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Fossil Focus — The ecology and evolution of the Lepospondyli

by Aodhán O'Gogain*1

Introduction and background

During the Pennsylvanian subperiod (roughly 318 million to 299 million years ago), lush tropical rainforests covered much of what is now North America and Europe, but were then near Earth's Equator. These tropical forests were teeming with animals, from 2-metre-long millipedes that scurried along among the roots to fish with fangs 10 centimetres in length that inhabited the associated rivers and estuaries. Living among these giants was a diverse group of small (less than 1 metre) vertebrates that resembled newts, lizards and snakes. These were the Lepospondyli, a sub-class of tetrapods that are characterized by having hourglass-shaped centrums, the central parts of their vertebrae. They had elongated, small bodies and short limbs, with one order losing their limbs completely. The lepospondyls first appear in the rock record in the mid-Mississippian subperiod (about 345 million years ago) and disappear by the end of the middle Permian period (265 million years ago), reaching their full diversity by the Pennsylvanian. They are mostly found in coal seams or sandstones and limestones deposited in estuaries, rivers and lakes. The fact that many specimens come from coal seams may explain why, despite being collected as far back as the mid-1850s, they are poorly understood: vertebrate fossils preserved in coal tend to be hard to investigate with the naked eye, and many specimens are destroyed or distorted by the dreaded pyrite disease, in which iron sulphate, or fool's gold, grows inside the fossil and breaks it up. There are five orders of lepospondyls, each with different characteristics.

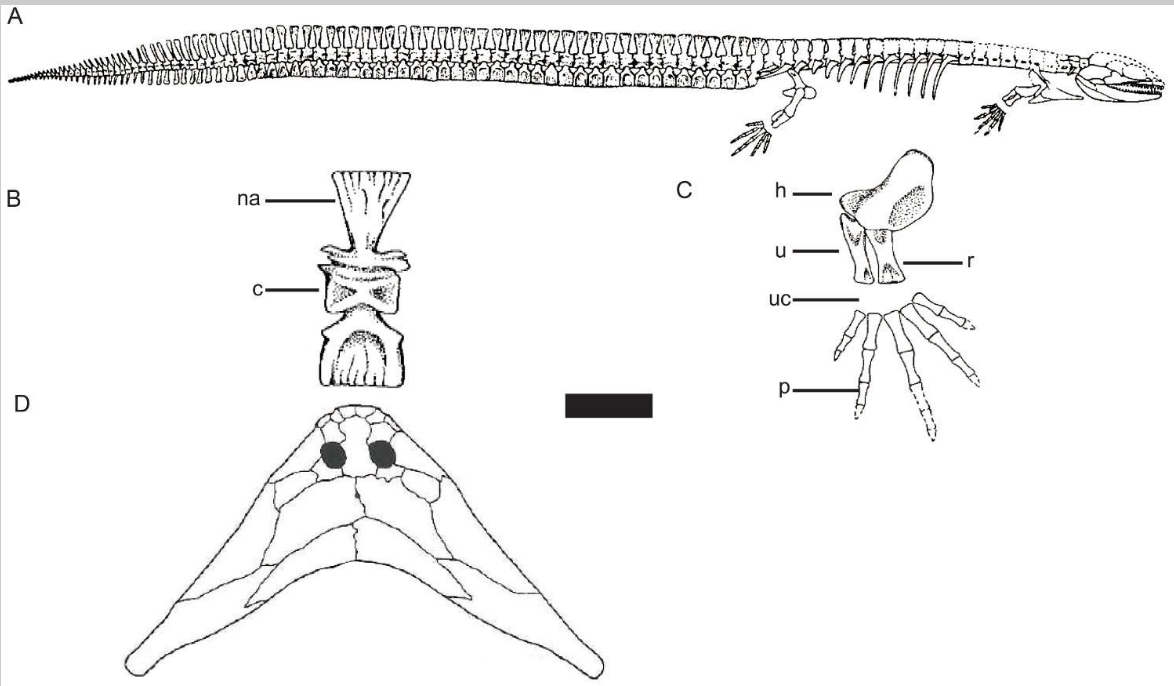

Figure 1 — A) The nectridean *Urocordylus wandesfordii* and B) associated tail vertebrae, showing the flattened neural and haemal arches and hourglass-shaped centrum. C) Forelimb showing a lack of a hard wrist bone. D) The skull of *Diplocaulus*. Abbreviations: c, centrum; h, humerus; ha, haemal arch; na, neural arch; p, phalanges; r, radius; u, ulna; uc, unossified carpals. Scale bar is 20 mm for A, 6 mm for B, 4 mm for C and 50 mm for D. Adapted from Carroll *et al*. 1998.

