Biology 356 - Major Features of Vertebrate Evolution
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Aquatic Reptiles

A return to the water is not uncommon among reptiles. It has been argued that because of the relatively low metabolic rates, tolerance to anoxia, and generally low body temperatures reptiles can make the transition from a terrestrial lifestyle to an aquatic one without major difficulties. It has been shown experimentally, in the modern marine iguana that the metabolic cost of swimming is only one-quarter that of walking. However, a return to the water to catch an easy meal is not the same as life in the water. Many reptiles today are amphibious and at home in the water but they do not live their entire lives there. Back in the Paleozoic and more notably in the Mesozoic many reptiles did evolve a fully aquatic lifestyle; it is these groups that we will study.

The relationships between Paleozoic and Mesozoic marine reptiles and their terrestrial relatives are difficult to assess, but the taxa discussed in this chapter are now generally considered to be derived from diapsids, probably lepidosauromorphs, with the lower temporal fenestra being without a lower temporal bar, and only the upper temporal fenestra being retained in its original form.

Nothosaurs are medium-sized aquatic reptiles restricted to the Triassic. They are one of the two major groups of sauropterygians (the other one being plesiosaurs). They range in length from 20 cm to 4 m in body length. Their skull is small. The lower temporal bar has been lost. The slender stapes and quadrate emargination suggest that they may have had a tympanum, and that they were probably related to saurians. The interpterygoid vacuity is closed. This type of palate links nothosaurs with plesiosaurs.

The ribs of nothosaurs were often **pachyostotic**. Their limbs and girdles are poorly ossified, but they have no striking aquatic adaptations. However, the pectoral girdle is very strange; the **interclavicle** has no posterior shaft, the **clavicle** is dorsal and medial to the scapula, and the clavicular blade is fused to the scapula. The interclavicle is ventral to the head of the clavicle. In most other amniotes, the interclavicle has a long posterior shaft, the clavicle is ventral and lateral to the scapula, and its shaft is free from the scapula. In almost all other tetrapods, the head of the clavicle is ventral to the interclavicle. The scapula and coracoid are poorly ossified, and there is a large fenestra in the ventral surface of the girdle. The distal limb elements are small compared to the propodials (humerus and femur). The carpus and tarsus are poorly ossified; several elements are not preserved and must have remained cartilaginous in the adults.

Nothosaurs probably swam relatively slowly by lateral undulation. The limbs were probably used for steering, although some people think that the forelimbs may also have been used for propulsion, because the coracoid is relatively large.

The **Plesiosauria** is a group of aquatic diapsids closely related to nothosaurs. They appeared in the Jurassic and became extinct at the end of the Cretaceous. They have a short trunk and a short tail. Their coracoid and to a certain extent their scapula, are greatly expanded ventrally. Young plesiosaurs had a shoulder similar to nothosaur's girdle; this may be an example of recapitulation. Plesiosaurs have massive ventral scales called **gastralia**. These scales may have strengthened the trunk. This would have been useful, because plesiosaurs used their limbs to swim.

The exact way in which the limbs were used is still debated. They may have swam much like the modern leatherback turtle (by subaqueous flight) or rowed like sea lions. According to some, the short scapular and iliac blades implies that the muscles elevating the limbs were weak and poorly suited for subaqueous flight. On the other hand, perhaps the origin of these muscles had just shifted medially, closer to the vertebral column. The massive coracoids would in any case provided a large surface for attachment of the forelimb retractor muscles. So, this question remains unsolved.

Placodonts are Triassic aquatic reptiles with robust tooth plates that strongly suggest that they had a durophageous diet; they may have fed on mollusks and arthropods. They had a short, stout body. They had no interptterygoid vacuity, which is not surprising, considering that their skull is extremely robust. The internal naris (choana) is a single, median opening. Their anterior dentary and premaxillary teeth are procumbent and spatulate; they were probably used to grab the prey.

Placodonts had long transverse processes, a derived character found in plesiosaurs and archosauromorphs. This may not indicate affinities, because large amniotes usually have long transverse processes. The interclavicle has a very short posterior stem and it is ventral to the clavicle, as in nothosaurs. The endochondral shoulder girdle is poorly ossified. Some genera had a carapace composed of polygonal dermal bones covered by epidermal scutes. In the most advanced members of this group the shoulder girdle has moved inside the armor and rib-cage, in a similar fashion to that seen in turtles. Some armored placodonts had lost their anterior teeth and may have had a horny beak instead.

