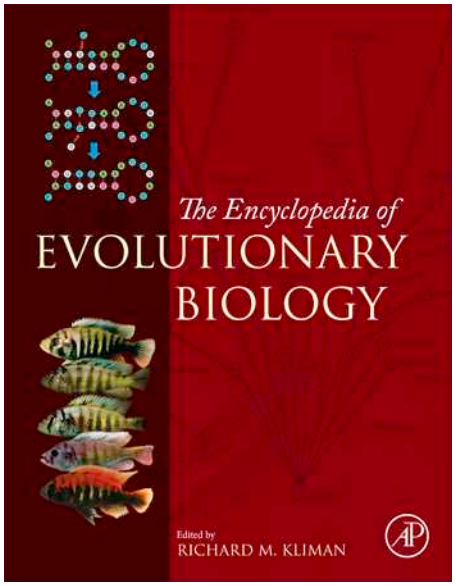

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Amniotes, Diversification of

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Glossary

Amniota A major clade of tetrapods, comprising reptiles, birds, mammals, and related forms. All amniotes have eggs that are characterized by the presence of an amnion, a membrane that encloses the embryo in a fluid-filled chamber.
Clade A group of organisms that comprises the last common ancestor of these organisms and all extant and extinct descendants of that ancestor is called clade.
Cranium The part of the skull that houses the brain and the organs of sense is called cranium.
Diapsida A clade of amniotes characterized by the presence of two openings behind the eye socket on either side of the cranium. Some diapsids no longer retain one or even both of these openings. Present-day diapsids comprise turtles (which have secondarily lost the openings), lizards, snakes, the tuatara, crocodylians, and birds.
Synapsida A clade of amniotes comprising mammals and their extinct close relatives (often misleadingly referred to as 'mammal-like reptiles'). Synapsids are characterized by the presence of a single opening behind the eye socket on either side of the cranium.
Taxon A group of one or more organisms deemed to be a unit within a hierarchical biological classification is called taxon.

Introduction

Reptiles, birds, and mammals and their closest relatives are grouped together as Amniota based on the shared possession of the amniotic (cleidoic) egg (Figure 1). This type of egg is laid on land and differs from that of amphibians in the presence of an outer shell and a set of extraembryonic membranes surrounding the embryo (Packard and Seymour, 1997; Stewart, 1997). The shell is either parchment-like or calcified and protects the egg's contents against desiccation and damage. (With the exception of the platypus and the echidnas, present-day mammals do not lay eggs.) The eggshell is semipermeable, permitting intake of oxygen for respiration and disposal of carbon dioxide. Four membranes surround the embryo. The first is the allantois, which forms a sac attached to the embryo and serves for storage of waste and for respiration. The second is the amnion, which encloses a fluid-filled chamber surrounding and protecting the embryo. The third is the chorion, which envelops the embryo and attached structures and is in close contact with the allantois and with the inside of the shell, facilitating respiration. The fourth is the membrane forming the yolk sac, which provides the developing embryo with nourishment. By contrast, present-day amphibians (and presumably their extinct precursors) typically deposit their eggs in water (Packard and Seymour, 1997). The egg is coated in a jelly-like substance, and the developing embryo receives oxygen and much of its nourishment from the surrounding water. A gilled larva hatches from the egg and continues its development in water. Finally, it undergoes a process of metamorphosis before emerging as an adult capable of life on land. The evolution of the cleidoic egg allowed amniotes to move into drier environments because they were no longer tied to permanent bodies of water for reproduction. No undisputed fossil eggs of amniotes are known from the Paleozoic to date but the fact that present-day reptiles, birds, and mammals all share the amniotic egg suggests that it had already evolved before the reptile-bird and mammal lineages diverged in the Carboniferous. In marsupials and placentals, the eggs develop in the uterus and thus lack a shell; however, the embryo is still surrounded by an amnion (Stewart, 1997).

