a total of nearly ten thousand species. The Neognathae have undergone adaptive radiation to produce the staggering diversity of form (especially of the bill and feet), function, and behavior that are seen today.

The orders comprising the Neognathae are:

Moa attacked by a Haast's Eagle

- Anseriformes—waterfowl
- Galliformes—fowl
- Charadriiformes—gulls, button-quails, plovers and allies
- Gaviiformes—loons
- Podicipediformes—grebes
- Procellariiformes—albatrosses, petrels, and allies
- Sphenisciformes—penguins

- Pelecaniformes—pelicans and allies
- Phaethontiformes—tropicbirds
- Ciconiiformes—storks and allies
- Cathartiformes—New World vultures
- Phoenicopteriformes—flamingos
- Falconiformes—falcons, eagles, hawks and allies
- Gruiformes—cranes and allies
- Pteroclidiformes—sandgrouse
- Columbiformes—doves and pigeons
- Psittaciformes—parrots and allies
- Cuculiformes—cuckoos and turacos
- Opisthocomiformes—hoatzin
- Strigiformes—owls
- Caprimulgiformes—nightjars and allies
- Apodiformes—swifts and hummingbirds
- Coraciiformes—kingfishers and allies
- Piciformes—woodpeckers and allies
- Trogoniformes—trogons
- Coliiformes—mousebirds
- Passeriformes—passerines

The radically different Sibley-Monroe classification (Sibley-Ahlquist taxonomy), based on molecular data, found widespread adoption in a few aspects, as recent molecular, fossil, and anatomical evidence supported the Galloanserae.

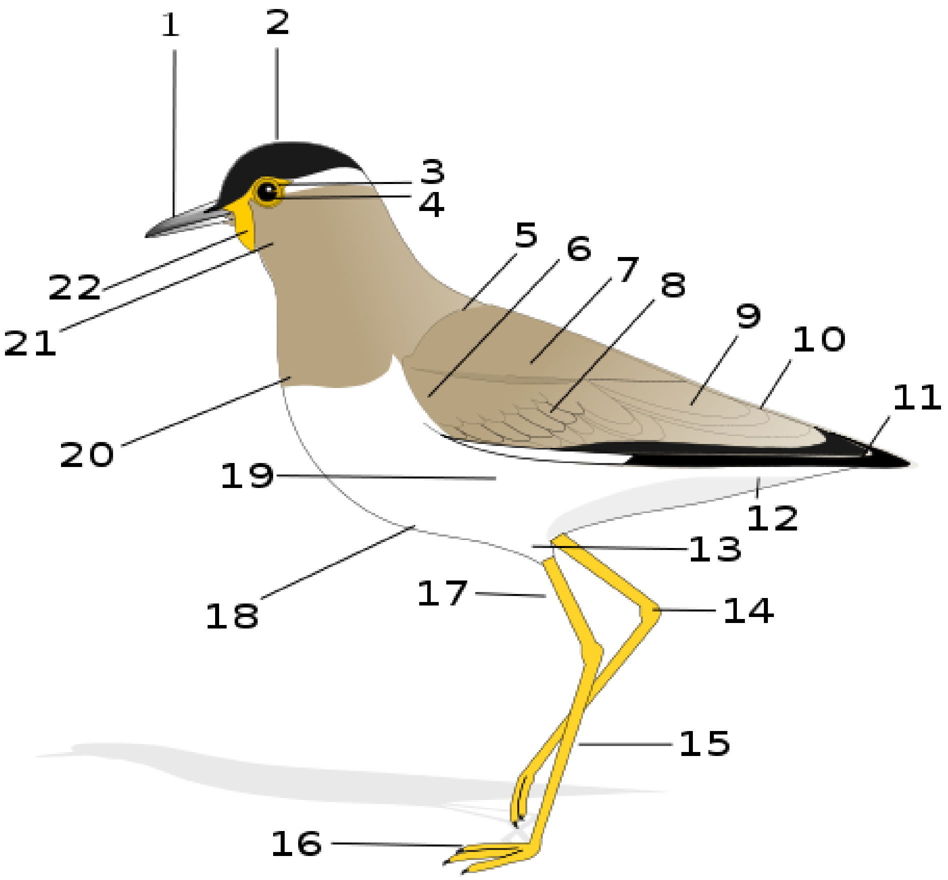
Distribution

The range of the House Sparrow has expanded dramatically due to human activities.

Birds live and breed in most terrestrial habitats and on all seven continents, reaching their southern extreme in the Snow Petrel's breeding colonies up to 440 kilometres (270 mi) inland in Antarctica. The highest bird diversity occurs in tropical regions. It was earlier thought that this high diversity was the result of higher speciation rates in the tropics, however recent studies found higher speciation rates in the high latitudes that were offset by greater extinction rates than in the tropics. Several families of birds have adapted to life both on the world's oceans and in them, with some seabird species coming ashore only to breed and some penguins have been recorded diving up to 300 metres (980 ft).

Many bird species have established breeding populations in areas to which they have been introduced by humans. Some of these introductions have been deliberate; the Ring-necked Pheasant, for example, has been introduced around the world as a game bird. Others have been accidental, such as the establishment of wild Monk Parakeets in several North American cities after their escape from captivity. Some species, including Cattle Egret, Yellow-headed Caracara and Galah, have spread naturally far beyond their original ranges as agricultural practices created suitable new habitat.

Anatomy and physiology



External anatomy of a bird: 1 Beak, 2 Head, 3 Iris, 4 Pupil, 5 Mantle, 6 Lesser coverts, 7 Scapulars, 8 Median coverts, 9 Tertials, 10 Rump, 11 Primaries, 12 Vent, 13 Thigh, 14 Tibio-tarsal articulation, 15 Tarsus, 16 Foot, 17 Tibia, 18 Belly, 19 Flanks, 20 Breast, 21 Throat, 22 Wattle

Compared with other vertebrates, birds have a body plan that shows many unusual adaptations, mostly to facilitate flight.

The skeleton consists of very lightweight bones. They have large air-filled cavities (called pneumatic cavities) which connect with the respiratory system. The skull bones in adults are fused and do not show cranial sutures. The orbits are large and separated by a bony septum. The spine has cervical, thoracic, lumbar and caudal regions with the number of cervical (neck) vertebrae highly variable and especially flexible, but movement is reduced in the anterior thoracic vertebrae and absent in the later vertebrae. The last few are fused with the pelvis to form the synsacrum. The ribs are flattened and the sternum is keeled for the attachment of flight muscles except in the flightless bird orders. The forelimbs are modified into wings.

Like the reptiles, birds are primarily uricotelic, that is, their kidneys extract nitrogenous wastes from their bloodstream and excrete it as uric acid instead of urea or ammonia via the ureters into the intestine. Birds do not have a urinary bladder or external urethral opening and (with exception of the Ostrich) uric acid is excreted along with feces as a semisolid waste. However, birds such as hummingbirds can be facultatively ammonotelic, excreting most of the nitrogenous wastes as ammonia. They also excrete creatine, rather than creatinine like mammals. This material, as well as the output of the intestines, emerges from the bird's cloaca. The cloaca is a multi-purpose opening: waste is expelled through it, birds mate by joining cloaca, and females lay eggs from it. In addition, many species of birds regurgitate pellets. The digestive system of birds is unique, with a crop for storage and a gizzard that contains swallowed stones for grinding food to compensate for the lack of teeth. Most birds are highly adapted for rapid digestion to aid with flight. Some migratory birds have adapted to use protein from many parts of their bodies, including protein from the intestines, as additional energy during migration.

Birds have one of the most complex respiratory systems of all animal groups. Upon inhalation, 75% of the fresh air bypasses the lungs and flows directly into a posterior air sac which extends from the lungs and connects with air spaces in the bones and fills them with air. The other 25% of the air goes directly into the lungs. When the bird exhales, the used air flows out of the lung and the stored fresh air from the posterior air sac is simultaneously forced into the lungs. Thus, a bird's lungs receive a constant supply of fresh air during both inhalation and exhalation. Sound production is achieved using the syrinx, a muscular chamber incorporating multiple tympanic membranes which diverges from the lower end of the trachea. The bird's heart has four chambers and the right aortic arch gives rise to systemic circulation (unlike in the mammals where the left arch is involved). The postcava receives blood from the limbs via the renal portal system. Unlike in mammals, the red blood cells in birds have a nucleus.

The nictitating membrane as it covers the eye of a Masked Lapwing

The nervous system is large relative to the bird's size. The most developed part of the brain is the one that controls the flight-related functions, while the cerebellum coordinates movement and the cerebrum controls behaviour patterns, navigation, mating and nest building. Most birds have a poor sense of smell with notable exceptions including kiwis, New World vultures and tubenoses. The avian visual system is usually highly developed. Water birds have special flexible lenses, allowing accommodation for vision in air and water. Some species also have dual fovea. Birds are tetrachromatic, possessing ultraviolet (UV) sensitive cone cells in the eye as well as green, red and blue ones. This allows them to perceive ultraviolet light, which is involved in courtship. Many birds show plumage patterns in ultraviolet that are invisible to the human eye; some birds whose sexes appear similar to the naked eye are distinguished by the presence of ultraviolet reflective patches on their feathers. Male Blue Tits have an ultraviolet reflective crown patch which is displayed in courtship by posturing and raising of their nape feathers. Ultraviolet light is also used in foraging—kestrels have been shown to search for prey by detecting the UV reflective urine trail marks left on the ground by rodents. The eyelids of a bird are not used in blinking. Instead the eye is lubricated by the nictitating membrane, a third eyelid that moves horizontally. The nictitating membrane also covers the eye and acts as a contact lens in many aquatic birds. The bird retina has a fan shaped blood supply system called the pecten. Most birds cannot move their eyes, although there are exceptions, such as the Great Cormorant. Birds with eyes on the sides of their heads have a wide visual field, while birds with eyes on the front of their heads, such as owls, have binocular vision and can estimate the depth of field. The avian ear lacks external pinnae but is covered by feathers, although in some birds, such as the *Asio*, *Bubo* and *Otus* owls, these feathers form tufts which resemble ears. The inner ear has a cochlea, but it is not spiral as in mammals.