The Nectridea

The nectrideans resembled newts, with many species having elongated, flattened tails. This was taken to the extreme in *Urocordylus wandesfordii* (Fig. 1a), whose tail made up two-thirds of its total body length. The flattening in the tail was caused by the neural and haemal arches: bone projections above and below the centrum, in the vertebrae, which formed thin blades (Fig. 1b). The nectrideans didn't have hard wrist or ankle bones (ossified carpals and tarsals; Fig. 1c), so their limbs were weak and probably not adapted to carry the animals' weight. Lateral lines — sense organs found in living aquatic animals and used to detect movement in water — have been observed in *Keraterpeton galvani*. The most iconic of the nectrideans, if not of the entire lepospondyls, is the boomerang-headed *Diplocalus* from the Permian of North America and Africa (Fig. 1d).

The Microsauria, the Lysorophia and the Adelospondyli

The microsaurs were the lepospondyl group with the most species, and possibly the most bizarre forms. They had elongated bodies with very small limbs (Fig. 2a). Many species were covered in scaly armour both on their back and on their belly. The microsaurs are generally grouped together because they all had vertebrae with no suture lines, features that mark the boundary between two separate, yet fused bones. The lysorophians (Fig. 2b) looked similar to the microsaurs, with elongated bodies and reduced limbs, but they were more specialized, with an unusual skull shape. This might suggest that they are in fact descended from the microsaurs. The adelospondyls (Fig. 2c) are known from only one location in Scotland. They have primitive traits and appear early in the rock record (in the Mississippian), and are often considered to be early microsaurs or ancestors of them.

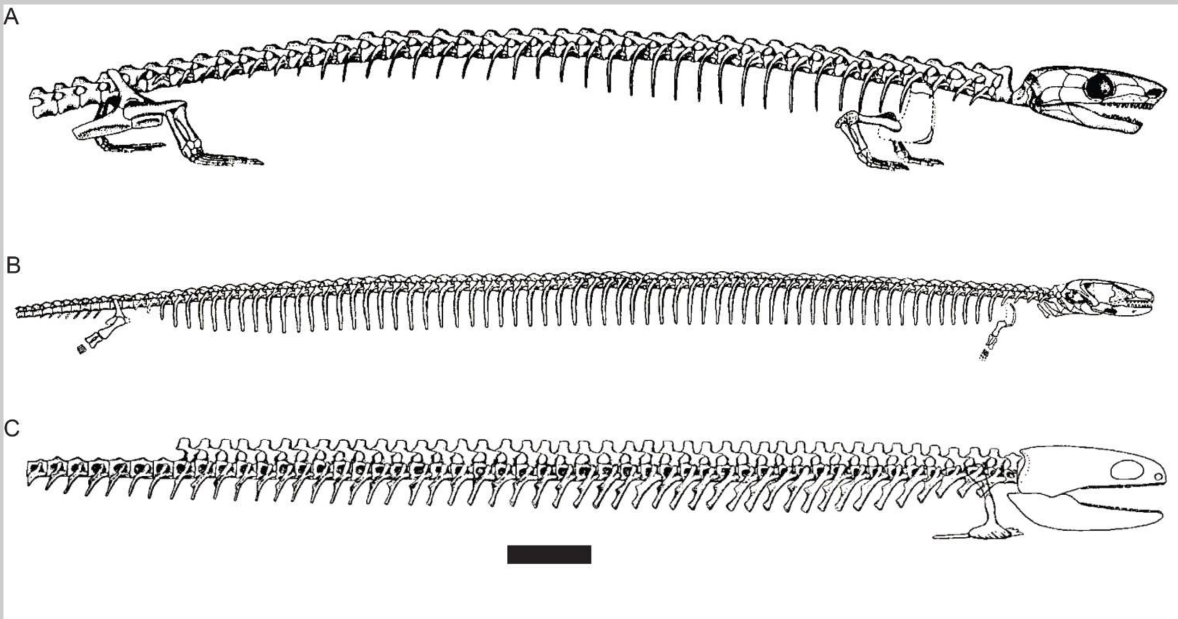

Figure 2 — A) The microsaur *Rhynchonkos*; B) the lysorophia *Brachydectes newberryi*; and C) the adelospondyl *Palaeomolgophis scoticus*. Scale bar is 6 mm for A, 7 mm for B and 10 mm for C. Adapted from Carroll 2001.

