

# Reptilia (Reptiles)

Michael J Benton, *University of Bristol, Bristol, UK*

Reptiles are a diverse group of vertebrates, including turtles, crocodiles, lizards and snakes, as well as the extinct dinosaurs, pterosaurs, plesiosaurs and ichthyosaurs. Reptiles lay cleidoic eggs (adapted to dry land), and they include the ancestors of birds and mammals.

## Introduction

The class Reptilia includes well-known cold-blooded animals such as turtles, lizards, snakes and crocodiles. The definition of class Reptilia, and the explanation of its rather disparate contents (Table 1), is an accident of evolutionary history and of traditional group definitions. In a cladistic sense, the group Reptilia is paraphyletic. In other words, it includes some, but not all, of the descendants of its common ancestor. The phylogenetic definition of Reptilia can be written as:

Reptilia = Amniota – (Mammalia + Aves)

Reptiles are all amniotes except birds and mammals.

The series Amniota is a true clade, a monophyletic group, one that includes all descendants of a common ancestor. Amniotes are diagnosed by the fact that they lay a cleidoic, or amniotic, egg, an enclosed egg that protects and nourishes the developing embryo. The cleidoic egg (Figure 1a) has two main characters, the external shell and the extraembryonic membranes. The shell of cleidoic eggs is typically hard and crystalline, made from calcium carbonate, as seen in birds and most reptiles. Some lizards and snakes, however, have leathery egg shells. In either case, the shell acts as a semipermeable membrane, allowing oxygen to pass in, and carbon dioxide out, but limiting the loss of water vapour. There are three extraembryonic membranes:

1. the amnion, which surrounds the embryo closely and functions in protection and gas transfer;
2. the chorion, which surrounds the embryo and yolk sac, and adheres closely to the inside of the shell, and also functions in protection and gas transfer; and
3. the allantois, a separate sac attached to the embryo, which also functions in respiration and stores waste materials.

The embryo is nourished by highly protein- and fat-rich yolk contained in the yolk sac. The yolk sac and chorion can be seen in an unfertilized hen's egg on the breakfast table. Reptiles and birds clearly lay such cleidoic eggs, but so also do mammals primitively. The living monotremes, the echidnas and the duck-billed platypus of Australasia lay eggs with hard shells, and many ancestral fossil mammals almost certainly laid eggs too. Egg laying was then suppressed in marsupials and placentals. **See also:** Classi-

## Introductory article

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fication; Reproduction in monotremes and marsupials.

The amniotic egg originated as an adaptation to life on land. The first tetrapods, land-living vertebrates, did not completely break free from their fishy ancestry. The basal tetrapods, the amphibians, still live a life half in water and half on land. Their eggs are in the form of spawn which is laid in water. There are typically many eggs, each containing a tiny embryo, and development passes through a water-living larval stage. The familiar tadpoles of frogs and salamanders live just like developing fishes in their first weeks, and then finally leave the water when they grow their limbs. Amniotes broke with that larval stage, and the cleidoic egg was the key to conquering new habitats away from permanent bodies of water. **See also:** Amphibia; Terrestrialization (Precambrian–Devonian).

The first reptiles, the first amniotes, arose from amphibian ancestors in the Mid Carboniferous, some 320 million years ago (Ma). These early forms almost certainly laid cleidoic eggs, although fossil eggs have not been found. Fossil eggs of later dinosaurs and other extinct reptiles are common enough, but the oldest fossil eggs come long after the origin of the reptiles. However, the fact that all main branches of Amniota lay identical eggs strongly suggests that such eggs originated only once, and at the point of divergence of the living groups. That point of ancestral divergence happened in the Mid Carboniferous. **See also:** Geological time: principles.

## Basic Design

The diversity of living reptiles, from lizards to crocodiles, and turtles to snakes (Table 1), makes it impossible to give a single account of their basic design. The anatomy of a basal amniote will be described, and then a brief account of each of the major living and extinct groups will be presented.

The first amniotes, such as *Paleothyris* from the Mid Carboniferous of Nova Scotia, Canada (**Figure 2a**), were small animals. They differed from their amphibian ancestors in having reorganized skull bones, with a loss or reduction of many of the elements at the back, a higher skull, and an ankle with two main bones, the astragalus and calcaneum (equivalent to our ankle and heel bones). Basal tetrapods (amphibians) typically have a flattened skull, but the elevated skull shape of the first amniotes is thought to have given them the ability to wrestle with large insects. A higher skull meant longer jaw muscles, and new muscle groups, set at an angle to the jaws. The first amniotes could have captured relatively large land-living insects, and punctured their tough cuticles using the strong mobile jaws. In the rest of its skeleton, *Paleothyris* has a long flexible backbone, relatively short limbs and a very long tail (not shown completely in the figure). The two bones of the ankle, a special feature of amniotes, represent a simplification and a strengthening from the basal tetrapod pattern. As reptiles became more land-adapted, the muscles of the limbs strengthened, and the astragalus and calcaneum provided a precise ankle hinge.