A few species are able to use chemical defenses against predators; some Procellariiformes can eject an unpleasant oil against an aggressor, and some species of pitohuis from New Guinea have a powerful neurotoxin in their skin and feathers.

Chromosomes

Birds have two sexes: male and female. The sex of birds is determined by the Z and W sex chromosomes, rather than by the X and Y chromosomes present in mammals. Male birds have two Z chromosomes (ZZ), and female birds have a W chromosome and a Z chromosome (WZ).

In nearly all species of birds, an individual's sex is determined at fertilization. However, one recent study demonstrated temperature-dependent sex determination among Australian Brush-turkeys, for which higher temperatures during incubation resulted in a higher female-to-male sex ratio.

Feathers, plumage, and scales

The plumage of the African Scops Owl allows it to blend in with its surroundings.

Feathers are a feature characteristic of birds (though also present in some dinosaurs not currently considered to be true birds). They facilitate flight, provide insulation that aids in thermoregulation, and are used in display, camouflage, and signaling. There are several types of feathers, each serving its own set of purposes. Feathers are epidermal growths attached to the skin and arise only in specific tracts of skin called pterylae. The distribution pattern of these feather tracts (pterylosis) is used in taxonomy and systematics. The arrangement and appearance of feathers on the body, called plumage, may vary within species by age, social status, and sex.

Plumage is regularly moulted; the standard plumage of a bird that has moulted after breeding is known as the "non-breeding" plumage, or – in the Humphrey-Parkes terminology – "basic" plumage; breeding plumages or variations of the basic plumage are known under the Humphrey-Parkes system as "alternate" plumages. Moulting is annual in most species, although some may have two moults a year, and large birds of prey may moult only once every few years. Moulting patterns vary across species. In passerines, flight feathers are replaced one at a time with the innermost primary being the first. When the fifth of sixth primary is replaced, the outermost tertiaries begin to drop. After the innermost tertiaries are moulted, the secondaries starting from the innermost begin to drop and this proceeds to the outer feathers (centrifugal moult). The greater primary coverts are moulted in synchrony with the primary that they overlap. A small number of species, such as ducks and geese, lose all of their flight feathers at once, temporarily becoming flightless. As a general rule, the tail feathers are moulted and replaced starting with the innermost pair. Centripetal moults of tail feathers are however seen in the Phasianidae. The centrifugal moult is modified in the tail feathers of woodpeckers and treecreepers, in that it begins with the second innermost pair of feathers and finishes with the central pair of feathers so that the bird maintains a functional climbing tail. The general pattern seen in passerines is that the primaries are replaced outward, secondaries inward, and the tail from center outward. Before nesting, the females of most bird species gain a bare brood patch by losing feathers close to the belly. The skin there is well supplied with blood vessels and helps the bird in incubation.

Red Lory preening

Feathers require maintenance and birds preen or groom them daily, spending an average of around 9% of their daily time on this. The bill is used to brush away foreign particles and to apply waxy secretions from the uropygial gland; these secretions protect the feathers' flexibility and act as an antimicrobial agent, inhibiting the growth of feather-degrading bacteria. This may be supplemented with the secretions of formic acid from ants, which birds receive through a behaviour known as anting, to remove feather parasites.

The scales of birds are composed of the same keratin as beaks, claws, and spurs. They are found mainly on the toes and metatarsus, but may be found further up on the ankle in some birds. Most bird scales do not overlap significantly, except in the cases of kingfishers and woodpeckers. The scales of birds are thought to be homologous to those of reptiles and mammals.

Flight

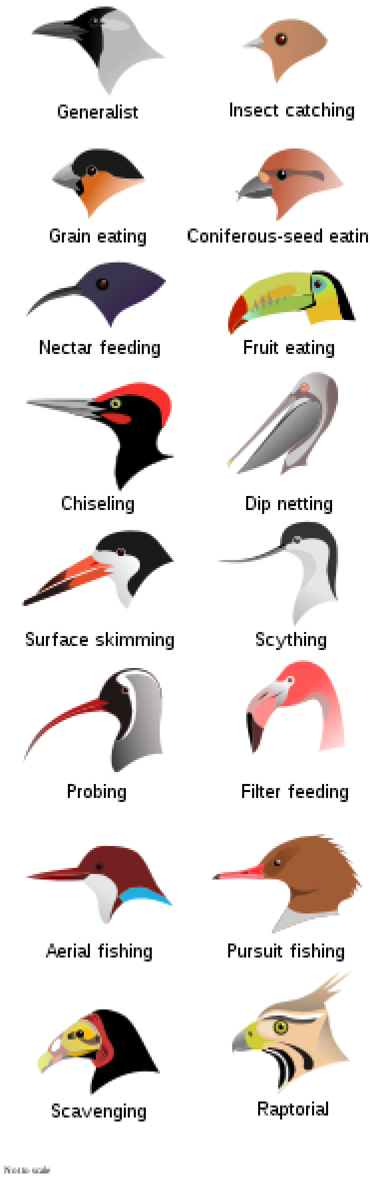
Restless Flycatcher in the downstroke of flapping flight

Most birds can fly, which distinguishes them from almost all other vertebrate classes. Flight is the primary means of locomotion for most bird species and is used for breeding, feeding, and predator avoidance and escape. Birds have various adaptations for flight, including a lightweight skeleton, two large flight muscles, the pectoralis (which accounts for 15% of the total mass of the bird) and the supracoracoideus, as well as a modified forelimb (wing) that serves as an aerofoil. Wing shape and size generally determine a bird species' type of flight; many birds combine powered, flapping flight with less energy-intensive soaring flight. About 60 extant bird species are flightless, as were many extinct birds. Flightlessness often arises in birds on isolated islands, probably due to limited resources and the absence of land predators. Though flightless, penguins use similar musculature and movements to "fly" through the water, as do auks, shearwaters and dippers.

Behaviour

Most birds are diurnal, but some birds, such as many species of owls and nightjars, are nocturnal or crepuscular (active during twilight hours), and many coastal waders feed when the tides are appropriate, by day or night.

Diet and feeding



Feeding adaptations in beaks

Birds' diets are varied and often include nectar, fruit, plants, seeds, carrion, and various small animals, including other birds. Because birds have no teeth, their digestive system is adapted to process unmasticated food items that are swallowed whole.

Birds that employ many strategies to obtain food or feed on a variety of food items are called generalists, while others that concentrate time and effort on specific food items or have a single strategy to obtain food are considered specialists. Birds' feeding strategies vary by species. Many birds glean for insects, invertebrates, fruit, or seeds. Some hunt insects by suddenly attacking from a branch. Those species that seek pest insects are considered beneficial 'biological control agents' and their presence encouraged in biological pest control programs. Nectar feeders such as hummingbirds, sunbirds, lories, and lorikeets amongst others have specially adapted brushy tongues and in many cases bills designed to fit co-adapted flowers. Kiwis and shorebirds with long bills probe for invertebrates; shorebirds' varied bill lengths and feeding methods result in the separation of ecological niches. Loons, diving ducks, penguins and auks pursue their prey underwater, using their wings or feet for propulsion, while aerial predators such as sulids, kingfishers and terns plunge dive after their prey. Flamingos, three species of prion, and some ducks are filter feeders. Geese and dabbling ducks are primarily grazers.

Some species, including frigatebirds, gulls, and skuas, engage in kleptoparasitism, stealing food items from other birds. Kleptoparasitism is thought to be a supplement to food obtained by hunting, rather than a significant part of any species' diet; a study of Great Frigatebirds stealing from Masked Boobies estimated that the frigatebirds stole at most 40% of their food and on average stole only 5%. Other birds are scavengers; some of these, like vultures, are specialised carrion eaters, while others, like gulls, corvids, or other birds of prey, are opportunists.

Water and drinking

Water is needed by many birds although their mode of excretion and lack of sweat glands reduces the physiological demands. Some desert birds can obtain their water needs entirely from moisture in their food. They may also have other adaptations such as allowing their body temperature to rise, saving on moisture loss from evaporative cooling or panting. Seabirds can drink seawater and have salt glands inside the head that eliminate excess salt out of the nostrils.

Most birds scoop water in their beaks and raise their head to let water run down the throat. Some species, especially of arid zones, belonging to the pigeon, finch, mousebird, button-quail and bustard families are capable of sucking up water without the need to tilt back their heads. Some desert birds depend on water sources and sandgrouse are particularly well-known for their daily congregations at waterholes. Nesting sandgrouse and many plovers carry water to their young by wetting their belly feathers. Some birds carry water for chicks at the nest in their crop or regurgitate it along with food. The pigeon family, flamingos and penguins have adaptations to produce a nutritive fluid called crop milk that they provide to their chicks.

Migration

Many bird species migrate to take advantage of global differences of seasonal temperatures, therefore optimising availability of food sources and breeding habitat. These migrations vary among the different groups. Many landbirds, shorebirds, and waterbirds undertake annual long distance migrations, usually triggered by the length of daylight as well as weather conditions. These birds are characterised by a breeding season spent in the temperate or arctic/antarctic regions and a non-breeding season in the tropical regions or opposite hemisphere. Before migration, birds substantially increase body fats and reserves and reduce the size of some of their organs. Migration is highly demanding energetically, particularly as birds need to cross deserts and oceans without refuelling. Landbirds have a flight range of around 2,500 km (1,600 mi) and shorebirds can fly up to 4,000 km (2,500 mi), although the Bar-tailed Godwit is capable of non-stop flights of up to 10,200 km (6,300 mi). Seabirds also undertake long migrations, the longest annual migration being those of Sooty Shearwaters, which nest in New Zealand and Chile and spend the northern summer feeding in the North Pacific off Japan, Alaska and California, an annual round trip of 64,000 km (39,800 mi). Other seabirds disperse after breeding, travelling widely but having no set migration route. Albatrosses nesting in the Southern Ocean often undertake circumpolar trips between breeding seasons.

The routes of satellite-tagged Bar-tailed Godwits migrating north from New Zealand. This species has the longest known non-stop migration of any species, up to 10,200 km (6,300 mi).