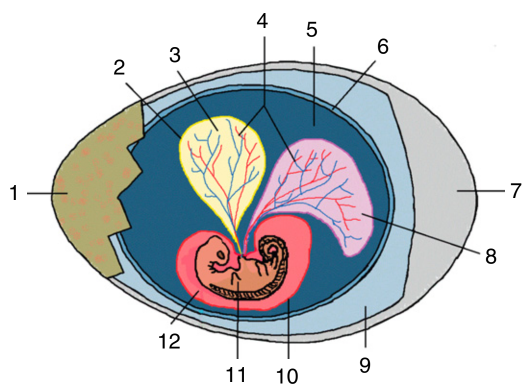

Figure 1 Diagram of the egg of a crocodile to show the basic structure of the amniotic egg. Numbers: (1) eggshell, (2) yolk sac, (3) yolk, (4) blood vessels, (5) coelomic cavity, (6) chorion, (7) air space, (8) allantois, (9) egg white, (10) amniotic sac, (11) embryo, and (12) amniotic cavity. Reproduced from Catsloveme207/Wikipedia.

Amniotic eggs acquire their shell in the oviduct of the female and thus must be fertilized before their encasement. Thus most male amniotes have special organs to deposit sperm inside the female reproductive tract.

Another major difference between amniotes and amphibians is the structure of the skin (Frolich, 1997). The skin of present-day amphibians is relatively thin, weakly keratinized, and rich in glands. By contrast, the skin of reptiles and birds is much less glandular and protected by keratin in the form of scales (Figure 2) or feathers. These features help to reduce water loss through the skin. Although richer in glands than that of reptiles, mammalian skin also contains keratin as well as lipids and is usually covered by hair.

In addition to filling and emptying their relatively small lungs through raising and lowering the floor of their mouth (buccal pumping), present-day amphibians rely extensively on

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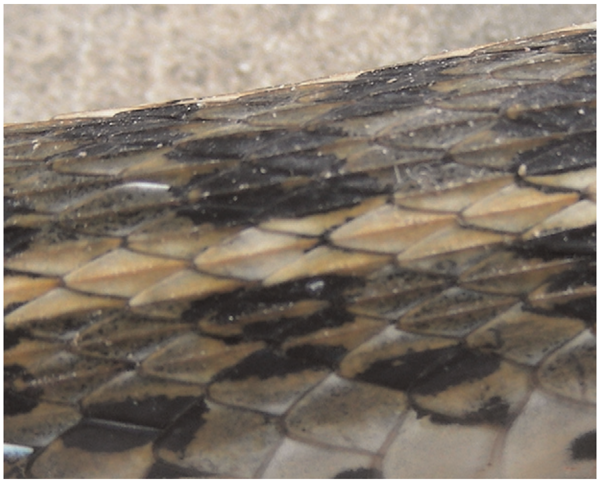

Figure 2 Keeled scales of the buff-striped keelback snake (*Amphiesma stolatum*). The scales protect the skin of reptiles against mechanical damage and help reduce water loss through the skin. Reproduced from AshLin/Wikipedia.

their skin for the intake of oxygen and excretion of carbon dioxide (Frolich, 1997). By contrast, amniotes largely abandoned cutaneous respiration. They fill and empty their larger, more complex lungs primarily by moving their ribs to alter the pressure within the thoracic cavity (Brainerd and Owerkowicz, 2006).

Present-day amniotes comprise six monophyletic groups or clades: mammals (Mammalia), turtles (Testudines), the tuatara (Rhynchocephalia), lizards and snakes (Squamata), crocodylians (Crocodylia), and birds (Aves) (Gauthier *et al.*, 1988). Mammals are characterized by the presence of hair, mammary glands, and many skeletal features. Turtles are distinguished by the possession of a bony shell, which is usually covered by scutes of keratin. Squamates are characterized by the presence of a mobile quadrate bone (along with loss of the lower temporal bar), paired hemipenes, and skin that is composed of superimposed layers of two types of keratin and is shed completely at regular intervals (Vitt and Caldwell, 2013). The tuatara is closely related to squamates but lacks the mobile quadrate bone and elaborate hemipenes. Crocodylians have air spaces in the skull bones surrounding the middle ear, elongate wrist bones, a modified pelvic girdle, and distinctive ankle structure (Nesbitt, 2011). Birds are especially characterized by the presence of wings and other features associated with powered flight, and a greatly reduced tail (Chiappe, 2007). The tuatara and squamates are classified together as Lepidosauria and crocodylians, and birds as Archosauria.