*Paleothyris* has an anapsid ('no-arch') skull, meaning that there are no temporal openings, holes through the skull bones behind the eye socket (**Figure 1b**). Anapsid reptiles are one of three major branches of reptile evolution that arose in the Carboniferous. There were a range of extinct anapsid groups, such as pareiasaurs and procolophonids, relatives of the living turtles. Turtles (**Figure 2b**) of course uniquely have a bony outer 'shell' encasing their body. The upper part of the shell, the carapace, is the most substantial, and the under part, the flattened plastron, is smaller. The carapace and plastron are attached to each other along the sides, and there are openings fore and aft for the head, tail and limbs to emerge. This arrangement obviously acts for protection, and when threatened, turtles typically withdraw their head and limbs inside the shell, and they are hard to get at. The carapace is composed of several large central plates of bone, surrounded by a rim of smaller plates. In life, the bone plates are covered by a horny outer cover that may carry patterns and colour. The main plates of the carapace are attached to the vertebrae and ribs, while the plastron is formed from expanded portions of the shoulder girdle and abdominal ribs. The carapace and plastron are massive and heavy, but they are reduced to a much more slender form, with many holes, in some aquatic forms, a weight-saving adaptation. The turtle shell is firmly attached to the internal skeleton, and a turtle cannot climb out and run about, as suggested in cartoons. **See also:** Comparative skeletal structure; Testudines (tortoises, turtles and terrapins).

The head of turtles is relatively small, and it is composed of thickened bone, part of the protective pattern. The jaws of living turtles are toothless, although the first turtles still had teeth. Modern turtle jaws are lined with sharpened horny material, quite effective in cutting plants and insect

cuticles. The neck is composed of strong vertebrae, and these allow the head to withdraw into the shell, by either bending sideways (pleurodire turtles) or up and down (cryptodire turtles). The limbs are short and powerful. The shoulder girdle is an elongated three-pronged structure, with a long coracoid running back, and a scapula with two separate heads, one pointing inwards, and one upwards. The pelvis is smaller. In swimming turtles, the hands and feet are converted into broad paddles.

The second main branch of amniote evolution consists of the synapsids. These amniotes have a single opening in the side of the cheek region of the skull, behind the eye socket (**Figure 1b**). The synapsids include modern mammals together with their amniote ancestors, a group often loosely referred to as the 'mammal-like reptiles'. These basal synapsids came in all shapes and sizes, and they were dominant in many terrestrial faunas during the Permian and earlier parts of the Triassic, 286 to 225 Ma. *Thrinaxodon*, a typical flesh-eating form (**Figure 2c**), is a superficially dog-like animal, but with sprawling limbs. The head is large, with a large brain, and the teeth are differentiated into incisors, canines and cheek teeth, as in modern mammals, and unlike other reptiles, which have undifferentiated teeth that are pretty well identical from front to back of the jaws. The neck is short. The body of *Thrinaxodon* is divided into two segments, a front thoracic portion, with ribs, and a back lumbar region, without ribs, again as in modern mammals, but different from other reptiles that have ribs all the way back to the hip region. The tail is short, again a feature of mammals, but not of most reptiles. **See also:** Synapsida ('mammal-like reptiles').

The third main line of amniote, and reptilian, evolution is represented by the diapsids, which had two openings in the side of the skull behind the eye socket. Diapsids include a variety of extinct forms, as well as living crocodiles, lizards and snakes. Diapsids fall into two major groupings, the archosaurs (crocodilians, birds, plus extinct pterosaurs and dinosaurs) and the lepidosaurs (lizards, snakes, sphenodontids, plus extinct relatives). The extinct marine reptiles, the ichthyosaurs and plesiosaurs, are also probably diapsids, perhaps related more closely to the lepidosaurs than to the archosaurs.

Crocodilians are a small group today, but they have a long and varied history. Early forms (**Figure 2d**) show the characteristic features. The skull is long and low, and the snout is usually narrow, with the nostrils at the tip. Inside the skull, there is a secondary palate, a bony plate that separates the nasal cavity from the mouth cavity. This allows crocodilians to breathe while underwater, with only the nostrils above the surface, or to eat and breathe at the same time. (Other reptiles must either breathe or eat, since the airway from the nostrils enters the mouth at the front. Mammals have independently evolved a secondary palate.) There are several specialized features in the crocodilian skull: deep pitting of the bones on top, a square shape to the posterior portion of the skull roof, an ear lid (a bony