Some bird species undertake shorter migrations, travelling only as far as is required to avoid bad weather or obtain food. Irruptive species such as the boreal finches are one such group and can commonly be found at a location in one year and absent the next. This type of migration is normally associated with food availability. Species may also travel shorter distances over part of their range, with individuals from higher latitudes travelling into the existing range of conspecifics; others undertake partial migrations, where only a fraction of the population, usually females and subdominant males, migrates. Partial migration can form a large percentage of the migration behaviour of birds in some regions; in Australia, surveys found that 44% of non-passerine birds and 32% of passerines were partially migratory. Altitudinal migration is a form of short distance migration in which birds spend the breeding season at higher altitudes elevations and move to lower ones during suboptimal conditions. It is most often triggered by temperature changes and usually occurs when the normal territories also become inhospitable due to lack of food. Some species may also be nomadic, holding no fixed territory and moving according to weather and food availability. Parrots as a family are overwhelmingly neither migratory nor sedentary but considered to either be dispersive, irruptive, nomadic or undertake small and irregular migrations.

The ability of birds to return to precise locations across vast distances has been known for some time; in an experiment conducted in the 1950s a Manx Shearwater released in Boston returned to its colony in Skomer, Wales, within 13 days, a distance of 5,150 km (3,200 mi). Birds navigate during migration using a variety of methods. For diurnal migrants, the sun is used to navigate by day, and a stellar compass is used at night. Birds that use the sun compensate for the changing position of the sun during the day by the use of an internal clock. Orientation with the stellar compass depends on the position of the constellations surrounding Polaris. These are backed up in some species by their ability to sense the Earth's geomagnetism through specialised photoreceptors.

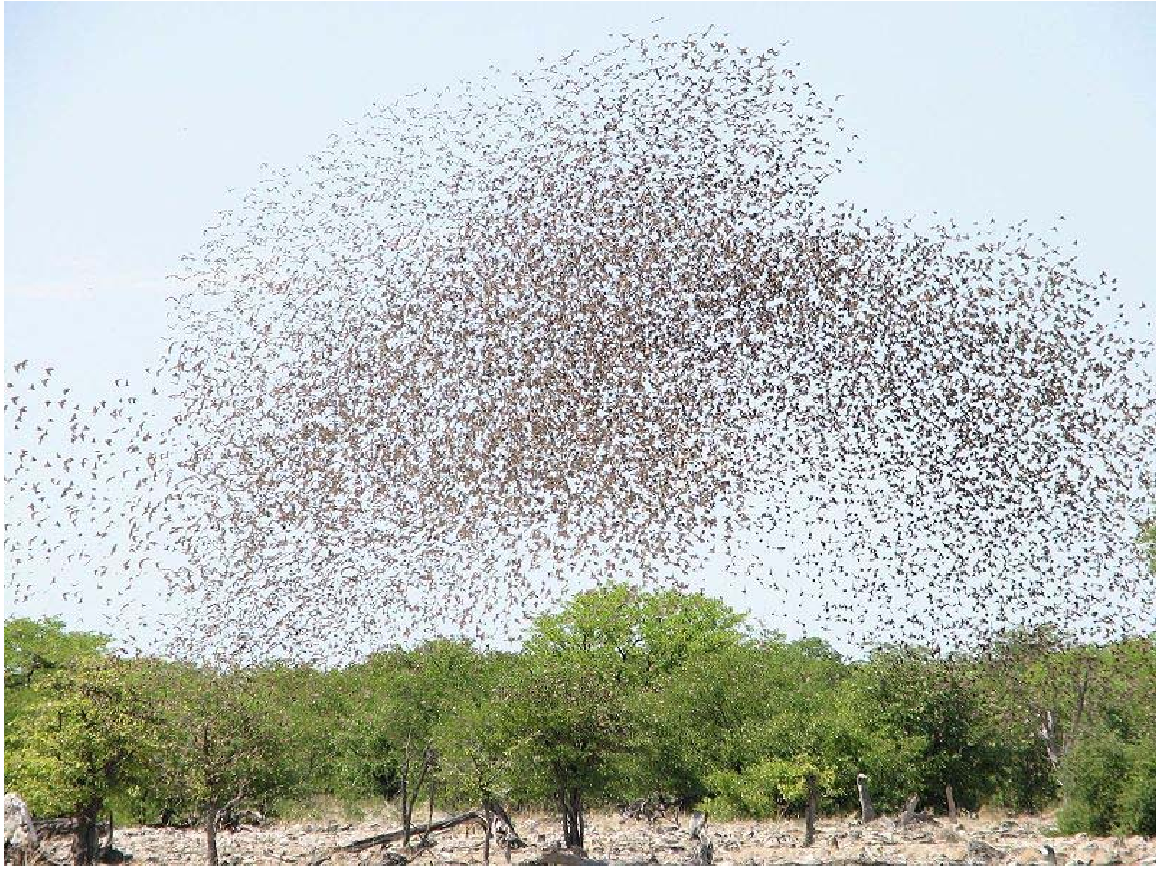
Communication

The startling display of the Sunbittern mimics a large predator.

Birds communicate using primarily visual and auditory signals. Signals can be interspecific (between species) and intraspecific (within species).

Birds sometimes use plumage to assess and assert social dominance, to display breeding condition in sexually selected species, or to make threatening displays, as in the Sunbittern's mimicry of a large predator to ward off hawks and protect young chicks. Variation in plumage also allows for the identification of birds, particularly between species. Visual communication among birds may also involve ritualised displays, which have developed from non-signalling actions such as preening, the adjustments of feather position, pecking, or other behaviour. These displays may signal aggression or submission or may contribute to the formation of pair-bonds. The most elaborate displays occur during courtship, where "dances" are often formed from complex combinations of many possible component movements; males' breeding success may depend on the quality of such displays.

Bird calls and songs, which are produced in the syrinx, are the major means by which birds communicate with sound. This communication can be very complex; some species can operate the two sides of the syrinx independently, allowing the simultaneous production of two different songs. Calls are used for a variety of purposes, including mate attraction, evaluation of potential mates, bond formation, the claiming and maintenance of territories, the identification of other individuals (such as when parents look for chicks in colonies or when mates reunite at the start of breeding season), and the warning of other birds of potential predators, sometimes with specific information about the nature of the threat. Some birds also use mechanical sounds for auditory communication. The *Coenocorypha* snipes of New Zealand drive air through their feathers, woodpeckers drum territorially, and Palm Cockatoos use tools to drum.



Red-billed Queleas, the most numerous species of bird, form enormous flocks—sometimes tens of thousands strong.

Flocking and other associations

While some birds are essentially territorial or live in small family groups, other birds may form large flocks. The principal benefits of flocking are safety in numbers and increased foraging efficiency. Defence against predators is particularly important in closed habitats like forests, where ambush predation is common and multiple eyes can provide a valuable early warning system. This has led to the development of many mixed-species feeding flocks, which are usually composed of small numbers of many species; these flocks provide safety in numbers but reduce potential competition for resources. Costs of flocking include bullying of socially subordinate birds by more dominant birds and the reduction of feeding efficiency in certain cases.

Birds sometimes also form associations with non-avian species. Plunge-diving seabirds associate with dolphins and tuna, which push shoaling fish towards the surface. Hornbills have a mutualistic relationship with Dwarf Mongooses, in which they forage together and warn each other of nearby birds of prey and other predators.

Resting and roosting

Many birds, like this American Flamingo, tuck their head into their back when sleeping

The high metabolic rates of birds during the active part of the day is supplemented by rest at other times. Sleeping birds often use a type of sleep known as vigilant sleep, where periods of rest are interspersed with quick eye-opening 'peeks', allowing them to be sensitive to disturbances and enable rapid escape from threats. Swifts are believed to be able to sleep in flight and radar observations suggest that they orient themselves to face the wind in their roosting flight. It has been suggested that there may be certain kinds of sleep which are possible even when in flight. Some birds have also demonstrated the capacity to fall into slow-wave sleep one hemisphere of the brain at a time. The birds tend to exercise this ability depending upon its position relative to the outside of the flock. This may allow the eye opposite the sleeping hemisphere to remain vigilant for predators by viewing the outer margins of the flock. This adaptation is also known from marine mammals. Communal roosting is common because it lowers the loss of body heat and decreases the risks associated with predators. Roosting sites are often chosen with regard to thermoregulation and safety.

Many sleeping birds bend their heads over their backs and tuck their bills in their back feathers, although others place their beaks among their breast feathers. Many birds rest on one leg, while some may pull up their legs into their feathers, especially in cold weather. Perching birds have a tendon locking mechanism that helps them hold on to the perch when they are asleep. Many ground birds, such as quails and pheasants, roost in trees. A few parrots of the genus *Loriculus* roost hanging upside down. Some hummingbirds go into a nightly state of torpor accompanied with a reduction of their metabolic rates. This physiological adaptation shows in nearly a hundred other species, including owlet-nightjars, nightjars, and woodswallows. One species, the Common Poorwill, even enters a state of hibernation. Birds do not have sweat glands, but they may cool themselves by moving to shade, standing in water, panting, increasing their surface area, fluttering their throat or by using special behaviours like urohidrosis to cool themselves.

Breeding

Social systems

Like others of its family the male Raggiana Bird of Paradise has elaborate breeding plumage used to impress females.

Ninety-five percent of bird species are socially monogamous. These species pair for at least the length of the breeding season or—in some cases—for several years or until the death of one mate. Monogamy allows for biparental care, which is especially important for species in which females require males' assistance for successful brood-rearing. Among many socially monogamous species, extra-pair copulation (infidelity) is common. Such behaviour typically occurs between dominant males and females paired with subordinate males, but may also be the result of forced copulation in ducks and other anatids. For females, possible benefits of extra-pair copulation include getting better genes for her offspring and insuring against the possibility of infertility in her mate. Males of species that engage in extra-pair copulations will closely guard their mates to ensure the parentage of the offspring that they raise.

Other mating systems, including polygyny, polyandry, polygamy, polygynandry, and promiscuity, also occur. Polygamous breeding systems arise when females are able to raise broods without the help of males. Some species may use more than one system depending on the circumstances.

Breeding usually involves some form of courtship display, typically performed by the male. Most displays are rather simple and involve some type of song. Some displays, however, are quite elaborate. Depending on the species, these may include wing or tail drumming, dancing, aerial flights, or communal lekking. Females are generally the ones that drive partner selection, although in the polyandrous phalaropes, this is reversed: plainer males choose brightly coloured females. Courtship feeding, billing and allopreening are commonly performed between partners, generally after the birds have paired and mated.