Traditional scenarios of vertebrate evolution held that reptiles separately gave rise to birds and to mammals (Romer, 1956). In recent decades, however, it has been established that the lineage leading to reptiles and their descendants, birds, and the lineage leading to mammals were already distinct by the time both first appear together in the fossil record some 310 million years ago (Gauthier *et al.*, 1988; Clack, 2012).

Amniotes have a vast fossil record worldwide, dating back more than 300 million years. There are over 20 000 known species of present-day reptiles and birds and some 5500 species of extant mammals. Although the Cenozoic is commonly known as the 'Age of Mammals' the combined number of species of reptiles and birds is now almost four times higher than that of mammals.

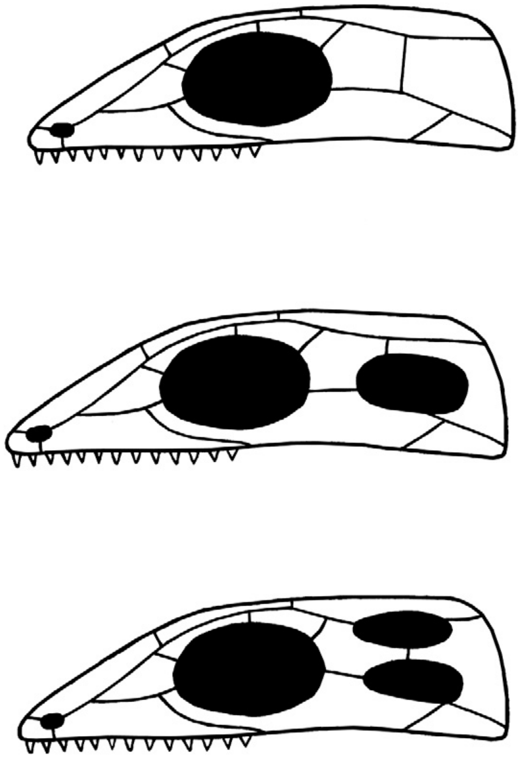

Figure 3 Diagrams of crania of amniote vertebrates. Top: anapsid condition (without temporal openings); center: synapsid condition (with one temporal opening); bottom: diapsid condition (with two temporal openings). Reproduced from H.-D. Sues/Public Domain.

Synapsida

The lineage leading to mammals is characterized by the presence of a single large opening behind the eye socket (orbit) on either side of the cranium (Kemp, 2005). This is known as the synapsid condition (**Figure 3, center**). The opening, called the temporal opening, lightens the skull, and its margins serve for attachment of jaw-closing muscles. Based primarily on this feature, mammals and their precursors are grouped together as Synapsida. Non-mammalian synapsids have traditionally been referred to as 'mammal-like reptiles' but this term has become scientifically meaningless. The earliest synapsids, often referred to as 'pelycosaurs,' are known from the Late Carboniferous and Permian (Kemp, 2005). They included forms with a range of shapes and sizes but superficially lizard-like in appearance. Some were among the first large herbivores whereas others, such as the 'fin-backed' *Dimetrodon* (**Figure 4**), were the first apex predators on land. They retained a sprawling gait, as in other early tetrapods. More derived synapsids, known as Therapsida, comprise a range of increasingly more mammal-like forms that came to dominate global land ecosystems during the latter half of the Permian and much of the Triassic