flap that covers the ear during diving), extra small bones in the eye socket to protect the eye and pneumatic spaces (air spaces) in the bones of the back of the skull. The crocodilian backbone is strong, and it is braced by a series of bony plates set into the skin. Small muscles link the vertebrae of the backbone with the bony plates, and this helps control up and down movements of the back. Crocodilian limbs are short. Crocodilians generally move slowly by bending the body from side to side, and using the limbs in a sprawling posture. However, they can hoist the body clear of the ground, and hold the legs erect, for faster running, and young ones have even been seen to gallop and jump, operating forelimbs and hindlimbs in pairs. The limbs, and limb girdles, of crocodilians show several unique features: the wrist bones are elongated, the coracoid (the lower element of the shoulder girdle) is long and narrow, the hip girdle is perforated in the middle, and the pubis, the front element of the hip girdle, is slender. **See also:** Crocodylia (including crocodiles and alligators).

The lepidosaurs include today the sphenodontids, lizards and snakes. The sphenodontids are the most primitive lepidosaurs, having arisen in the Late Triassic, 220 Ma. Sphenodontids included several fossil forms, but there is only one living representative, the tuatara, *Sphenodon*, from New Zealand (**Figure 2e**). *Sphenodon* is often described as a ‘living fossil’, since it belongs to a long-lived group; but also since its anatomy is primitive in comparison to lizards and snakes, its skull does not show the extra points of flexibility seen in lizards and snakes (see below), and other features of the skull and skeleton are close to those of the ancestors of lizards.

Lizards are generally small, although there are some large forms like the Komodo dragon, *Varanus komodoensis*, 3 m long. The skull is specialized by being kinetic, that is, mobile. Lizard skulls contain extra joints in addition to the normal jaw joint, between:

1. frontal and parietal in the skull roof, and a matching joint in the palate, which allows lizards to tip their snouts up and down;
2. braincase and skull; and
3. quadrate and squamosal, in the back of the cheek region, and pterygoid and lower jaw, in the palate, to allow the skull to move backwards and forwards relative to the lower jaw.

This mechanism allows lizards to open their mouths wider than expected, but also to manipulate their food efficiently. Normally, when an animal closes its jaws, pressure is exerted on a food item from above and below, but also partly forward, since closing jaws are like closing blades of a pair of scissors. There is a risk that the food may be propelled out of the mouth. The kinetic lizard system means that pressure is exerted only onto the food, and not forward. **See also:** Sauria (Lizards).

Lizards generally have slender bodies and long limbs and feet. The astragalus and calcaneum, the two main ankle bones, are fused, and the fifth metatarsal (the top joint in the little toe) is L-shaped, features that perhaps give lizards more control over their foot actions during climbing. There were several extinct groups of varanid lizards that were fully marine, most spectacular of which were the mosasaurs of the Late Cretaceous (100–65 Ma), which ranged in length from 3 to 10 m. Some lizards have reduced their limbs, and others have lost them altogether.

Snakes arose from typical lizards in the Early Cretaceous, perhaps 130 Ma. Snakes have even more highly kinetic skulls than those seen in lizards, with as many as seven joints, as well as others linking the tooth-bearing bones, the maxilla and premaxilla. Snakes, as is well known, can dislocate their jaws when feeding on large prey. Snakes have lost their limbs, and increased the length of their backbones to 120–500 vertebrae. Snakes are predators, which kill their prey either by constriction (suffocation) or by poison. **See also:** Serpentes (snakes).

## Diversity

Living reptiles number about 8160 species made up of 25 families and include 305 species of turtles, eight genera and 23 species of crocodilians, about 4880 species of lizards, 2955 species of snakes and one (or perhaps two) species of sphenodontid, *Sphenodon*. Extinct reptiles account for a considerable diversity as well, with some 300 genera of mammal-like reptiles (nonmammalian synapsids), known from the Late Carboniferous to the Late Jurassic, perhaps 500 genera of dinosaurs, and 100 genera of large marine reptiles.

Living reptiles are most diverse in the tropics. Moving away from the equator, diversity decreases, and large species become rarer and rarer. Some lizards live as far north as the Arctic Circle, and as far south as the southern tip of South America. Lizards are especially adept at surviving in deserts, both hot and cold. Relatively few modern reptiles live in the sea: sea turtles, a few species of crocodilian, the marine iguanas of the Galapagos Islands, and some sea snakes, all of these equatorial in distribution. **See also:** Diversity of life.

## Habits and Lifestyles

Living reptiles are highly diverse, and it is not possible to synthesize their habits and lifestyles readily. Specific details will be found in the articles on turtles, crocodilians, lizards and snakes. One feature of reptiles that sets them apart from birds and mammals, however, is their ‘cold-bloodedness’ or ectothermy.