Territories, nesting and incubation

Many birds actively defend a territory from others of the same species during the breeding season; maintenance of territories protects the food source for their chicks. Species that are unable to defend feeding territories, such as seabirds and swifts, often breed in colonies instead; this is thought to offer protection from predators. Colonial breeders defend small nesting sites, and competition between and within species for nesting sites can be intense.

Male Common Blackbird (*Turdus merula*) feeding its chicks

All birds lay amniotic eggs with hard shells made mostly of calcium carbonate. Hole and burrow nesting species tend to lay white or pale eggs, while open nesters lay camouflaged eggs. There are many exceptions to this pattern, however; the ground-nesting nightjars have pale eggs, and camouflage is instead provided by their plumage. Species that are victims of brood parasites have varying egg colours to improve the chances of spotting a parasite's egg, which forces female parasites to match their eggs to those of their hosts.

Male Golden-backed Weavers construct elaborate suspended nests out of grass

Bird eggs are usually laid in a nest. Most species create somewhat elaborate nests, which can be cups, domes, plates, beds scrapes, mounds, or burrows. Some bird nests, however, are extremely primitive; albatross nests are no more than a scrape on the ground. Most birds build nests in sheltered, hidden areas to avoid predation, but large or colonial birds—which are more capable of defence—may build more open nests. During nest construction, some species seek out plant matter from plants with parasite-reducing toxins to improve chick survival, and feathers are often used for nest insulation. Some bird species have no nests; the cliff-nesting Common Guillemot lays its eggs on bare rock, and male Emperor Penguins keep eggs between their body and feet. The absence of nests is especially prevalent in ground-nesting species where the newly hatched young are precocial.

Nest of an Eastern Phoebe that has been parasitised by a Brown-headed Cowbird

Incubation, which optimises temperature for chick development, usually begins after the last egg has been laid. In monogamous species incubation duties are often shared, whereas in polygamous species one parent is wholly responsible for incubation. Warmth from parents passes to the eggs through brood patches, areas of bare skin on the abdomen or breast of the incubating birds. Incubation can be an energetically demanding process; adult albatrosses, for instance, lose as much as 83 grams (2.9 oz) of body weight per day of incubation. The warmth for the incubation of the eggs of megapodes comes from the sun, decaying vegetation or volcanic sources. Incubation periods range from 10 days (in woodpeckers, cuckoos and passerine birds) to over 80 days (in albatrosses and kiwis).

Parental care and fledging

At the time of their hatching, chicks range in development from helpless to independent, depending on their species. Helpless chicks are termed *altricial*, and tend to be born small, blind, immobile and naked; chicks that are mobile and feathered upon hatching are termed *precocial*. Altricial chicks need help thermoregulating and must be brooded for longer than precocial chicks. Chicks at neither of these extremes can be semi-precocial or semi-altricial.

A female Calliope Hummingbird feeding fully grown chicks

The length and nature of parental care varies widely amongst different orders and species. At one extreme, parental care in megapodes ends at hatching; the newly hatched chick digs itself out of the nest mound without parental assistance and can fend for itself immediately. At the other extreme, many seabirds have extended periods of parental care, the longest being that of the Great Frigatebird, whose chicks take up to six months to fledge and are fed by the parents for up to an additional 14 months.

In some species, both parents care for nestlings and fledglings; in others, such care is the responsibility of only one sex. In some species, other members of the same species—usually close relatives of the breeding pair, such as offspring from previous broods—will help with the raising of the young. Such alloparenting is particularly common among the Corvida, which includes such birds as the true crows, Australian Magpie and Fairy-wrens, but has been observed in species as different as the Rifleman and Red Kite. Among most groups of animals, male parental care is rare. In birds, however, it is quite common—more so than in any other vertebrate class. Though territory and nest site defence, incubation, and chick feeding are often shared tasks, there is sometimes a division of labour in which one mate undertakes all or most of a particular duty.

The point at which chicks fledge varies dramatically. The chicks of the *Synthliboramphus* murrelets, like the Ancient Murrelet, leave the nest the night after they hatch, following their parents out to sea, where they are raised away from terrestrial predators. Some other species, such as ducks, move their chicks away from the nest at an early age. In most species, chicks leave the nest just before, or soon after, they are able to fly. The amount of parental care after fledging varies; albatross chicks leave the nest on their own and receive no further help, while other species continue some supplementary feeding after fledging. Chicks may also follow their parents during their first migration.

Brood parasites

Reed Warbler raising a Common Cuckoo, a brood parasite.

Brood parasitism, in which an egg-layer leaves her eggs with another individual's brood, is more common among birds than any other type of organism. After a parasitic bird lays her eggs in another bird's nest, they are often accepted and raised by the host at the expense of the host's own brood. Brood parasites may be either *obligate brood parasites*, which must lay their eggs in the nests of other species because they are incapable of raising their own young, or *non-obligate brood parasites*, which sometimes lay eggs in the nests of conspecifics to increase their reproductive output even though they could have raised their own young. One hundred bird species, including honeyguides, icterids, estrildid finches and ducks, are obligate parasites, though the most famous are the cuckoos. Some brood parasites are adapted to hatch before their host's young, which allows them to destroy the host's eggs by pushing them out of the nest or to kill the host's chicks; this ensures that all food brought to the nest will be fed to the parasitic chicks.

Ecology

The South Polar Skua (left) is a generalist predator, taking the eggs of other birds, fish, carrion and other animals. This skua is attempting to push an Adelie Penguin (right) off its nest

Birds occupy a wide range of ecological positions. While some birds are generalists, others are highly specialised in their habitat or food requirements. Even within a single habitat, such as a forest, the niches occupied by different species of birds vary, with some species feeding in the forest canopy, others beneath the canopy, and still others on the forest floor. Forest birds may be insectivores, frugivores, and nectarivores. Aquatic birds generally feed by fishing, plant eating, and piracy or kleptoparasitism. Birds of prey specialise in hunting mammals or other birds, while vultures are specialised scavengers. Avivores are animals that are specialized at predating birds.

Some nectar-feeding birds are important pollinators, and many frugivores play a key role in seed dispersal. Plants and pollinating birds often coevolve, and in some cases a flower's primary pollinator is the only species capable of reaching its nectar.

Birds are often important to island ecology. Birds have frequently reached islands that mammals have not; on those islands, birds may fulfill ecological roles typically played by larger animals. For example, in New Zealand the moas were important browsers, as are the Kereru and Kokako today. Today the plants of New Zealand retain the defensive adaptations evolved to protect them from the extinct moa. Nesting seabirds may also affect the ecology of islands and surrounding seas, principally through the concentration of large quantities of guano, which may enrich the local soil and the surrounding seas.

A wide variety of Avian ecology field methods, including counts, nest monitoring, and capturing and marking, are used for researching avian ecology.

Chapter 13

Snake

Snakes
Temporal range: 145–0 Ma
Cretaceous – Recent

Coast garter snake,
Thamnophis elegans terrestris

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Superfamily:	Varanoidea
(unranked):	Pythonomorpha
Suborder:	**Serpentes** Linnaeus, 1758

Infraorders

- Alethinophidia – Nopcsa, 1923

- Scolecophidia – Cope, 1864

World range of snakes
(rough range of sea snakes in blue)

Snakes are elongate, legless, carnivorous reptiles of the suborder **Serpentes** that can be distinguished from legless lizards by their lack of eyelids and external ears. Like all squamates, snakes are ectothermic, amniote vertebrates covered in overlapping scales. Many species of snakes have skulls with many more joints than their lizard ancestors, enabling them to swallow prey much larger than their heads with their highly mobile jaws. To accommodate their narrow bodies, snakes' paired organs (such as kidneys) appear one in front of the other instead of side by side, and most have only one functional lung. Some species retain a pelvic girdle with a pair of vestigial claws on either side of the cloaca.

Living snakes are found on every continent except Antarctica and on most islands. Fifteen families are currently recognized, comprising 456 genera and over 2,900 species. They range in size from the tiny, 10 cm-long thread snake to pythons and anacondas of up to 7.6 metres (25 ft) in length. The recently discovered fossil *Titanoboa* was 15 metres (49 ft) long. Snakes are thought to have evolved from either burrowing or aquatic lizards during the Cretaceous period (*c* 150 Ma). The diversity of modern snakes appeared during the Paleocene period (*c* 66 to 56 Ma).

Most species are nonvenomous and those that have venom use it primarily to kill and subdue prey rather than for self-defense. Some possess venom potent enough to cause painful injury or death to humans. Nonvenomous snakes either swallow prey alive or kill by constriction.

Etymology

The English word *snake* comes from Old English *snaca*, itself from Proto-Germanic **snak-an-* (cf. German *Schnake* "ring snake," Swedish *snok* "grass snake"), from Proto-Indo-European root **(s)nēg-o-* "to crawl, creep," which also gave *sneak* as well as Sanskrit *nāgá* "snake." The word ousted *adder*, as *adder* went on to narrow in meaning, though in Old English *nœddre* was the general word for snake. The other term, *serpent*, is from French, ultimately from Indo-European **serp-* (to creep), which also gave Greek *érpo* (ερπω) "I crawl."

Evolution

The fossil record of snakes is relatively poor because snake skeletons are typically small and fragile, making fossilization uncommon. However, 150 million-year-old specimens, readily identifiable as snakes, yet with lizard-like skeletal structures, have been uncovered in South America and Africa Based on comparative anatomy, there is consensus that snakes descended from lizards

Pythons and boas—primitive groups among modern snakes—have vestigial hind limbs: tiny, clawed digits known as anal spurs, which are used to grasp during mating. The Leptotyphlopidae and Typhlopidae groups also possess remnants of the pelvic girdle, sometimes appearing as horny projections when visible.