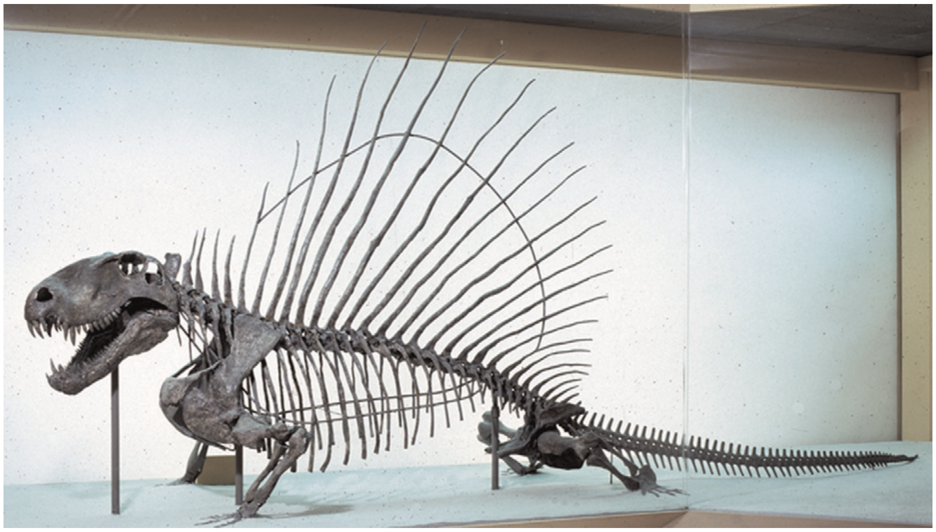

Figure 4 Skeleton of *Dimetrodon grandis*, an Early Permian synapsid. Superficially resembling certain reptiles, *Dimetrodon* is actually closely related to mammals. Reproduced from National Museum of Natural History/Public Domain.

(Kemp, 2005). Therapsids have a much larger temporal opening than 'pelycosaurs.' They also have a relatively larger upper canine, a groove for the ear canal on the squamosal bone, and the angular bone bears a distinct process, which supported the precursor of the eardrum in mammals. The girdle bones of therapsids are less massive and their limb bones are more slender than those of early synapsids, suggesting greater freedom of limb movement and greater ability to lift the body further off the ground. One therapsid group, Cynodontia, includes the immediate antecedents of mammals (Kemp, 2005). Cynodonts have dentitions differentiated into incisors, canines, and postcanine (cheek) teeth, a typically closed secondary bony palate, and a lower jaw in which the tooth-bearing dentary is the principal element whereas the bones behind the dentary became much smaller. The bones behind the dentary subsequently became detached from the lower jaw, attached to the cranium, and formed a chain of three small bones (incus, malleus, and stapes) in the middle ear of mammals. Based on the structure of the dentary bone, the jaw-closing muscles in early cynodonts had already attained a mammal-like differentiation with a superficial masseter and deeper masseter and temporalis muscles. The crowns of cynodont cheek teeth have large cusps and shelves composed of small cusps (cingula), indicating various degrees of oral food processing. The trunk region comprises a thorax with long, mobile ribs at the front and a lumbar region with short ribs further back. The femur (thigh bone) was held closer to the body unlike in 'pelycosaurs,' in which it extended nearly horizontally from the body. Presumably maintenance of a constant high body temperature and higher basic metabolic rates evolved among cynodonts, if not earlier. Development of these physiological attributes was likely accompanied by the development of hair for insulation.