The ectothermy of modern reptiles is in one sense a primitive characteristic which they inherited from their basal tetrapod and fish ancestors. Warm-blooded birds and mammals evolved their particular systems of endothermy ('warm-bloodedness') independently. Reptiles are classically thought to be cold, clammy and unpleasant to the touch. This view stemmed from an old prejudice, expressed in the Bible, which classed reptiles as evil and degraded animals. However, reptile body temperatures are frequently warmer than ours, especially on a hot day. Reptiles are highly successful animals, and they clearly do control their body temperatures in various ways. **See also:** Vertebrate metabolic variation.

Classic field studies in the 1940s showed that reptiles have a complex system of behavioural thermoregulation. During the night, when air temperatures are cool or cold, many reptiles enter a state of inaction, or torpor. When the sun rises, they crawl out of their hiding places and bask on a rock. They absorb heat by direct radiation from the sun, but also by conduction through the rock, and by reflection from surrounding rocks. When they have absorbed enough heat to become active, reptiles go about their business, until the air temperature becomes too high at midday. Then, they may shelter in a dark spot until air temperatures cool down. **See also:** Thermoregulation in vertebrates.

These behavioural mechanisms involve considerable adaptation and sophistication. Unlike endotherms, reptiles can operate efficiently at a range of body temperatures, from 4 to 40°C. The rate of heat absorption and loss can be controlled by varying the orientation of the body to the sun, the body shape, the body colour and the rate of blood flow in the peripheral regions of the body. These mechanisms allow many reptiles to divorce themselves much more than had been expected from daily temperature changes: active lizards living above the timberline in temperate regions may be 30°C warmer than air temperature.

The conclusion from modern physiological studies is that reptile thermoregulation is not necessarily inferior to the endothermy of birds and mammals. The diversity of reptiles of course should prove that. It turns out that reptiles have many advantages because of their ectothermy. For example, ectothermy uses far less food than endothermy, and hence reptiles can survive in environments where food is hard to find, and they can devote far less time of their lives to eating. Typically, about nine-tenths of the food eaten by an endotherm goes into temperature control, so an ectothermic reptile only has to eat about one-tenth of the amount of food of an endotherm of the same body weight. A second major advantage is that reptiles require far less water than endotherms. This is partly because of their ectothermy, and partly because reptiles, like birds, rid their body of waste nitrogen in the form of uric acid, a solid, rather than as urea, which must be dissolved in water before being voided as liquid urine. **See also:** Thermoregulation in vertebrates: acclimation, acclimatization and adaptation.

## Life Histories

All reptiles lay eggs, although some lizards and snakes have suppressed egg-laying, and produce live young ones. However, this form of live-bearing is different from that of placental mammals in that the mother lizard or snake retains the eggs inside until hatching time. This habit evolved many times, and it is seen in sea snakes and in lizards and snakes that live in colder areas, so the mother can bask in the sun to keep the eggs warm. Most lizards and snakes, however, lay eggs, often elongate and with leathery shells, instead of hard mineralized shells. The nest is usually abandoned, and the young hatch and fend for themselves independently. Unusually, some pythons incubate their eggs. **See also:** Reproductive strategies.

Female turtles lay 4–100 eggs in nests scooped in the ground. The egg-laying of large marine turtles is well known, where the mother hauls herself high on a beach, scoops a hole in the sand with her hind paddles, deposits a large number of spherical eggs, and then leaves them. The young hatch some 60 days later, scurgle up through the sand, and head straight for the water. The young are vulnerable at this time, and many are killed by predators.

Crocodylians, on the other hand, exhibit parental care. The female creates a nest on a river bank, either on a mound of vegetation, if the ground is marshy, or in a hollow scooped in the earth. She lays the eggs, and covers them with twigs and leaves. In many, or all, living crocodylians, the mother guards the nest against predators, and when she hears her young ones squeaking, she helps them out of the nest, and carries them in her mouth to the water. This helping behaviour was formerly interpreted as cannibalism – the unpleasant reptilian mother eating her own young!

## Oddities within the Class

The class Reptilia is a paraphyletic group, a ragbag assemblage of turtles, crocodylians, lizards and snakes (see above). Hence, it is hard to generalize about all reptiles, and so it is also not easy to identify 'oddities within the class'.

## Fossil History

Reptiles arose in the Mid Carboniferous, some 320 Ma. It is easier to think of reptiles as part of a larger clade, the series Amniota, which also includes birds and mammals, and to document the broader evolution of that group (**Figure 3**). The three main lines of amniote evolution manifested themselves as early as the Late Carboniferous, when it is possible to discern the anapsid, synapsid and diapsid lines of evolution (**Figure 1b**). Excellent fossil specimens of these most ancient reptiles are found mainly in North

America. The oldest reptile specimens, animals like *Paleothyris* (Figure 2a), are preserved in an unusual sedimentary situation in coal deposits of Nova Scotia, Canada. These earliest amniotes are found in ancient tree stumps. Evidently, during floods, the large trees were knocked down, leaving only the stumps. Over time, the stumps rotted inside, and they became inhabited by insects and early reptiles. Eventually, another flood covered the stumps and filled them with sediment, hence preserving a whole little ecosystem undamaged. **See also:** Fossil record; Fossil record: quality.