The Aïstopoda

The last group of lepospondyls, the aïstopods (Fig. 3), is also the first to appear in the rock record. As a group they show the fewest similarities to the common ancestor of the lepospondyls. Being limbless, they resemble snakes, but members of the group still have part of the shoulder, which suggests that they evolved from a limbed ancestor. They became elongated by adding extra vertebrae. The highest number of vertebrae is found in *Phlegethontia linearis*, which had at least 250. More primitive aïstopods, such as *Oestocephalus amphiuminus*, were large by lepospondyl standards and had ovoid bony plates on their backs and around their heads, along with gastralia, or bony structures in the skin, protecting their undersides. These may have acted as armour to fend off predators. More specialized aïstopods tended to be smaller and lack the armour.

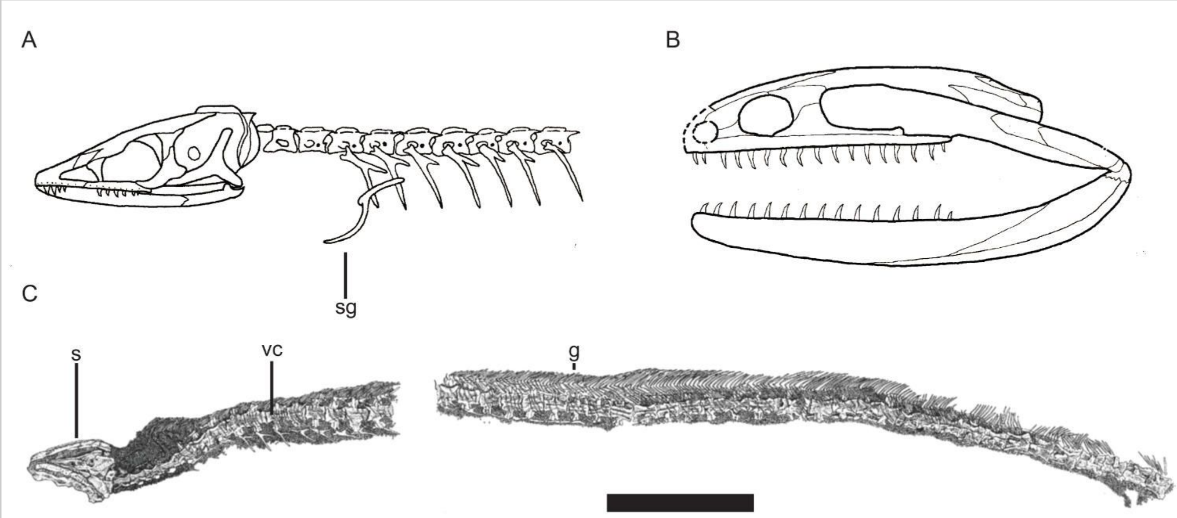

Figure 3 — The aïstopods A) *Phlegethontia longissima* and B,C) *Oestocephalus amphiuminus*. Abbreviations: g, gastralia; s, skull; sg, shoulder girdle; vc, vertebral column. Scale bar is 2 mm for A, 5 mm for B and 15 mm for C. Adapted from Anderson (2002, 2003).

Lepospondyl palaeoecology

The appearance of diverse groups of lepospondyls in coal seams and associated rocks of the Pennsylvanian suggests that they thrived during this sub-period and that they were a major component of the ecosystems of the earliest tropical forests. These forests were highly variable, with interconnected estuary, river, swamp and forest-floor ecosystems. Which of these ecosystems different lepospondyls inhabited is not yet fully understood. The majority of nectrideans seem to have spent most, if not all, of their lives in the water. This is indicated by the presence of 1) lateral lines in *Keraterpeton galvani*, a sensory system that can function only in water; 2) flattened tails adapted to move the animal along by undulating during swimming (the tails of *Urocordylus wandesfordii* would have been very cumbersome on land); and 3) the lack of wrist or ankle bones, which suggests that the limbs were not adapted for support but instead to serve as paddles for swimming. The exception to this is the nectridean *Scincosaurus*, which had stronger bones and a less flattened, shorter tail and would have inhabited the river and swamp banks of the forest.