Mammaliaformes, defined as the group comprising Mammalia and their closest extinct relatives, dates back to the Late Triassic (Kemp, 2005). Mammalia, defined as the most recent common ancestor of monotremes, metatherians (marsupials and their closest relatives), and eutherians (placentals and their closest relatives) and all descendants of that ancestor, first appears in the Middle Jurassic. Mammaliaformes is characterized by the possession of a well-developed joint formed by the dentary bone of the lower jaw and the squamosal (temporal) bone of the cranium. (By contrast, the articular bone of the lower jaw and the quadrate bone of the cranium form the jaw joint in other amniotes.) The roots of the cheek teeth are divided, and, in most forms, the upper and lower teeth met in a precise manner (occlusion) to facilitate the chewing of food. Additional characteristic features are present in the structure of the ear region and the braincase, the latter related to a major increase in brain size. Exquisitely preserved fossils from the Early Cretaceous of northeastern China have established that metatherian and eutherian mammals were already distinct groups more than 120 million years ago (Luo *et al.*, 2011). However, the diversification of evolutionary lineages represented by present-day mammals largely postdated the extinction of dinosaurs other than birds some 66 million years ago (Rose, 2006). Today, placentals are the most widely distributed and diverse group of mammals worldwide whereas marsupials are restricted to the Americas and to Australia.

Reptilia

Among reptiles, there are two principal types of skull structure (Rieppel, 1993). In the first type, there are no temporal openings behind the orbit on either side of the cranium (**Figure 3**, top). This is the anapsid condition, which is found only in turtles among present-day amniotes. In the second type, two large openings perforate the side of the cranium behind the orbit (**Figure 3**, bottom). This is the diapsid condition, which is present (often in highly modified form) in most extant and extinct reptiles as well as in birds.

The oldest known reptiles, of Late Carboniferous age, were small and lightly built (Clack, 2012). One group lacks temporal openings but has other skeletal features, such as long

Figure 5 Florida gopher tortoise (*Gopherus polyphemus*). Reproduced from Tomfriedel/Wikipedia.

and slender limbs with slender hands and feet that ally it to diapsid reptiles.

Parareptilia represents an entirely extinct group of early reptiles that were once considered closely related to turtles (Tsuji and Müller, 2009). They ranged in time from the end of the Carboniferous to the end of the Triassic. Some parareptiles have openings behind the eye socket in the cranium but others lack such features. Most have an embayment formed by the squamosal and quadratojugal at the back of the cranium, which probably supported an eardrum. Together with the slender stapes (which conducts sound vibrations from the eardrum to the inner ear), the eardrum formed an impedance-matching ear. This hearing mechanism evolved quite independently from those in other reptiles and in mammals.

All other reptilian groups are united as Eureptilia. Turtles are easily distinguished from other reptiles by their bony shell (**Figure 5**). The shell comprises a dorsal carapace and a ventral plastron, which are linked by a bony 'bridge' on either side (Romer, 1956). Parts of the shoulder girdle and the ribs are integrated into the bony shell. The head, neck, and limbs can be withdrawn into the shell in most present-day turtles. Turtles lack true temporal openings although the back of the cranium is distinctly emarginated in many species (Rieppel, 1993). Thus, most paleontologists assumed that turtles evolved from the earliest known reptiles (Romer, 1956). However, recent discoveries have established that turtles evolved from early diapsid reptiles and some stem-turtles retained two temporal openings on either side of the cranium (Schoch and Sues, 2015).

Aside from turtles, diapsid reptiles comprise archosaurs, lepidosaurs, and their closest extinct relatives. In addition to the two temporal openings, diapsids also share the presence of a large opening in the bony palate, the suborbital fenestra (Rieppel, 1993). Archosaurs and lepidosaurs (which are united as Sauria; Gauthier *et al.*, 1988) share a number of features related to the development of an impedance-matching hearing system with an eardrum (tympanic membrane): the quadrate bone is bowed, the retroarticular process of the lower jaw is long, and the stapes is slender (Rieppel, 1993). These features are still lacking in the oldest known diapsid reptiles. Diapsids also have a more or less L-shaped ('hooked') fifth metatarsal bone, which supports the fifth toe and is thought to assist in extending the foot. The early evolutionary history of diapsid reptiles is still poorly known due to the scarcity of well-preserved fossils from the late Paleozoic. However, from the early Mesozoic onward, diapsids have a rich and varied fossil record (Benton, 2014).