During the subsequent Permian period, 286–250 Ma, the synapsids held sway on land worldwide. The early synapsids, especially abundant specimens of pelycosaurs, are known from the American midwest, and the later Permian synapsids are well known from South Africa and central Russia. Various anapsid groups, such as the large knobby herbivorous pareiasaurs, and the smaller procolophonids, were also important members of ecosystems in the Late Permian. At the end of the Permian, a huge mass extinction wiped out most of these animals. **See also:** Extinction: end-Permian mass extinction.

In the Triassic, 250–200 Ma, terrestrial ecosystems recovered, but synapsids did not retrieve their former prominence. The diapsids, already present in the Carboniferous and Permian, became dominant carnivores in many settings. Especially successful at this point were the archosaurs, some of which became effective top predators, and as much as 5 m in length. They preyed on synapsids, other archosaurs, and a variety of other reptiles and amphibians. The Early and Mid Triassic terrestrial ecosystems, to some extent rebuilt from Permian forms, were dealt a final blow near the beginning of the Late Triassic, 225 Ma. The major herbivores, dicynodonts and chiniquodontids (two groups of medium to large synapsids), and the rhynchosaurs (a diapsid group related to archosaurs), died out, perhaps as a result of drying of climates and changes in vegetation. A suite of new groups replaced them: dinosaurs, pterosaurs, turtles, crocodylians and mammals (at this point, small insectivorous forms that had evolved from the older synapsids). Dinosaurs, large and small, sometimes very large, ruled terrestrial ecosystems for the next 160 million years, until the end of the Cretaceous. In the air, the pterosaurs, close relatives of the dinosaurs, were important flying forms, some achieving huge size. **See also:** Biotic recoveries after extinction; Dinosauria (dinosaurs); Post-Permian radiation; Pterosauria (pterosaurs).

In the sea, reptiles were important predators. The first reptiles to become adapted to marine conditions were the mesosaurs, an enigmatic group in the Mid Permian, possibly related to anapsids. One or two diapsid groups also tried the experiment in the Late Permian, and two succeeded impressively, the euryapsids and the ichthyosaurs (Table 1). The euryapsids radiated in the Triassic into three main groups, the small fish-eating pachypleurosaurs and nothosaurs, and the mollusc-eating placodonts. The not-

hososaurs gave rise to plesiosaurs and pliosaurs, long and short-necked predators, respectively, which were hugely successful in the Jurassic and Cretaceous. The ichthyosaurs evolved a dolphin-like body structure early in the Triassic, and remained the same until the Late Cretaceous.

Various modern reptile groups evolved during these times, but they were generally small animals, not noticeable beside the impressive dinosaurs, pterosaurs, plesiosaurs and ichthyosaurs. First to arrive on the scene were the turtles, crocodylians and sphenodontids, in the Late Triassic. Next came the lizards in the Mid Jurassic, and the snakes in the Early Cretaceous. The diversity of all these groups increased during the Late Cretaceous and, when the dinosaurs and other giant reptiles became extinct at the end of the Cretaceous, 65 Ma, during another mass extinction, all of them increased further in diversity. So too did the birds and mammals, which were also present during the age of dinosaurs, but were small and relatively rare. It was not clear then which of the groups would rise to dominance on land, and certain birds and reptiles competed with the mammals for dominance. In South America, for example, certain groups of crocodylians became highly terrestrial and they were effective top predators for a period of time. In the end, mammals became the dominant, large land animals, but current reptilian diversity (about 8160 species) is not much less than the diversity of birds (9930 species) and it is greater than the current diversity of mammals (4840 species). **See also:** Extinction: K–T mass extinction.

## Phylogeny

The phylogeny of reptiles (Figure 3) is fairly well agreed in broad outlines, but much work is yet to be done on finer details. A large number of broad-scale cladistic analyses have been carried out since the mid-1980s (see Further Reading), and these have confirmed the existence of three main lines of amniote evolution, the Synapsida, the Anapsida and the Diapsida, each characterized by a range of synapomorphies.

The Synapsida had always been recognized as distinctive, and as the group containing mammal-like reptiles and mammals. The Anapsida, however, was often seen as a ragbag group of basal reptiles, sharing only the primitive character of having no temporal opening in the posterior skull wall (Figure 1b). However, further study has shown that anapsids, including various extinct groups (pareiasaurs, procolophonids) and the modern turtles, share a number of synapomorphies of the skull and skeleton. The Diapsida has had a chequered history, recognized as a clade by many, but rejected by others who had thought that lizards and crocodiles had entirely independent origins. Diapsids, however, share the possession of two temporal openings (Figure 1b), as well as other features of the skull and skeleton.