Ichthyosaurs were similar to dolphins and sharks in size and shape. They appeared in the Lower Triassic, were numerous in the Jurassic, and became extinct well before the end of the Cretaceous. Of all the Paleozoic and Mesozoic marine diapsids, they were the most highly adapted to a marine existence. Typical ichthyosaurs (from the Jurassic and Cretaceous) had a relatively short, fusiform trunk, a dorsal fin, a high, lunate caudal fin. We know about the dorsal fin because some specimens have the body outline preserved as a carbonaceous film. These features suggest that ichthyosaurs could swim fairly fast. We know that ichthyosaurs were viviparious, because some of them died while giving birth and were preserved with the young ichthyosaur still in the pubic canal.

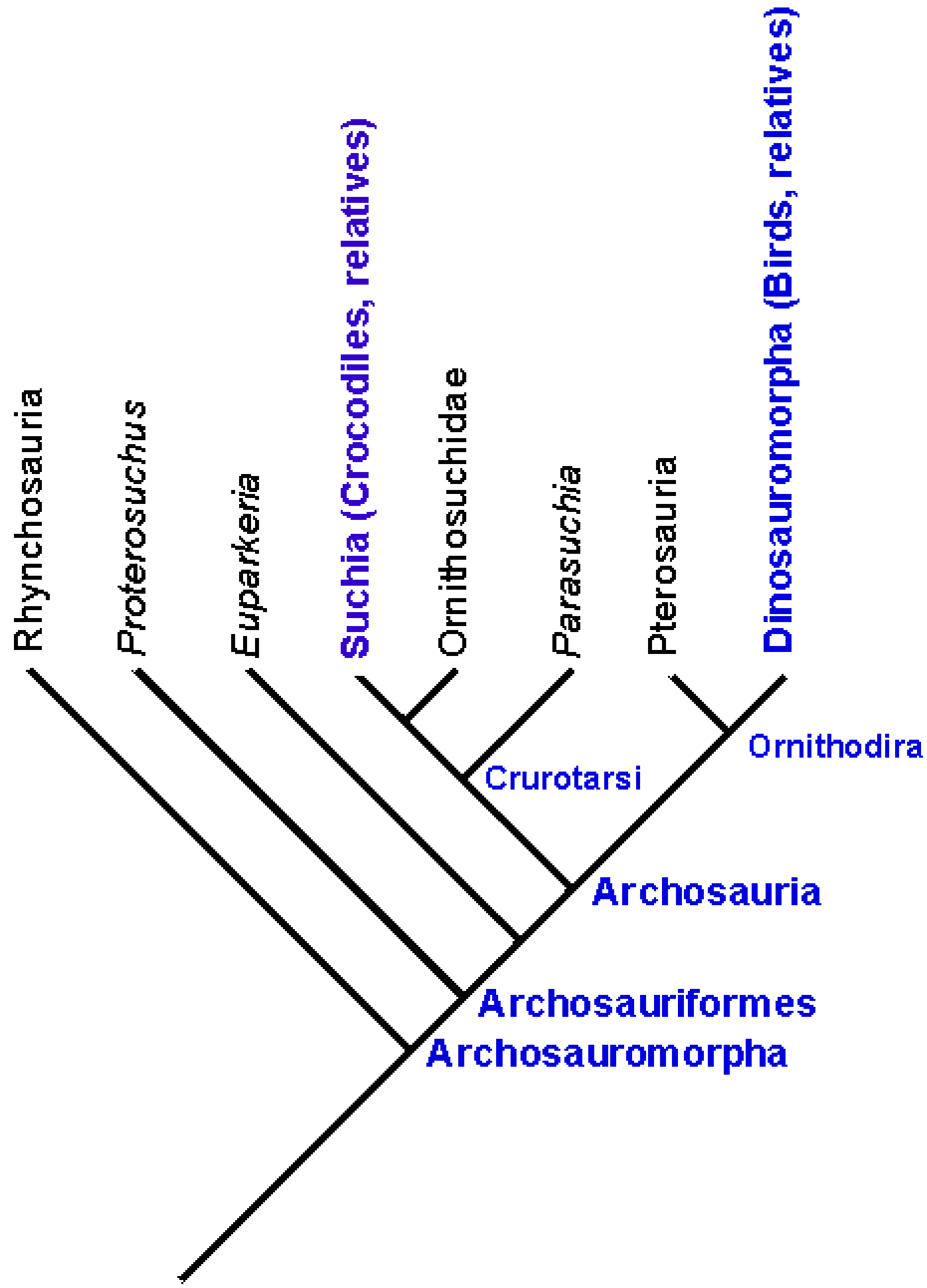
The orbit was large and the eye was protected by a well ossified scletrotic ring. The snout was long and bore several homodont, sharp teeth (in most genera). The quadrate was not notched posteriorly and the stapes was relatively massive and articulated with the quadrate distally, so there was probably no tympanum (it would not have been useful under water). The vertebrae of ichthyosaurs were short, wide amphicoelous disks. The neural arches never fused to the centra and there were no transverse processes.