Present-day lepidosaurs include lizards, snakes, and the tuatara (Vitt and Caldwell, 2013). The known fossil record of the tuatara and its relatives (Rhynchocephalia) dates back to the Triassic whereas the oldest fossil lizards are known from the Jurassic and the oldest fossil snakes are known from the Cretaceous. The skulls of lizards have additional joints that allow them to increase the gape of their mouths and manipulate their food more effectively. Lizards generally have slender bodies with long limbs. The two principal anklebones, the astragalus and calcaneum, are fused. Lizards do not grow indefinitely, unlike many other reptiles, and their limb bones have separate ossifications (epiphyses) at their joint ends. Many species reduce or even lose their limbs. Snakes evolved from limbed lizards although their precise relationships remain contentious (Hsiang *et al.*, 2015). They completely lost their forelimbs and shoulder girdle, and the much elongated vertebral column sometimes comprises over 400 vertebrae. The bones of the upper jaws and palate in snakes are loosely joined to each other and to the braincase, and, along with a ligamentous connection between the lower jaws, facilitate the capture and manipulation of prey (Rieppel, 1993). Snakes use constriction or venoms to subdue and kill their prey (**Figures 6–8**).

During the Mesozoic, a number of groups of diapsid reptiles independently adapted to life in the sea (Motani, 2009). They included ichthyosaurs, which are often remarkably fish-like in their body plan, and plesiosaurs, which used four flipper-like limbs for swimming. These groups may be more closely related to lepidosaurs than to archosaurs.

Archosaurs include dinosaurs (including birds), pterosaurs (flying reptiles), crocodylians, and the extinct close relatives of these groups (Nesbitt, 2011). They date back to the Early Triassic. Only birds and crocodylians survived to the present

Figure 6 Tuatara (*Sphenodon punctatus*). The tuatara is the lone present-day survivor of a once diverse group of reptiles closely related to lizards and snakes. Reproduced from Samsara/Wikipedia.

Figure 7 Desert iguana (*Dipsosaurus dorsalis*). Reproduced from Wilson44691/Wikipedia.

day. Birds descended from small predatory dinosaurs and evolved active, flapping flight (Chiappe, 2007). Most researchers now agree that birds should be classified as a subgroup of dinosaurs. Many features commonly associated with birds, such as feathers, the furcula (wishbone), and a specialized wrist joint, were already present in small predatory dinosaurs. A wide range of often exquisitely preserved fossils, especially from the Jurassic and Cretaceous of China, documents a series of intermediate stages in the evolution of the bird skeleton and flight adaptations in great detail (Chiappe, 2007). The major diversification of birds, during which most major modern groups evolved, took place only during the Cenozoic (Mayr, 2014). Starting at the end of the Triassic, dinosaurs became the dominant carnivores and herbivores in continental ecosystems for much of the Mesozoic (Fastovsky and Weishampel, 2012). They included the largest animals that ever lived on land. Pterosaurs are closely related to dinosaurs and evolved active flight long before and independently from birds (Witton, 2013). The wing membrane was attached to the enormously elongated fourth finger. Pterosaurs dominated the air for much of the Mesozoic and included the largest flying animals of all time. Present-day crocodylians are represented only by some 25 species, which are mostly amphibious ambush predators (Grigg and Kirshner, 2015; **Figure 9**). However, crocodylians and their closest relatives were far more diverse during earlier geological periods. Their earliest precursors were land-dwelling pursuit predators.

Figure 8 Western diamondback rattlesnake (*Crotalus atrox*). Reproduced from Gary Stolz, USFW/Public Domain.

Figure 9 American crocodile (*Crocodylus acutus*). Reproduced from Tomás Castelazo/Wikipedia.

Amniotes represent one of the great success stories in the evolution of vertebrates. They attained a global distribution and are found everywhere except in the greatest depths of the ocean.

See also: Amniotes, the Origin of. Birds, Diversification of. Mammalian Diversification

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