004126.p0038 Some alternative phylogenies of amniotes have been presented. One of these has birds and mammals paired as very close relatives, with the remaining amniotes more distantly related. This view, though supported by some molecular data, is opposed by a huge amount of morphological, and particularly fossil, data. The long and detailed fossil records that document the origin of birds from theropod dinosaurs, and of mammals from among the Permian synapsids, cannot be ignored, and they show an early split of the bird and mammal lines back in the Mid Carboniferous, 320 Ma, and not in the Triassic, 220 Ma, the alternative view. Another proposal made in 1998 and 1999, supported by some molecular and morphological evidence, and disputed by others, is that turtles are really diapsids, but whether they are closer to the lepidosaurs or the archosaurs is debated. If accepted, this view will be hard to square with the evidence of cladograms compiled from fossils. **See also:** Aves (birds); Mammalia (mammals).

## Synopsis

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004126.p0039 Reptiles are a paraphyletic group, the residue of the clade Amniota, when birds and mammals are removed. Modern reptiles – turtles, crocodylians, lizards and snakes – are a disparate group, but they give little indication of the rich fossil history of amniotes, which includes such major extinct groups as the mammal-like reptiles, dinosaurs, pterosaurs, plesiosaurs and ichthyosaurs. Reptiles lay eggs on land, and some exhibit parental care. They have adaptations for water-saving and for food-saving, possibly because their ectothermy requires far less food and water than endothermy. Reptiles today are particularly well adapted to arid and hot conditions.

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## Glossary

*Amniote*#A vertebrate that lays an amniotic, or cleidoic, egg; includes reptiles, birds and mammals.

*Amniotic egg*#An enclosed egg with a shell and amniotic membranes that protect and nourish the developing embryo (same as cleidoic egg).

*Clade*#A monophyletic group, one that has a single ancestor, and includes all descendants of that ancestor.

*Cleidoic egg*#An enclosed egg incorporating much yolk to nourish the developing embryo (same as amniotic egg).

*Ectothermy*#'Cold-bloodedness'; the condition in which an animal does not generate heat to warm its body by internal means.

*Endothermy*#'Warm-bloodedness'; the condition in which an animal generates heat to warm its body by internal means.

*Kinesis*#Mobility (of a skull, typically) about particular joints.

*Monophyletic*#Pertaining to a group that has a single ancestor, and includes all descendants of that ancestor, a clade.

*Paraphyletic*#Pertaining to a group that has a single ancestor, but does not include all descendants of that ancestor.

*Phylogenetic*#Relating to phylogeny (patterns of evolution and relationships).

*Synapomorphy*#A shared derived character; in cladistics, a character that defines a clade.

004126.t0001 **Table 1** Classification of the reptiles, a consensus view based on the latest cladistic analyses (from Benton, 2004)

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Series Amniota

Class Reptilia

Subclass Synapsida

Order Pelycosauria (paraphyletic)

The extinct early mammal-like reptiles, including sail-backed forms (Late Carboniferous to Mid Permian)

Order Therapsida

Later mammal-like reptiles, with more mammalian characters, and including class Mammalia (Late Permian to Recent)

Subclass Anapsida

Family Procolophonidae

Extinct small broad-skulled herbivores and insectivores (Late Permian to Late Triassic)

Family Pareiasauridae

Extinct bulky herbivores (Late Permian)

Order Testudines (Chelonia)

Turtles and tortoises (Late Triassic to Recent)

Subclass Diapsida

Infraclass Lepidosauromorpha

Division Euryapsida

Pachypleurosaurs, nothosaurs, plesiosaurs, pliosaurs, and placodonts, extinct marine reptiles (Triassic to Cretaceous)

Division Ichthyosauria

Ichthyosaurs, extinct marine reptiles (Triassic to Cretaceous)

Superorder Lepidosauria

Order Sphenodontida

The sphenodontids, extinct and living (Late Triassic to Recent)

Order Squamata

Suborder Lacertilia (Sauria)

Lizards (Mid Jurassic to Recent)

Suborder Serpentes (Ophidia)

Snakes (Early Cretaceous to Recent)

Infraclass Archosauromorpha

Division Archosauria

Subdivision Crurotarsi

Superorder Crocodylomorpha

Order Crocodylia

Crocodiles, alligators, gavials, and extinct relatives (Late Triassic to Recent)