Microsaurs, lysorophians and adelospondyls all had a semi-terrestrial lifestyle, and it is thought that their elongated bodies with reduced limbs evolved to help them navigate the root systems and leaf litter of the coal forests. However, these adaptations could also have helped them to navigate shallow river systems and lakes, indicating that these animals were eel-like.

Whether aïstopods were aquatic, terrestrial or both is still debated. The lack of evidence for lateral-line systems and flattened tail vertebrae has led to the suggestion that they were strictly terrestrial. However, primitive aïstopods are more common than derived ones in aquatic deposits, which might indicate that the early aïstopods were aquatic and the later ones were terrestrial. This coincides with the suggestion that the skull of the derived aïstopod *Phlegethontia* was adapted for digging, and that these animals burrowed in the forest floor.

There is no direct evidence about the diet of lepospondyls, but they had backwards-pointing, sharp teeth, which indicates that they were carnivores. They were probably not at the top of their food chains, because they shared their ecosystems with larger carnivorous tetrapods and fish. Fluid-dynamic studies of water flow over the boomerang head of the nectridean *Diplocalus* suggests that it would swim along the bottom of a river or lake; once it spotted some prey swimming above it, it would tilt its head up. This acted as a wing, giving extra lift and helping the *Diplocalus* to catch its unfortunate prey. By contrast, the lower jaw of the nectridean *Keraterpeton galvani* protruded behind the skull, where a large muscle attached to it. Like a lever system, this muscle allowed for rapid opening of the lower jaw (Fig. 4a). In water, this rapid opening of the mouth would create a vacuum, sucking in any prey caught in its pull. This feeding method is common in modern fish. The aïstopod *Ophiderpeton brownriggi*, the microsaur *Cardiocephalus* and the nectridean *Keraterpeton* all have rounded denticles, or small tooth-like structures, on the roofs of their mouths. These would have allowed them to crush up the hard outer bodies of arthropods — arachnids, insects and their relations, which were abundant in the ecosystems at the time.

