Palaeobiology of Carboniferous/Permian Aïstopod Amphibians

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Abstract:

Aïstopods are the most striking order among the Palaezoic lepospondyl amphibians. Most noticably is the complete reduction of limbs as well as the pelvic girdle. Further characteristics are the extremely elongate body with a long vertebral column and highly fenestrate skulls.
It is assumed that aïstopods lived in the same ecological nices as modern day snakes. Some taxa also appear to be secondary aquatic.

1. Introduction

The order Aïstopoda represents palaeozoic tetrapods. They occur in the Carboniferous and Early Permian of Europe as well as North America (BENTON, 2004), their first appearance beeing in the Mid-Visean, Wardie shore, Edinburgh Wardie Shales, Middle of Lower Oil Shale Group with the taxon *Lethiscus stocki*.

They were elongate, snakelike animals with limbs as well as the pelvic girdle reduced already in the primitive forms. Traces of the pectoral girdle might still be found in Lethiscus and other forms, suggesting a secondary loss of limbs instead of having evolved from a limbless fish ancestor (BENTON 2004). Their length ranged from 50 cm to 1 m, with up to 230-250 vetrebrae total (CARROLL et al., 1998). Further characteristics are their typically light skulls with large fenestrae, and their holospondylous vertebra. Due to extra joints on the skull, it is also suggested that some aïstopods may have been able to open their jaws unsually wide, as is common in modern snakes (BENTON 2004).

They may have filled the same ecological niches as snakes do today, beeing terrestiral or secondary aquatic.

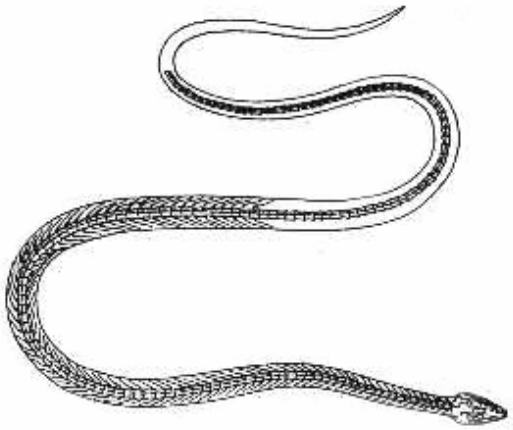

Fig. 1. The aïstopod *Phlegethontia*. From BAIRD (1965)

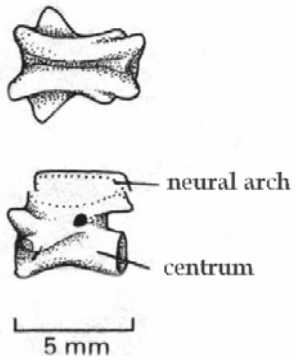

Fig. 2. Trunk vertebra of Aornerpeton in dorsal and lateral views. From BENTON (2004)

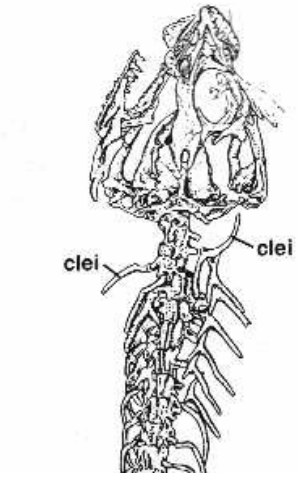

Fig. 3. Anterior portion of Phlegethontia linearis; Linton, Ohio, Westphalian D; showing cleithrum . From CARROLL et al. 1998

2. Morphology

2. 1. Vertebrae and Ribs

Aïstopods had 60-65 precaudal vertebrae with 230-250 vertebrae total (ANDERSON 2003). Each vertebra is holospondylus, meaning that it is formed from a single element. The neural arch is fused to the centrum. All centra are amphicoelous (funnel-like on both ends) and notochordal (CARROLL et al. 1998).

The ribs of *Lethiscus* are stout and double headed. In later forms they become more slender and develop a K-shaped structure (ibid.).

2. 2. Appendicular Skeleton

Remnants of the appendicular skeleton are still found in primitive aïstopods. The pelvic girdle ('hip') is completely reduced but remains of the pectoral girdle ('shoulder') are still visible in *Lethiscus* (scapulae, coracoids, putative clavicle); *Ophiderpeton nanum* (interclavicle); *Oestocephalus, Phlegethontia* and *Aornerpeton* (rods that resemble cleithra in other Palaeozoic tetrapods). However, due to the very small size of the remains a doubtless identification of these structures is difficult (CARROLL et al. 1998).