Early archosauromorphs and crocodiles

Archosauromorphs include archosaurs (crocodiles, birds, dinosaurs and pterosaurs) and their close relatives. They share the following synapomorphy:

- A dorsolateral process of the premaxilla extending below the external naris.

Rhynchosaurs were the most common and widespread early archosauromorphs. They are found throughout the Triassic. They have been used for biostratigraphic correlations. They have a single, median external naris and a premaxillary beak. Mesosuchus is a Lower Triassic rhynchosaur, more primitive than later rhynchosaurs in retaining premaxillary teeth and in having a single row of maxillary and dentary teeth. Later rhynchosaurs have multiple tooth rows and a very broad skull. Rhynchosaurs were among the most abundant large herbivores in the Middle and Upper Triassic. Their extinction at the end of the Triassic may support the existence of a mass extinction event at that time. The relationships between prolacertiforms, rhynchosaurs, Trilophosaurus and other archosauromorphs are unclear, so we can summarize what we know of archosauromorph phylogeny with this cladogram:



Archosauromorph phylogeny. Extant groups are in bold, blue type.

The remaining archosauromorphs are included in the **Archosauriformes**. This group includes archosaurs and their closest relatives. It includes Proterosuchus, the Erythrosuchidae, Euparkeria, the Proterochampsidae and archosaurs. In our classification, archosaurs are crocodiles, birds, and all the descendants of their last common ancestor. Animals like Proterosuchus and Euparkeria, which used to be classified in the Archosauria (because they looked like archosaurs), are now excluded from it, because they are not derived from their last common ancestor. Archosaurs can be divided into two major groups: the **Crurotarsi**, which includes crocodiles and their fossil relatives, and the **Ornithodira**, which includes birds and their fossil relatives.

We can now study archosauriforms.

Proterosuchus is known from the Lower Triassic of Southern Africa and China. It was about 1.5 m long and was probably an aquatic carnivore. It retained a sprawling posture, as shown by its straight femur. Proterosuchus is united to other archosauriforms by the following synapomorphy: An **antorbital fenestra**. This was probably just a pneumatic structure, as in modern birds. It made the skull lighter.

Next we come to **Euparkeria**, a small archosauriform (body length around 50 cm including the tail) from the Lower Triassic of South Africa. Euparkeria had a semi-erect posture, but it was probably not bipedal, even though it has usually been reconstructed that way.

The **Archosauria** is one of the most successful groups of reptiles. Birds and crocodiles are the only living representatives of this highly diverse group that included dinosaurs, flying reptiles, and other spectacular forms. The earliest archosaurs have traditionally been collected together as the **Thecodontia**. The name refers to the fact that the teeth are implanted in deep sockets in the jaws. This type of tooth implantation is also found in mosasaurs and the mammal-like reptiles. Thecodonts first appeared in the Upper Permian and diversified throughout the Triassic. The term **Thecodontia** is no longer valid because it does not include the descendants of thecodonts, the dinosaurs, birds, and crocodiles. From now on, I will call them early archosaurs.

Recent attempts at classification of the early archosaurs have used the structure of the ankle joint. Four different types of ankle joints can be identified according to where the hinge is located.

