Biology 356 - Major Features of Vertebrate Evolution
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Lepospondyls and Lissamphibians

Lepospondyls, frogs, caecilians and salamanders

Lepospondyls appeared in the Mississippian. They all lack an otic notch. They are united by a few synapomorphies: They are all relatively small, they lack **labyrinthine** infolding in the teeth, the **centrum** of lepospondyls is large and **cylindrical**. They usually have a single central element (at least in the presacral series), although recently quite a few taxa have been discovered to have small presacral intercentra. In the groups having a single central element, we are therefore fairly certain that the major vertebral element is a pleurocentrum.

There are 4 major groups of lepospondyls: Aïstopoda, Nectridea, Microsauria, and Lysorophidae.

We will study **aïstopods** first. All aïstopods looked superficially like snakes. They are represented in the fossil record from the Mississippian to the Lower Permian. The oldest known member of this group, Lethiscus, known from the Lower Mississippian of Europe is one of the oldest known post Devonian tetrapods. Despite its old age, it has only remnants of limbs. However, it does have intercentra, and large pleurocentra. Younger aistopods share the following features: Their skull had large **fenestrae**. They had a long body and **no limbs**; they had no trace of limbs or even girdles. They had **no intercentra** (even in the tail) and no free haemal arches. The neural arch is low and is **fused** to the centrum. Their rib heads are shaped like a **K**.

Nectrideans known from the Lower Pennsylvanian until the Lower Permian, were an aquatic group of lepospondyls. They retained limbs with five fingers primitively (manus and pes), but this number was reduced to four in the hand in late nectrideans. They are diagnosed by several synapomorphies: Most nectrideans (but not Sauropleura, have a flat, wide, short skull shaped like a **boomerang**. The **tabular** and **squamosal** are very large and project posterolaterally into a **tabular horn**. There is no **intertemporal** bone on the skull table. The **basicranial** articulation is fused. Like the temnospondyls the palate is open (there are large interpterygoid vacuities).

Their tail was long and laterally compressed. It was probably used for swimming. The **neural spines** and the **haemal spines expanded** dorsally and were fused to the centra.

The trunk vertebrae had **accessory articular surfaces**. Among nectrideans, two forms, from the Early Permian, Diplocaulus and Diploceraspis develop enormous

tabular horns which have been interpreted as protective structures for these aquatic, possibly mud dwelling **lepospondyls**.

Microsaurs were the most diverse and successful lepospondyls. 11 families are currently recognized. They range in time from the Mississippian to the Lower Permian. They all have limbs, although the limbs are often small. Many lacked lateral-line canal grooves and they have no adaptations to an aquatic habitat, so these taxa were probably terrestrial. They superficially look like lizards, and the microsaurs were initially thought to be early reptiles. This explains their name, which means “small lizards”. Like other lepospondyls, their centra are cylindrical and fused to the neural arches, but some genera have presacral intercentra. Microsaurs share several synapomorphies: No intertemporal, no supratemporal. They had a broad **occipital cotyle** (depression) articulating against the atlantal condyle. This is the opposite of what is found in amniotes.

Like, the dissorophoids, some scientists have suggested that microsaurs are the only lepospondyls that may have left descendants. It has been argued that salamanders and caecilians are derived from microsaurs.

Two major groups of microsaurs can be recognized on the basis of their skull morphology: These two morphologies are exemplified by the taxa Tuditanus and Pantylus, clearly terrestrial forms which had a postfrontal-tabular contact, and by Microbrachis, an aquatic form, which had no postfrontal-tabular contact. Possibly a third, distinct morphological type, one that is more closely related to Tuditanus than Microbrachis is the long bodied, short limbed Rhynchonchos, which has been proposed as a possible relative of apodan lissamphibians (see next section)

Lysorophids also looked like small snakes. They had a very long body with up to 99 presacral vertebrae and no limbs or very small ones. They also had a very open skull with large fenestrae. They have lost the intertemporal, supratemporal, postfrontal, and jugal.

“Lissamphibians”

Extant amphibians (anurans, caecilians, and urodeles) represent one of the great controversies in vertebrate evolution. Although generally accepted as having been derived from Paleozoic tetrapods, the specific relationships of the three groups remains highly controversial. The three groups of modern amphibians have been united into a taxon called the Lissamphibia because they share several derived characters: **Cylindrical centra**. A problem with this character is that several groups of early tetrapods had this (microsaurs, Doleserpeton, stereospondyls, amniotes). **Pedicellate teeth**. This refers to the fact that the crown of the teeth is separated from the root by a zone of fibrous tissue. This is perhaps the most interesting character. Among Paleozoic tetrapods, it is only

known in some dissorophoids. A problem with this character is that the teeth of some fossil salamanders are not pedicellate. **Bicuspid teeth**. Most modern amphibians have two cusps per tooth. Juvenile dissorophoids also had bicuspid teeth.