Frontal limbs are nonexistent in all snakes. This is caused by the evolution of Hox genes, controlling limb morphogenesis. The axial skeleton of the snakes' common ancestor, like most other tetrapods, had regional specializations consisting of cervical (neck), thoracic (chest), lumbar (lower back), sacral (pelvic), and caudal (tail) vertebrae. Early in snake evolution, the Hox gene expression in the axial skeleton responsible for the development of the thorax became dominant. As a result, the vertebrae anterior to the hindlimb buds (when present) all have the same thoracic-like identity (except from the atlas, axis, and 1–3 neck vertebrae). In other words, most of a snake's skeleton is an extremely extended thorax. Ribs are found exclusively on the thoracic vertebrae. Neck, lumbar and pelvic vertebrae are very reduced in number (only 2–10 lumbar and pelvic vertebrae are present), while only a short tail remains of the caudal vertebrae. However, the tail is still long enough to be of important use in many species, and is modified in some aquatic and tree-dwelling species.

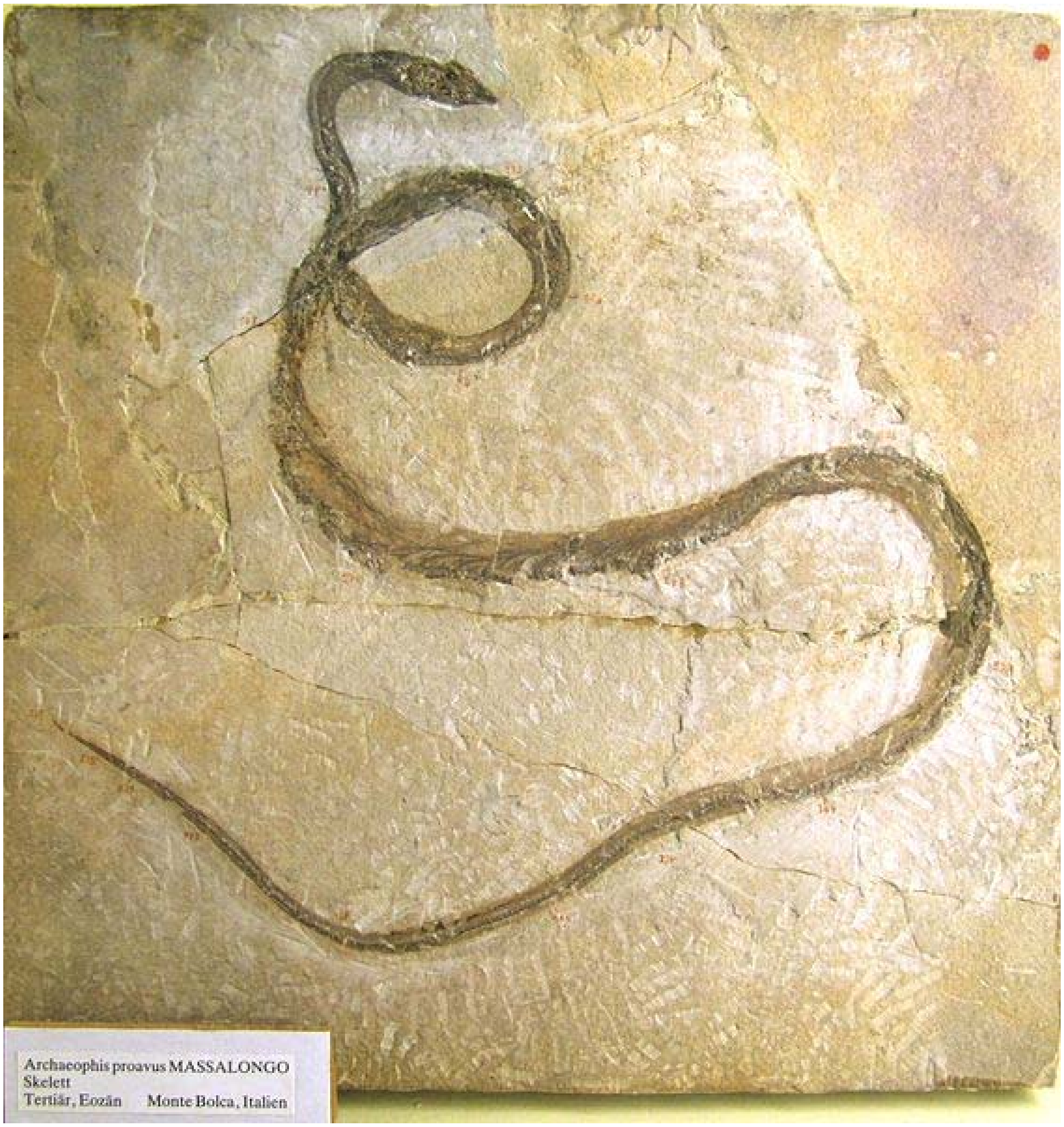
Modern snakes greatly diversified during the Paleocene. This occurred alongside the adaptive radiation of mammals, following the extinction of (non-avian) dinosaurs. The colubrids, one of the more common snake groups, became particularly diverse due to preying on rodents, an especially successful mammal group. There are over 2,900 species of snakes ranging as far northward as the Arctic Circle in Scandinavia and southward through Australia and Tasmania. Snakes can be found on every continent (with the exception of Antarctica), in the sea, and as high as 16,000 feet (4,900 m) in the Himalayan Mountains of Asia.There are numerous islands from which snakes are absent, such as Ireland, Iceland, and New Zealand.

Origins

The origin of snakes remains an unresolved issue. There are two main hypotheses competing for acceptance.

Burrowing Lizard Hypothesis

There is fossil evidence to suggest that snakes may have evolved from burrowing lizards, such as the varanids (or a similar group) during the Cretaceous Period. An early fossil snake, *Najash rionegrina*, was a two-legged burrowing animal with a sacrum, and was fully terrestrial. One extant analog of these putative ancestors is the earless monitor *Lanthanotus* of Borneo (though it also is semiaquatic). Subterranean species evolved bodies streamlined for burrowing, and eventually lost their limbs. According to this hypothesis, features such as the transparent, fused eyelids (brille) and loss of external ears evolved to cope with fossorial difficulties, such as scratched corneas and dirt in the ears. Some primitive snakes are known to have possessed hindlimbs, but their pelvic bones lacked a direct connection to the vertebrae. These include fossil species like *Haasiophis*, *Pachyrhachis* and *Eupodophis*, which are slightly older than *Najash*.



Fossil of *Archaeophis proavus*. Aquatic Mosasaur Hypothesis

An alternative hypothesis, based on morphology, suggests the ancestors of snakes were related to mosasaurs—extinct aquatic reptiles from the Cretaceous—which in turn are thought to have derived from varanid lizards. According to this hypothesis, the fused, transparent eyelids of snakes are thought to have evolved to combat marine conditions (corneal water loss through osmosis), and the external ears were lost through disuse in an aquatic environment. This ultimately lead to an animal similar to today's sea snakes. In the Late Cretaceous, snakes recolonized land, and continued to diversify into today's snakes. Fossilized snake remains are known from early Late Cretaceous marine sediments, which is consistent with this hypothesis; particularly so, as they are older than the terrestrial *Najash rionegrina*. Similar skull structure, reduced or absent limbs, and other anatomical features found in both mosasaurs and snakes lead to a positive cladistical correlation, although some of these features are shared with varanids.

Genetic studies in recent years have indicated snakes are not as closely related to monitor lizards as was once believed—and therefore not to mosasaurs, the proposed ancestor in the aquatic scenario of their evolution. However, more evidence links mosasaurs to snakes than to varanids. Fragmented remains found from the Jurassic and Early Cretaceous indicate deeper fossil records for these groups, which may potentially refute either hypothesis.

Taxonomy

All modern snakes are grouped within the suborder *Serpentes* in Linnean taxonomy, part of the order Squamata, though their precise placement within squamates is controversial.

There are two infraorders of *Serpentes*: Alethinophidia and Scolecophidia. This separation is based on morphological characteristics and mitochondrial DNA sequence similarity. Alethinophidia is sometimes split into Henophidia and Caenophidia, with the latter consisting of "colubroid" snakes (colubrids, vipers, elapids, hydrophiids, and attractaspids) and acrochordids, while the other alethinophidian families comprise Henophidia. While not extant today, the Madtsoiidae, a family of giant, primitive, python-like snakes, was around until 50,000 years ago in Australia, represented by genera such as Wonambi.

There are numerous debates in the systematics within the group. For instance, many sources classify Boidae and Pythonidae as one family, while some keep the Elapidae and Hydrophiidae (sea snakes) separate for practical reasons despite their extremely close relation.

Recent molecular studies support the monophyly of the clades of modern snakes, scolecophidians, typhlopids + anomalepidids, alethinophidians, core alethinophidians, uropeltids (*Cylindrophis*, *Anomochilus*, uropeltines), macrostomatans, booids, boids, pythonids and caenophidians.

Families

Infraorder **Alethinophidia** 15 families

Family	Taxon author	Genera	Species	Common name	Geographic range
Acrochordidae	Bonaparte, 1831	1	3	Wart snakes	Western India and Sri Lanka through tropical Southeast Asia to the Philippines, south through the Indonesian/Malaysian island group to Timor, east through New Guinea to the northern coast of Australia to Mussau Island, the Bismark Archipelago and Guadalcanal Island in the Solomon Islands.
Aniliidae	Stejneger, 1907	1	1	False coral snake	Tropical South America.
Anomochilidae	Cundall, Wallach, 1993	1	2	Dwarf pipe snakes	West Malaysia and on the Indonesian island of Sumatra.
Atractaspididae	Günther, 1858	12	64	Burrowing asps	Africa and the Middle East.
Boidae	Gray, 1825	8	43	Boas	Northern, Central and South America, the Caribbean, southeastern Europe and Asia Minor, Northern, Central and East Africa, Madagascar and Reunion Island, the Arabian Peninsula, Central and southwestern Asia, India and Sri Lanka, the Moluccas and New Guinea through to Melanesia and Samoa.
Bolyeriidae	Hoffstetter, 1946	2	2	Splitjaw snakes	Mauritius.
Colubridae	Oppel, 1811	304	1938	Typical snakes	Widespread on all continents, except Antarctica.
Cylindrophiidae	Fitzinger, 1843	1	8	Asian pipe snakes	Sri Lanka east through Myanmar, Thailand, Cambodia, Vietnam and the

					Malay Archipelago to as far east as Aru Islands off the southwestern coast of New Guinea. Also found in southern China (Fujian, Hong Kong and on Hainan Island) and in Laos.
Elapidae	Boie, 1827	61	235	Elapids	On land, worldwide in tropical and subtropical regions, except in Europe. Sea snakes occur in the Indian Ocean and the Pacific.
Loxocemidae	Cope, 1861	1	1	Mexican burrowing snake	Along the Pacific versant from Mexico south to Costa Rica.
Pythonidae	Fitzinger, 1826	8	26	Pythons	Subsaharan Africa, India, Myanmar, southern China, Southeast Asia and from the Philippines southeast through Indonesia to New Guinea and Australia.
Tropidophiidae	Brongersma, 1951	4	22	Dwarf boas	From southern Mexico and Central America, south to northwestern South America in Colombia, (Amazonian) Ecuador and Peru, as well as in northwestern and southeastern Brazil. Also found in the West Indies.
Uropeltidae	Müller, 1832	8	47	Shield-tailed snakes	Southern India and Sri Lanka.
Viperidae	Oppel, 1811	32	224	Vipers	The Americas, Africa and Eurasia.
Xenopeltidae	Bonaparte, 1845	1	2	Sunbeam snakes	Southeast Asia from the Andaman and Nicobar Islands, east through Myanmar to southern China, Thailand, Laos, Cambodia, Vietnam, the Malay Peninsula and the East Indies to Sulawesi, as well as the Philippines.