Subdivision Ornithodira

Order Pterosauria

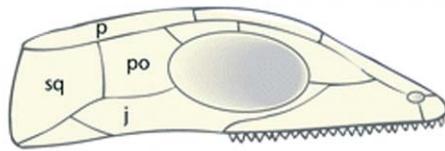
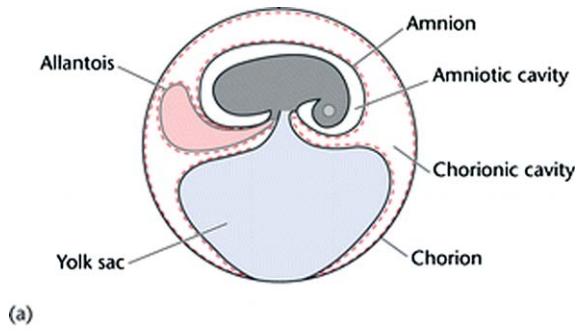
Extinct flying reptiles (Late Triassic to Cretaceous)

Superorder Dinosauria

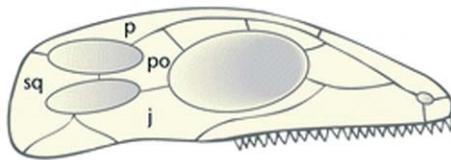
Large to giant extinct land reptiles, and including class Aves (Late Triassic to Recent)

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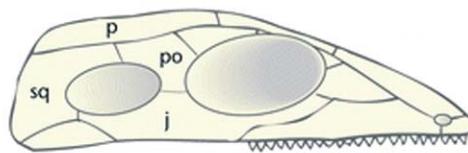
*Note:* Aves(birds) are included, as a part of the larger clade Archosauria



Anapsid



Diapsid



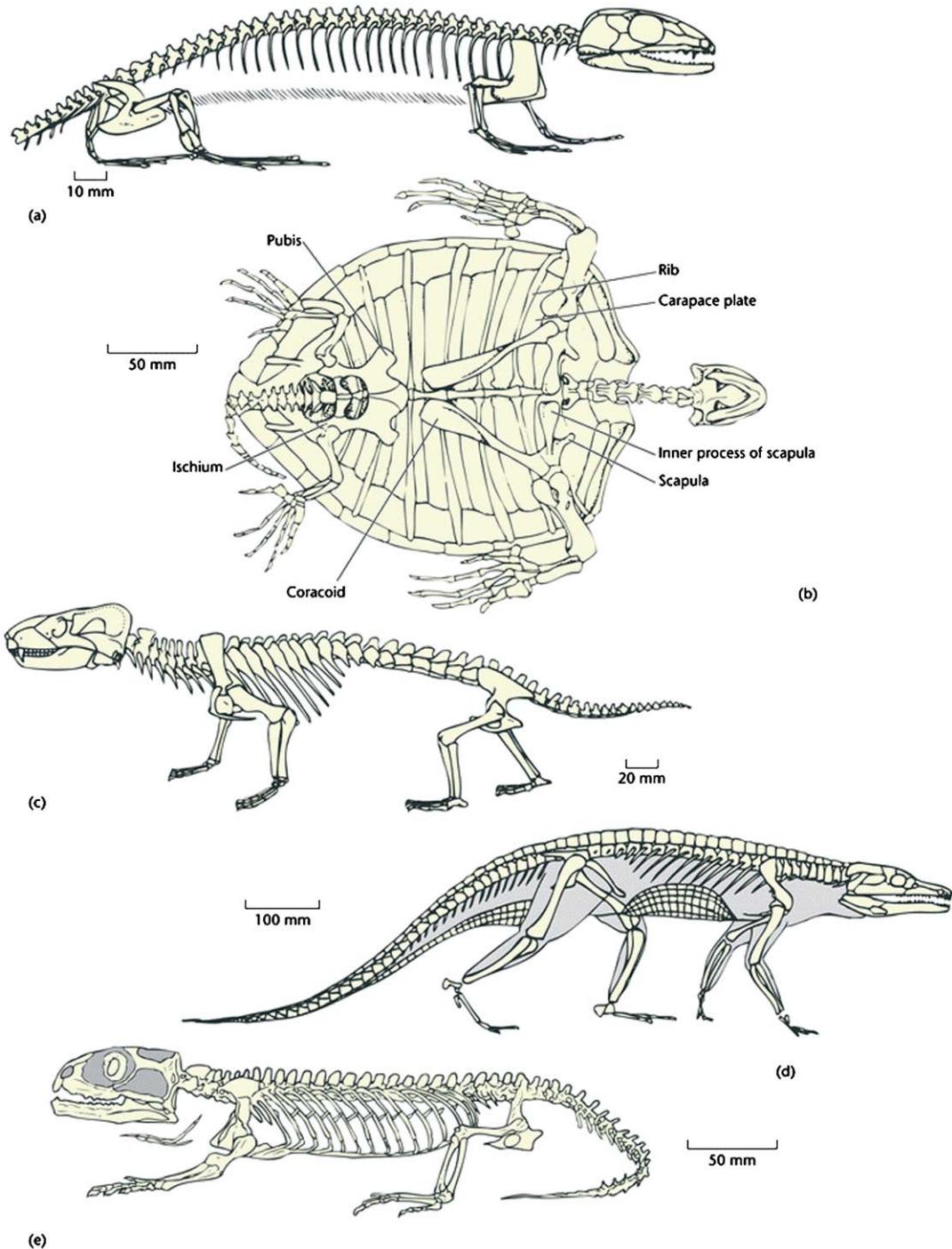
Synapsid

(b)