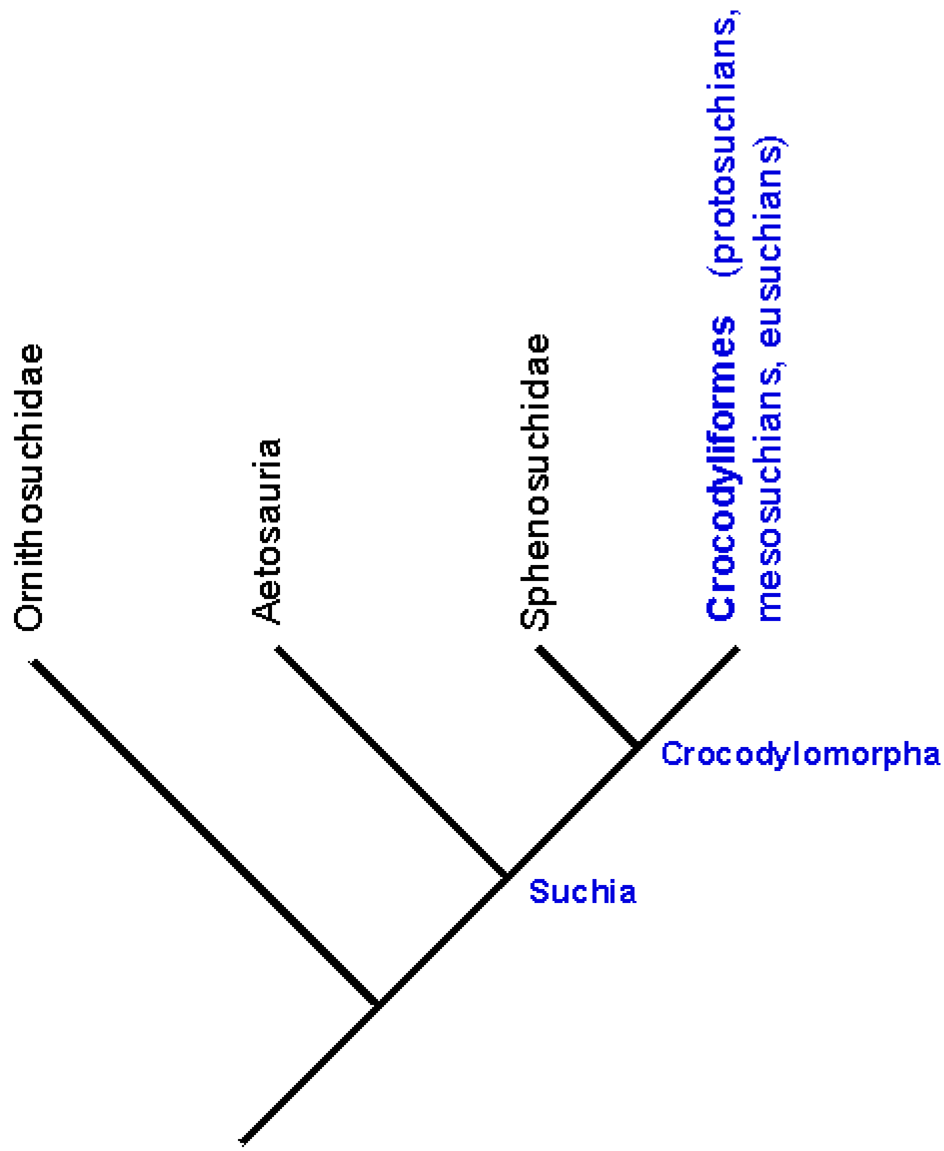
In basal diapsids, the hinge is between the two main ankle bones, the astragalus and calcaneum, and the tarsals. This is called the **primitive mesotarsal** joint. The earliest archosauriforms perhaps even Euparkeria, have this type of ankle. Dinosaurs and birds have a second type of ankle called an **advanced mesotarsal** joint. The axis is in the same place, but the astragalus and calcaneum are attached to the tibia and fibula. The other two types of ankle joints have a hinge between the astragalus and calcaneum. In one, called the **crocodile-normal** found in living crocodiles, a peg on the astragalus fits into a socket on the calcaneum. The other is the **crocodile-reverse** which, as the name suggests, is opposite. That is, the peg is on the calcaneum and the socket on the astragalus. A dinosaur specialist, Sereno argued quite convincingly that the distinction between crocodile-normal and crocodile-reverse articulations are not nearly as useful to reconstruct the phylogeny of archosaurs as we used to think. The crocodile-normal joint is found in the Suchia, whereas the crocodile-reversed joint is found in the Ornithosuchia.