Infraorder **Scolecophidia** 3 families					
Family	**Taxon author**	**Genera**	**Species**	**Common name**	**Geographic range**
Anomalepidae	Taylor, 1939	4	15	Primitive blind snakes	From southern Central America to northwestern South America. Disjunct populations in northeastern and southeastern South America.
Leptotyphlopidae	Stejneger, 1892	2	87	Slender blind snakes	Africa, western Asia from Turkey to northwestern India, on Socotra Island, from the southwestern United States south through Mexico and Central to South America, though not in the high Andes. In Pacific South America they occur as far south as southern coastal Peru, and on the Atlantic side as far as Uruguay and Argentina. In the Caribbean they are found on the Bahamas, Hispaniola and the Lesser Antilles.
Typhlopidae	Merrem, 1820	6	203	Typical blind snakes	Most tropical and many subtropical regions around the world, particularly in Africa, Madagascar, Asia, islands in the Pacific, tropical America and in southeastern Europe.

Biology

When compared, the skeletons of snakes are radically different from those of most other reptiles (such as the turtle, right), being made up almost entirely of an extended ribcage.

Skeleton

The skeleton of most snakes consists solely of the skull, hyoid, vertebral column, and ribs, though henophidian snakes retain vestiges of the pelvis and rear limbs. The skull of the snake consists of a solid and complete braincase, to which many of the other bones are only loosely attached, particularly the highly mobile jaw bones, which facilitate manipulation and ingestion of large prey items. The left and right sides of the lower jaw are joined only by a flexible ligament at the anterior tips, allowing them to separate widely, while the posterior end of the lower jaw bones articulate with a quadrate bone, allowing further mobility. The bones of the mandible and quadrate bones can also pick up ground borne vibrations. The hyoid is a small bone located posterior and ventral to the skull, in the 'neck' region, which serves as an attachment for muscles of the snake's tongue, as it does in all other tetrapods.

The vertebral column consists of anywhere between 200 to 400 (or more) vertebrae. Tail vertebrae are comparatively few in number (often less than 20% of the total) and lack ribs, while body vertebrae each have two ribs articulating with them. The vertebrae have projections that allow for strong muscle attachment enabling locomotion without limbs.

Autotomy of the tail, a feature found in some lizards is absent in most snakes. Caudal autotomy in snakes is rare and is intervertebral, unlike that in lizards, which is intravertebral—that is, the break happens along a predefined fracture plane present on a vertebra.

In some snakes, most notably boas and pythons, there are vestiges of the hindlimbs in the form of a pair of pelvic spurs. These small, claw-like protrusions on each side of the cloaca are the external portion of the vestigial hindlimb skeleton, which includes the remains of an ilium and femur.

Internal organs

The snake's heart is encased in a sac, called the *pericardium*, located at the bifurcation of the bronchi. The heart is able to move around, however, owing to the lack of a diaphragm. This adjustment protects the heart from potential damage when large ingested prey is passed through the esophagus. The spleen is attached to the gall bladder and pancreas and filters the blood. The thymus gland is located in fatty tissue above the heart and is responsible for the generation of immune cells in the blood. The cardiovascular system of snakes is also unique for the presence of a renal portal system in which the blood from the snake's tail passes through the kidneys before returning to the heart.

The vestigial left lung is often small or sometimes even absent, as snakes' tubular bodies require all of their organs to be long and thin. In the majority of species, only one lung is functional. This lung contains a vascularized anterior portion and a posterior portion that does not function in gas exchange. This 'saccular lung' is used for hydrostatic purposes to adjust buoyancy in some aquatic snakes and its function remains unknown in terrestrial species. Many organs that are paired, such as kidneys or reproductive organs, are staggered within the body, with one located ahead of the other.

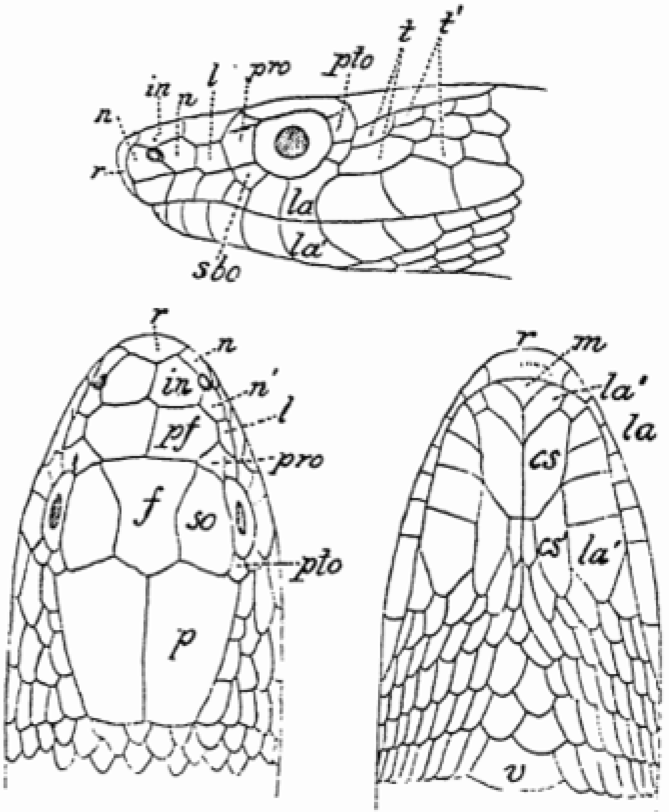
Snakes have no lymph nodes.

An adult Barbados threadsnake, Leptotyphlops carlae, on an American quarter dollar.

Size

The now extinct *Titanoboa cerrejonensis* snakes found were 12–15 meters (39–49 ft) in length. By comparison, the largest extant snakes are the reticulated python, which measures about 9 meters (30 ft) long, and the anaconda, which measures about 7.5 meters (25 ft) long and is considered the heaviest snake on Earth.

At the other end of the scale, the smallest extant snake is *Leptotyphlops carlae*, with a length of about 10 centimeters (4 in). Most snakes are fairly small animals, approximately 3 feet in length.



Three views of head of *Zamenis ventrimaculatus*, to explain the terminology of the head-shields.

cs. Chin-shields (anterior).
cs'. Chin-shields (posterior).
f. Frontal.
in. Internasal.
l. Loreal.
la. Upper labial.
la'. Lower labial.
m. Mental.
n. Nasal.
p. Parietal.
pf. Præfrontal.
pro. Præocular.
pto. Postocular.
r. Rostral.
sbo. Subocular.
so. Supraocular.
t. Temporals (first row).
t'. Temporals (second row).
v. First ventral.

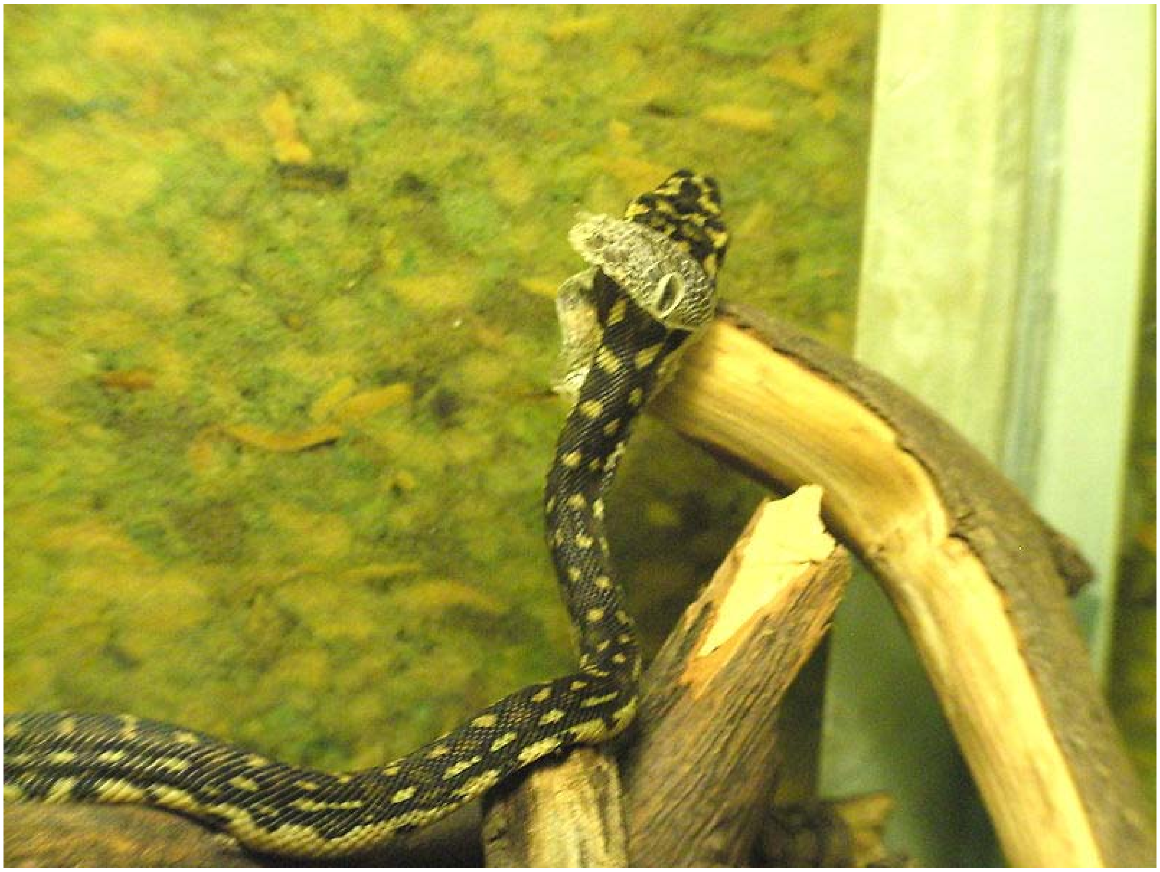
A line diagram from G.A. Boulenger's Fauna of British India (1890) illustrating the terminology of shields on the head of a snake.