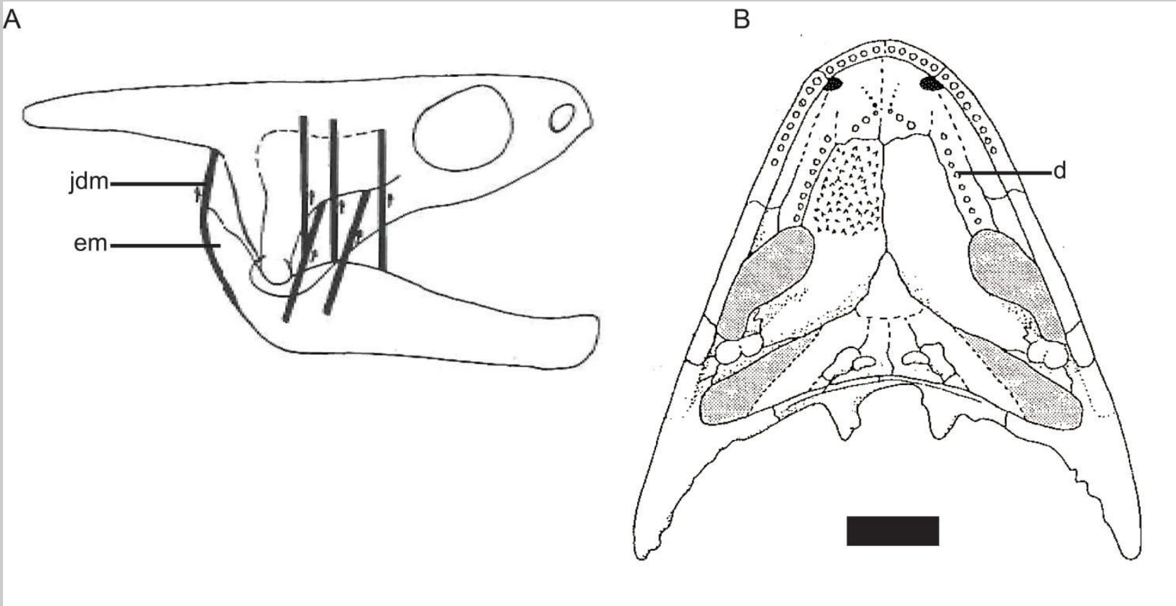

Figure 4 — The skull of the nectridean *Keraterpeton galvani* A) in side view, showing how the extend lower jaw would act as a lever; and B) showing the roof of the mouth, highlighting the rounded denticles. Abbreviations: d, denticle; em, extended mandible; jdm, jaw depressing mandible. Adapted from Milner (1980) and Carroll *et al.* (1998).

The formation of the supercontinent Pangaea towards the end of the Pennsylvanian led to the drying up and collapse of the coal-forest ecosystems, causing a huge loss in lepospondyl diversity into the Permian. Lepospondyls became restricted to river and lake systems, before becoming extinct by the mid-Permian (265 million years ago).

Lepospondyl evolution

The first lepospondyl to appear in the fossil record is the mid-Mississippian aïstopod *Lethiscus stocki*, which was already highly specialized and limbless. This led to the hypothesis that the aïstopods evolved from a separate lineage to the rest of the tetrapods, directly from the lobe-finned fish. However, unlike fish, *L. stocki* has a neck separating the skull and the shoulder. This suggests that it is related to the tetrapods, supporting the idea that all tetrapods evolved from a single ancestor. The occurrence of highly specialized aïstopods in the mid-Mississippian deposits also suggests an early split from other tetrapods, possibly as far back as the Devonian period (419 million to 359 million years ago), when tetrapods were first coming onto land.

When considering early tetrapod evolution, there are two major questions: from which group did modern amphibians (frogs, toads, newts, salamanders and limbless caecilians) evolve; and from which group did amniotes (animals with amniotic sacs, including reptiles and mammals) evolve?

There are currently two competing hypotheses for the origins of the amphibians. The lepospondyl hypothesis suggests that either some (i.e. only the caecilians), or all, modern amphibians originated from the lepospondyls. This idea focuses on the similar-shaped vertebrae of the two groups and is supported by a palaeontology technique called cladistics analysis, which compares the characteristics of various groups. The lepospondyl hypothesis links modern caecilians with aïstopods, normally on the basis that both groups are limbless. However, limblessness is not uncommon in animals, having evolved once in snakes and around 30 times independently in lizards. Also, a major problem with this hypothesis is that lepospondyls went extinct before modern amphibians originated, in the Triassic period (252 million to 201 million years ago).

The competing hypothesis, which most people believe, is that amphibians are descended from tetrapods called temnospondyls. This idea is supported by other cladistics analyses. Temnospondyls were the most diverse group of tetrapods in the Pennsylvanian, and went extinct only during the Cretaceous period (146 million to 66 million years ago), so they overlap with the amphibians.

A key to resolving this issue is to look at how lepospondyls, temnospondyls and amphibians develop from juveniles to adults. Modern amphibians have a wide range of developmental patterns but the basic method of growth is considered to involve a larval juvenile stage that undergoes a short period of metamorphosis into an adult, for example a tadpole changing into a frog. A larval stage is seen in some temnospondyl fossils, with juveniles having external gills similar to tadpoles and losing them in adulthood. In lepospondyls, both the aïstopods and the nectrideans show a gradual series of growth stages, suggesting that they did not have a metamorphosis stage. Therefore, on the basis of growth and development, the amphibians probably originated from the temnospondyls. If that is the case, where do the lepospondyls fit? General cladistics consensus suggests that they shared a closer common ancestor with the amniotes than with the amphibians, but that the amniotes originated from a different group of tetrapods.

Although no modern lineage of animal is descended from the lepospondyls, understanding their evolution and ecology is still important because it tells us about the evolution of early tetrapods and the evolution of terrestrial ecosystems. Understanding how the collapse of their ecosystems caused all but a few species to die out can teach us the importance of conserving our modern equatorial rain forests.

Suggestions for further reading

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