An **operculum**. In frogs and salamanders, there is a small bone between the footplate of the stapes and the fenestra ovalis (hole of the braincase in which the stapes fits in early tetrapods and amniotes). The operculum is linked with the shoulder girdle by the opercularis muscle. This complex may be involved in hearing and balance. The problem with this character is that caecilians don't seem to have an operculum. Further, the operculum is not present in all salamanders, and it is fused to the stapes in most anurans. Therefore, it may have appeared more than once, and it may have been present but unrecognized or unpreserved in several early tetrapods.

Loss of posterior skull bones. All modern amphibians lack the supratemporal, intertemporal, tabular and postparietal. However, several of these bones were lost in microsaurs as well as in dissorophoids. Small, widely separated pterygoids. Primitively, the pterygoids are large and closely appressed medially. However, small, widely separated pterygoids are found in temnospondyls and in nectrideans. Wide cultriform process of the parasphenoid. Primitively in tetrapods, the cultriform process il long and narrow. However, a wide cultriform process is found in some microsaurs (Rhynchonchos) and lysorophids. **Double occipital condyle**. Most early tetrapods have a single, median occipital condyle.

Several characters taken from the soft anatomy have also been used to support the monophyly of the Lissamphibia, but they cannot be evaluated in fossil tetrapods. Therefore, these characters are not very useful and we will not study them.

Most herpetologists working on modern amphibians accept the monophyly of the Lissamphibia, and several paleontologists do. However, some paleontologists, including myself, are not convinced, and we will consider this matter unresolved.

Anura

Triadobatrachus, the earliest known frog, lived in the Lower Triassic in Madagascar. Although relatively ancient, it is redily recognizable as a frog because it shares the following derived characters with other anurans: Median fronto-parietal (parietals and frontals fused into a single median bone). There are only 14 trunk vertebrae and 6 caudal vertebrae. This is more than in modern frogs but it is much less than in typical temnospondyls and microsaurs. It has a long ilium (but not as long as in modern frogs), a stricture necessary for jumping behavior. These are good derived characters, but Triadobatrachus is so much

more primitive than modern frogs that some people are not certain that it is related to frogs.

After *Triadobatrachus*, the next oldest fossil frog is Vieraella, from the Lower Jurassic of South America. **Vieraella** is the first undoubted frog in the fossil record (oldest one). Vieraella and later anurans are characterized by the following derived characters: There is no jugal. There are five to nine trunk vertebrae in the adult, and no free caudal vertebrae because the proximal caudals are fused into an **urostyle**, a unique anuran feature. In addition, there are long hind limbs with fused tibiae and fibulae, obviously used for jumping and swimming. The fused tibiofibula is stronger than a discrete tibia and fibula would be. Probably the most strikin feature for a fossil taxon is the presence of a special type of larva, the **tadpole**. Most tadpoles are herbivorous suspension feeders or algae grazers, but the adults are insectivorous. Although many fossil and extant amphibians have larval stages, only frogs have the distinct tadpole.

Urodeles

Salamanders appear in the fossil record in the Upper Jurassic of Russia (Karaurus). Seven of the eight living families are known by the Paleocene. Probably the most distinct feature of salamanders is the presence of a deep cheek emargination between the maxilla, squamosal and quadrate.

Salamanders are presumed to have been derived from temnospondyls, just like frogs, but this theory has several problems because urodeles have no otic notch and no tympanum, but dissorophoids and most other temnospondyls do. Therefore, salamanders would have lost their otic notch and tympanum according to this theory. On the other hand, if salamanders were derived from microsaurs, we would not have to postulate that they lost these structures.

Caecilians or gymnophiones

These limbless living amphibians also called apodans appear in the fossil record in the Lower Jurassic. They are poorly known. All live in the tropics and are aquatic or burrowers. There are four families and 34 genera but little or no fossil record, except for the the Lower Jurassic form Eocaecilia. Caecilians are peculiar, small amphibians with small orbits sometimes completely covered by bone, and a **tentacle**, a tactile or chemosensory organ located in front of the orbit. They have up to 200 trunk vertebrae but a very short tail. They have no girdles or limbs. Eocaecilia is more primitive than all other apodans in possessing intercentra, and remnants of limbs.

Carroll and Currie have argued that caecilians are closely related to some microsaurs. There is some evidence to support this theory: The jaw articulation is

located in front of the occiput, the snout projects beyond tooth row anteriorly, the palate and lower jaws have a medial row of teeth parallel to the marginal tooth row. In addition some microsaurs have a long trunk, as in Rhynchonkos , a small microsaur which has 36 trunk vertebrae, and also small limbs.

Nevertheless, the origin of caecilians remains controversial.