Skin

The skin of a snake is covered in scales. Contrary to the popular notion of snakes being slimy because of possible confusion of snakes with worms, snakeskin has a smooth, dry texture. Most snakes use specialized belly scales to travel, gripping surfaces. The body scales may be smooth, keeled, or granular. The eyelids of a snake are transparent "spectacle" scales, which remain permanently closed, also known as brille.

The shedding of scales is called *ecdysis* (or in normal usage, *moulting* or *sloughing*). In the case of snakes, the complete outer layer of skin is shed in one layer. Snake scales are not discrete, but extensions of the epidermis—hence they are not shed separately but as a complete outer layer during each moult, akin to a sock being turned inside out.

The shape and number of scales on the head, back, and belly are often characteristic and used for taxonomic purposes. Scales are named mainly according to their positions on the body. In "advanced" (Caenophidian) snakes, the broad belly scales and rows of dorsal scales correspond to the vertebrae, allowing scientists to count the vertebrae without dissection.



Eye scales visible during the moult of a Diamond Python.

Snakes' eyes are covered by their clear scales (the brille) rather than movable eyelids. Their eyes are always open, and for sleeping, the retina can be closed or the face buried among the folds of the body.

Moulting

Moulting serves a number of functions. Firstly, the old and worn skin is replaced; secondly, it helps get rid of parasites such as mites and ticks. Renewal of the skin by moulting is supposed to allow growth in some animals such as insects; however, this has been disputed in the case of snakes.

A snake shedding its skin.

Moulting occurs periodically throughout a snake's life. Before a moult, the snake stops eating and often hides or moves to a safe place. Just before shedding, the skin becomes dull and dry looking and the eyes become cloudy or blue-colored. The inner surface of the old skin liquefies. This causes the old skin to separate from the new skin beneath it. After a few days, the eyes clear and the snake "crawls" out of its old skin. The old skin breaks near the mouth and the snake wriggles out, aided by rubbing against rough surfaces. In many cases, the cast skin peels backward over the body from head to tail in one piece, like pulling a sock off inside-out. A new, larger, brighter layer of skin has formed underneath.

An older snake may shed its skin only once or twice a year. But a younger snake, still growing, may shed up to four times a year. The discarded skin gives a perfect imprint of the scale pattern, and it is usually possible to identify the snake if the discarded skin is reasonably intact. This periodic renewal has led to the snake being a symbol of healing and medicine, as pictured in the Rod of Asclepius.

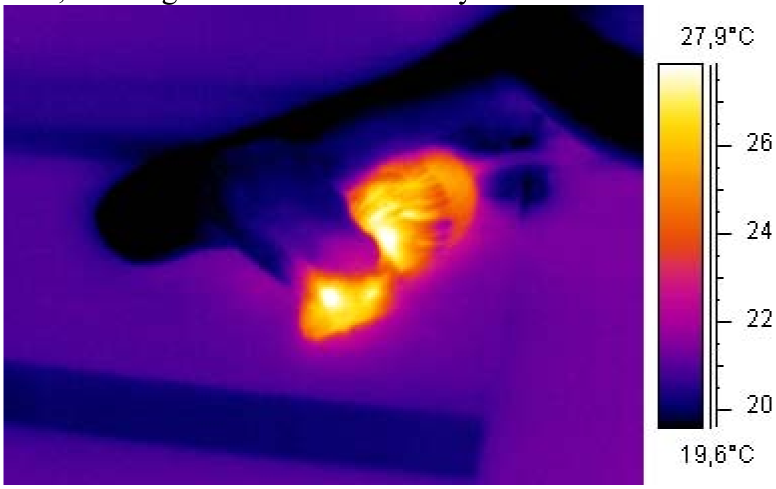
Perception

Eyesight

Snake vision varies greatly, from only being able to distinguish light from dark to keen eyesight, but the main trend is that their vision is adequate although not sharp, and allows them to track movements. Generally, vision is best in arboreal snakes and weakest in burrowing snakes. Some snakes, such as the Asian vine snake (genus *Ahaetulla*), have binocular vision, with both eyes capable of focusing on the same point. Most snakes focus by moving the lens back and forth in relation to the retina, while in the other amniote groups, the lens is stretched.

Smell

Snakes use smell to track their prey. They smell by using their forked tongues to collect airborne particles, then passing them to the vomeronasal organ or *Jacobson's organ* in the mouth for examination. The fork in the tongue gives snakes a sort of directional sense of smell and taste simultaneously. They keep their tongues constantly in motion, sampling particles from the air, ground, and water, analyzing the chemicals found, and determining the presence of prey or predators in the local environment. In water-dwelling snakes, such as the Anaconda, the tongue functions efficiently under water.



Thermographic image of a snake eating a mouse

Vibration sensitivity

The part of the body in direct contact with the ground is very sensitive to vibration; thus, a snake can sense other animals approaching by detecting faint vibrations in the air and on the ground.

Infrared sensitivity

Pit vipers, pythons, and some boas have infrared-sensitive receptors in deep grooves between the nostril and eye, although some have labial pits on their upper lip just below the nostrils (common in pythons), which allow them to "see" the radiated heat of warm-blooded prey mammals.

Venom

Milk snakes are often mistaken for coral snakes, whose venom is deadly to humans.

Cobras, vipers, and closely related species use venom to immobilize or kill their prey. The venom is modified saliva, delivered through fangs. The fangs of 'advanced' venomous snakes like viperids and elapids are hollow to inject venom more effectively, while the fangs of rear-fanged snakes such as the boomslang merely have a groove on the posterior edge to channel venom into the wound. Snake venoms are often prey specific, their role in self-defense is secondary.

Venom, like all salivary secretions, is a predigestant that initiates the breakdown of food into soluble compounds, facilitating proper digestion. Even nonvenomous snake bites (like any animal bite) will cause tissue damage.

Certain birds, mammals, and other snakes (such as kingsnakes) that prey on venomous snakes have developed resistance and even immunity to certain venoms. Venomous snakes include three families of snakes, and do not constitute a formal classification group used in taxonomy.

The term **poisonous snake** is mostly incorrect. Poison is inhaled or ingested, whereas venom is injected. There are, however, two exceptions: *Rhabdophis* sequesters toxins from the toads it eats, then secretes them from nuchal glands to ward off predators, and a small population of garter snakes in Oregon retains enough toxin in their liver from the newts they eat to be effectively poisonous to small local predators (such as crows and foxes).

Snake venoms are complex mixtures of proteins, and are stored in poison glands at the back of the head. In all venomous snakes, these glands open through ducts into grooved or hollow teeth in the upper jaw. These proteins can potentially be a mix of neurotoxins (which attack the nervous system), hemotoxins (which attack the circulatory system), cytotoxins, bungarotoxins and many other toxins that affect the body in different ways. Almost all snake venom contains *hyaluronidase*, an enzyme that ensures rapid diffusion of the venom.

Venomous snakes that use hemotoxins usually have fangs in the front of their mouths, making it easier for them to inject the venom into their victims. Some snakes that use neurotoxins (such as the mangrove snake) have fangs in the back of their mouths, with the fangs curled backwards. This makes it both difficult for the snake to use its venom and for scientists to milk them. *Elapids*, however, such as cobras and kraits are *proteroglyphous*—they possess hollow fangs that cannot be erected toward the front of their mouths, and cannot "stab" like a viper. They must actually bite the victim.

It has recently been suggested that all snakes may be venomous to a certain degree, with harmless snakes having weak venom and no fangs. Most snakes currently labelled “nonvenomous” would still be considered harmless according to this theory, as they either lack a venom delivery method or are incapable of delivering enough to endanger a human. This theory postulates that snakes may have evolved from a common lizard ancestor that was venomous—and that venomous lizards like the gila monster, beaded lizard, monitor lizards, and the now-extinct mosasaurs may also have derived. They share this venom clade with various other saurian species.