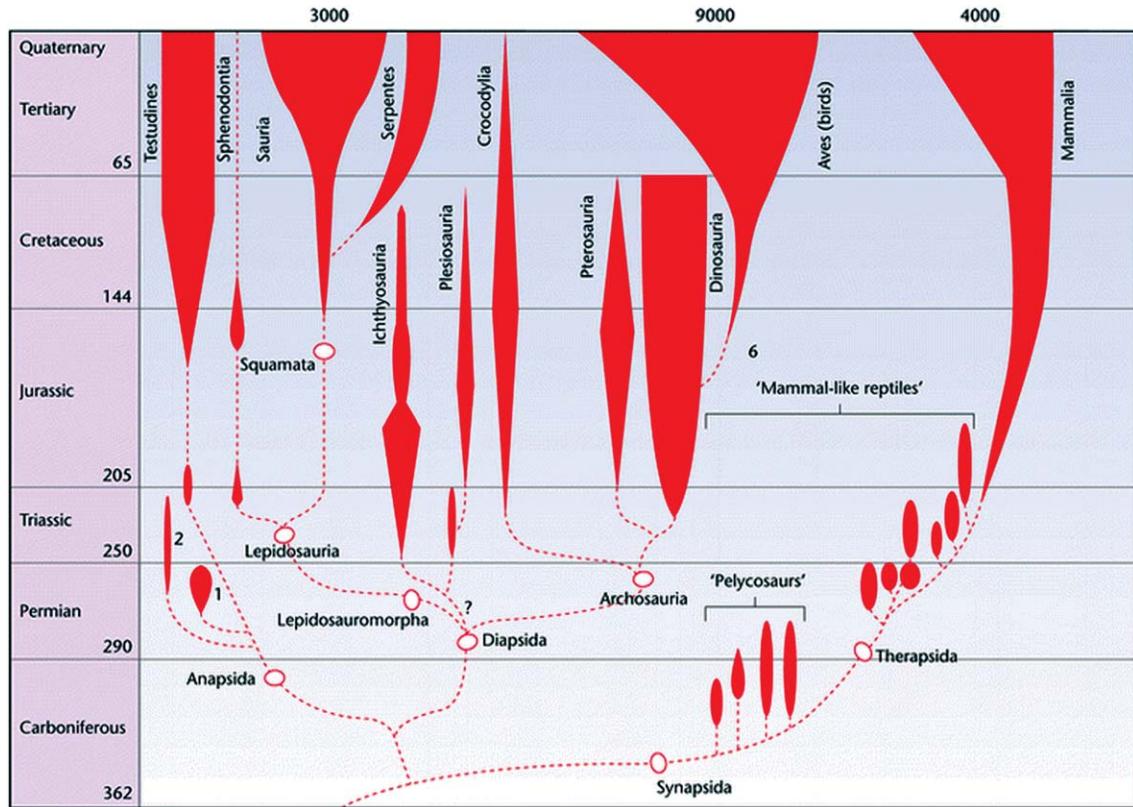
004126.f0001 **Figure 1** Basic amniote characters. (a) The cleidoic egg, showing the semipermeable shell and the extraembryonic membranes. (b) The main skull designs seen in reptiles, and amniotes in general: anapsid, diapsid and synapsid. Abbreviations: j, jugal; p, parietal; po, postorbital; sq, squamosal. Based on various sources.

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## Reptilia (Reptiles)



004126.f0002 **Figure 2** Basic design of a diversity of reptiles. (a) The basal amniote *Paleothyris*, from the Mid Carboniferous of Canada. (b) The living marine turtle *Chelone* seen from below, with the plastron removed. (c) The extinct synapsid *Thrinaxodon*, from the Early Triassic of South Africa. (d) The extinct crocodylian *Protosuchus* from the Early Jurassic of North America. (e) The living sphenodontid *Sphenodon*, the tuatara. Based on various sources.



004126.0003 **Figure 3** Phylogeny of the Amniota, focusing on the major groups of reptiles, their fossil history and current diversity. 1, Pareiasauridae; 2, Procolophonidae.