Phytosaurs (Parasuchia) are distant relatives of crocodiles. Therefore, it is not surprising that they are the most crocodile-like of the archosaurs in both morphology and probable habits. They are especially similar to the modern gavial. They were large reptiles with body lengths between 2 and 4 meters. They had a sprawling posture. Phytosaurs can be easily distinguished from crocodiles by one feature. The nostrils of phytosaurs are placed on a prominent bump on the top of the head. This adaptation allowed a phytosaur to lie in waiting under water with only the eyes and the nostrils visible. Crocodiles, on the other hand, have their nostrils at the tip of the snout. Phytosaurs were abundant during the Upper Triassic in North America, India, and central Europe. Their extinction near the end of the Triassic opened up an ecological niche that was soon occupied by true crocodiles.

Phytosaurs are united to other Crurotarsi by the presence a pair of paramedian **osteoderms** per dorsal vertebra. There is one scute on each side of the neural spine (there is no body armor primitively in pterosaurs and dinosaurs).

Ornithosuchids were large quadrupedal carnivores from the Upper Triassic of Scotland and Argentina. They bore numerous resemblances to some dinosaurs, especially the carnosaurs. They had a diastema in the posterior half of the premaxilla. Two large anterior dentary teeth fit in it. There was a frontal-lacrimal contact. There was a fenestra medial to the suborbital fenestra. Their ankle joint was the crocodile-reverse, unique among thecodonts. They had an erect posture.

The phylogeny of the Suchia is as follows:



Phylogeny of the Suchia. Extant groups are in bold, blue type.

Aetosaurs are a group of large, quadrupedal suchians with heavy body armor consisting of large, overlapping plates. These plates covered most of the body and tail. Some had long spikes that projected outwards. Aetosaurs are known from the Upper Triassic of North America and Europe. They ranged in size from 1 to 4 meters. One of the best known aetosaurs is Stagonolepis from Europe. The skull and teeth are unusual. The tip of the snout is flat and blunt, giving the animal a sort of pig-like appearance. The teeth are not the typical sharp-edged cutting blades of carnivores. Instead, the teeth are leaf-shaped suggesting that aetosaurs were herbivores. Unlike the phytosaurs, aetosaurs were erect walkers with the hind limb held beneath the body. Aetosaurs are united to rauisuchians by the horizontal orientation of their acetabulum. This seems to have been an adaptation for an erect posture.

The **Sphenosuchidae** is a group of early crocodiles. Sphenosuchids are known primarily from the Upper Triassic of Europe, North and South America and the Lower Jurassic of South Africa. Sphenosuchids had an erect, bipedal posture. The loss of the postfrontal unites crocodiles to sphenosuchids.

True crocodiles (**crocodyliforms**) first appeared in the Upper Triassic.

The skull of true crocodiles is large, massively built, and low. The skull roof is flat and has heavy pitting on the surface. The antorbital fenestra is small in primitive crocodiles and absent in living crocodiles. Living crocodiles have a long secondary palate to separate the passage of air from the mouth, as in mammals.

Modern crocodiles are in the suborder **Eusuchia**. Eusuchians first appear in the Upper Cretaceous. Modern crocodiles are semiaquatic and their limb posture is different from their ancestors. Eusuchians have semi-erect posture; this means that the limbs are held to the side as well as down. This posture allows them to use both a sprawling walk as well as an erect run or gallop. Most people think of crocodiles as slow animals, but Webb and Gans (1982) reported that the australian species *Crocodylus johnstoni* can reach speads of over **16 km/h** while galloping on an irregular forest floor. *C. johnstoni* inhabits isolated bodies of temporary water in dry areas, so it may be somewhat more terrestrial than other crocodiles. *C. johnstoni* may have recently acquired this ability to run, but it is also possible that this is a primitive character for crocodiles, because their early relatives, the sphenosuchians and protosuchians had a fully erect stance and were more terrestrial.