Venomous snakes are classified in two taxonomic families:

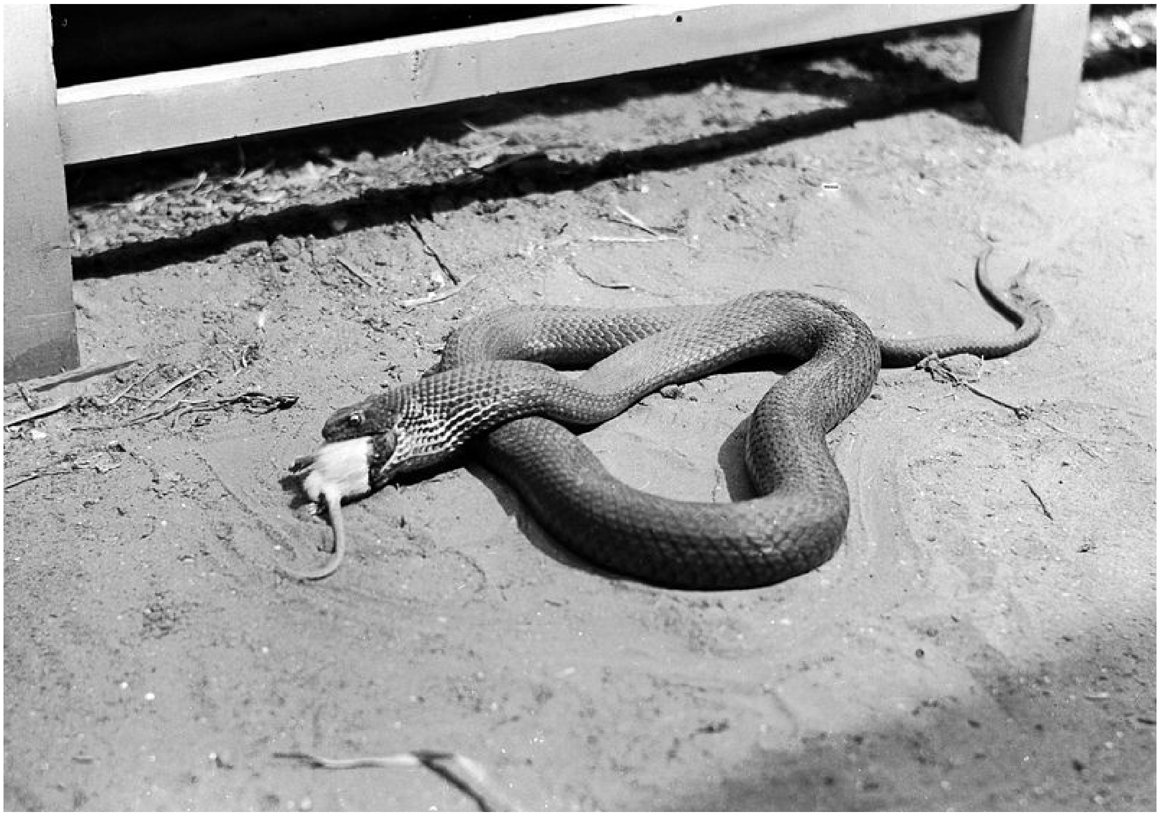
- Elapids – cobras including king cobras, kraits, mambas, Australian copperheads, sea snakes, and coral snakes.
- Viperids – vipers, rattlesnakes, copperheads/cottonmouths, adders and bushmasters.

There is a third family containing the *opistoglyphous* (rear-fanged) snakes (as well as the majority of other snake species):

- Colubrids – boomslangs, tree snakes, vine snakes, mangrove snakes, although not all colubrids are venomous.

Behavior

Feeding and diet



Snake eating a rodent.

Carpet python constricting and consuming a chicken.

All snakes are strictly carnivorous, eating small animals including lizards, other snakes, small mammals, birds, eggs, fish, snails or insects. Because snakes cannot bite or tear their food to pieces, they must swallow prey whole. The body size of a snake has a major influence on its eating habits. Smaller snakes eat smaller prey. Juvenile pythons might start out feeding on lizards or mice and graduate to small deer or antelope as an adult, for example.

African egg-eating snake.

The snake's jaw is a complex structure. Contrary to the popular belief that snakes can dislocate their jaws, snakes have a very flexible lower jaw, the two halves of which are not rigidly attached, and numerous other joints in their skull, allowing them to open their mouths wide enough to swallow their prey whole, even if it is larger in diameter than the snake itself, as snakes do not chew. For example, the African egg-eating snake has flexible jaws adapted for eating eggs much larger than the diameter of its head. This snake has no teeth, but does have bony protrusions on the inside edge of its spine, which it uses to break shells when it eats eggs.

While the majority of snakes eat a variety of prey animals, there is some specialization by some species. King cobras and the Australian bandy-bandy consume other snakes.

Pareas iwesakii and other snail-eating colubrids of subfamily Pareatinae have more teeth on the right side of their mouths than on the left, as the shells of their prey usually spiral clockwise

Some snakes have a venomous bite, which they use to kill their prey before eating it. Other snakes kill their prey by constriction. Still others swallow their prey whole and alive.

After eating, snakes become dormant while the process of digestion takes place. Digestion is an intense activity, especially after consumption of large prey. In species that feed only sporadically, the entire intestine enters a reduced state between meals to conserve energy. The digestive system is then 'up-regulated' to full capacity within 48 hours of prey consumption. Being ectothermic ("cold-blooded"), the surrounding temperature plays a large role in snake digestion. The ideal temperature for snakes to digest is 30 °C (86 °F). So much metabolic energy is involved in a snake's digestion that in the Mexican rattlesnake (*Crotalus durissus*), surface body temperature increases by as much as 1.2 °C (2.2 °F) during the digestive process. Because of this, a snake disturbed after having eaten recently will often regurgitate its prey to be able to escape the perceived threat. When undisturbed, the digestive process is highly efficient, with the snake's digestive enzymes dissolving and absorbing everything but the prey's hair (or feathers) and claws, which are excreted along with waste.

Locomotion

The lack of limbs does not impede the movement of snakes. They have developed several different modes of locomotion to deal with particular environments. Unlike the gaits of limbed animals, which form a continuum, each mode of snake locomotion is discrete and distinct from the others; transitions between modes are abrupt.

Lateral undulation

Lateral undulation is the sole mode of aquatic locomotion, and the most common mode of terrestrial locomotion. In this mode, the body of the snake alternately flexes to the left and right, resulting in a series of rearward-moving "waves." While this movement appears rapid, snakes have rarely been documented moving faster than two body-lengths per second, often much less. This mode of movement has the same net cost of transport (calories burned per meter moved) as running in lizards of the same mass.

Terrestrial

Terrestrial lateral undulation is the most common mode of terrestrial locomotion for most snake species. In this mode, the posteriorly moving waves push against contact points in the environment, such as rocks, twigs, irregularities in the soil, etc. Each of these environmental objects, in turn, generates a reaction force directed forward and towards the midline of the snake, resulting in forward thrust while the lateral components cancel out. The speed of this movement depends upon the density of push-points in the environment, with a medium density of about 8 along the snake's length being ideal. The wave speed is precisely the same as the snake speed, and as a result, every point on the snake's body follows the path of the point ahead of it, allowing snakes to move through very dense vegetation and small openings.

Aquatic

Banded sea krait, *Laticauda sp*.

When swimming, the waves become larger as they move down the snake's body, and the wave travels backwards faster than the snake moves forwards. Thrust is generated by pushing their body against the water, resulting in the observed slip. In spite of overall similarities, studies show that the pattern of muscle activation is different in aquatic versus terrestrial lateral undulation, which justifies calling them separate modes. All snakes can laterally undulate forward (with backward-moving waves), but only sea snakes have been observed reversing the motion (moving backwards with forward-moving waves).

Sidewinding

A Mojave rattlesnake (Crotalus scutulatus) sidewinding.

Most often employed by colubroid snakes (colubrids, elapids, and vipers) when the snake must move in an environment that lacks irregularities to push against (rendering lateral undulation impossible), such as a slick mud flat, or a sand dune. Sidewinding is a modified form of lateral undulation in which all of the body segments oriented in one direction remain in contact with the ground, while the other segments are lifted up, resulting in a peculiar "rolling" motion. This mode of locomotion overcomes the slippery nature of sand or mud by pushing off with only static portions on the body, thereby minimizing slipping. The static nature of the contact points can be shown from the tracks of a sidewinding snake, which show each belly scale imprint, without any smearing. This mode of locomotion has very low caloric cost, less than ⅓ of the cost for a lizard or snake to move the same distance. Contrary to popular belief, there is no evidence that sidewinding is associated with the sand being hot.

Concertina

When push-points are absent, but there is not enough space to use sidewinding because of lateral constraints, such as in tunnels, snakes rely on concertina locomotion. In this mode, the snake braces the posterior portion of its body against the tunnel wall while the front of the snake extends and straightens. The front portion then flexes and forms an anchor point, and the posterior is straightened and pulled forwards. This mode of locomotion is slow and very demanding, up to seven times the cost of laterally undulating over the same distance. This high cost is due to the repeated stops and starts of portions of the body as well as the necessity of using active muscular effort to brace against the tunnel walls.

Rectilinear

The slowest mode of snake locomotion is rectilinear locomotion, which is also the only one where the snake does not need to bend its body laterally, though it may do so when turning. In this mode, the belly scales are lifted and pulled forward before being placed down and the body pulled over them. Waves of movement and stasis pass posteriorly, resulting in a series of ripples in the skin. The ribs of the snake do not move in this mode of locomotion and this method is most often used by large pythons, boas, and vipers when stalking prey across open ground as the snake's movements are subtle and harder to detect by their prey in this manner.

Other

The movement of snakes in arboreal habitats has only recently been studied. While on tree branches, snakes use several modes of locomotion depending on species and bark texture. In general, snakes will use a modified form of concertina locomotion on smooth branches, but will laterally undulate if contact points are available. Snakes move faster on small branches and when contact points are present, in contrast to limbed animals, which do better on large branches with little 'clutter'.

Gliding snakes (*Chrysopelea*) of Southeast Asia launch themselves from branch tips, spreading their ribs and laterally undulating as they glide between trees. These snakes can perform a controlled glide for hundreds of feet depending upon launch altitude and can even turn in midair.

Reproduction

Although a wide range of reproductive modes are used by snakes, all snakes employ internal fertilization. This is accomplished by means of paired, forked hemipenes, which are stored, inverted, in the male's tail. The hemipenes are often grooved, hooked, or spined in order to grip the walls of the female's cloaca.

Most species of snakes lay eggs, but most snakes abandon the eggs shortly after laying. However, a few species (such as the King cobra) actually construct nests and stay in the vicinity of the hatchlings after incubation. Most pythons coil around their egg-clutches and remain with them until they hatch. A female python will not leave the eggs, except to occasionally bask in the sun or drink water. She will even “shiver” to generate heat to incubate the eggs.

Some species of snake are ovoviviparous and retain the eggs within their bodies until they are almost ready to hatch. Recently, it has been confirmed that several species of snake are fully viviparous, such as the boa constrictor and green anaconda, nourishing their young through a placenta as well as a yolk sac, which is highly unusual among reptiles, or anything else outside of placental mammals. Retention of eggs and live birth are most often associated with colder environments, as the retention of the young within the female.