2. 3. Skull

The most distinct feature of aïstopod skulls are their large temporal fenestra, which do extend approximately one-half of the length of the skull. However, the area of the orbit is seperated by a postorbital bar. While the skulls of lethiscids and ophiderpetontids resembles the typical architecture of other Paleozoic tetrapods, the skull of phlegethontiids is changed.

3. Taxonomy

3. 1. Lepospondyl Amphibians and their Relations

Palaeozoic amphibians are divided into two major groups, namely the labyrinthodonts and the lepospondyls. The most distinct feature of labyrinthodonts is the labyrinthine enfolding of the teeth, an attribute linking them to

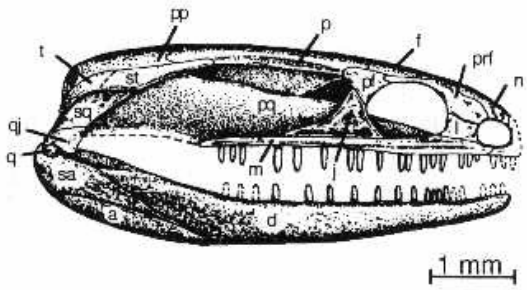

Fig. 4. Skull of the ophiderpetontid *Oestocephalus* sp., lateral view. Reconstruction of the skull based on material from Mazon Creek, Illinois. This specimen is assumed to be immature. From CARROLL et al. 1998

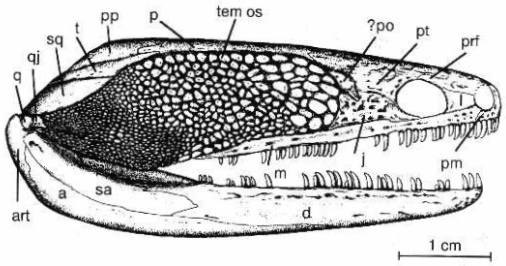

Fig. 5. Skull of *Oestocephalus amphiuminum*, lateral view. Reconstruction of the skull based on material of assumed mature individuals from Linton, Ohio. From CARROLL et al. 1998

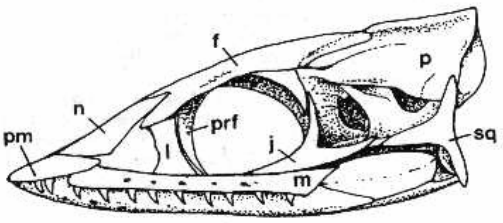

Fig. 6. Reconstruction of the skull of *Phlegethontia linearis*, lateral view. Specimen from Linton, Ohio (Westphalian D). From CARROLL et al. 1998

Abbreviations: a=angular, art=articular, d=dentary, f=frontal, l=lacrimal, m=maxilla, n=nasal, p=parietal, pf=postfrontal, pm=premaxilla, po=postorbital, pp=postparietal, pq=palatoquadrate, prf=prefrontal, pt=pterygoid, q=quadrate, qj=quadratojugal, sa=surangular, sq=squamosal, st=supratemporal, t=tabular, tem os=temporal ossicles

osteolepiform fish. Labyrinthodons are typically large, having a skull-length of 10 cm or more. Lepospondyls on the other hand are rather small, with skulls no longer than 5 cm. They lack palatal fang and pit pairs (as are common in labyrinthodonts), and almost no specimen show a labyrinthine enfolding of the teeth (Carroll et al. 1998) . All labyrinthodonts, including Aïstopods, show a spool shaped centra, usually the neural arch is fused to the centra. In contrast to labyrinthodonts, these ossify already early in the ontogenesis.

Lepospondyls are extremely divergent in their appearance. Furthermore, even the first specimen appearing in the fossil record (the aïstopod *Lethiscus*) are already highly specialized.

The taxonomy of the lepospondyl amphibian orders as established by ANDERSON (2001):

Superclass: Tetrapoda
Class: Amphibia
Subclass: Lepospondyli
Order: Adelospondyli
Order: Aïstopoda
Order: Nectridea
Superorder: Microsauria
Order: Lysorophia

No evolutionary sequence between lepospondyls and any modern ambibian group can be established. Lepospondyls occupied the same ecological environments as modern ambibians and might consequently have had similar features. According to BOLT (1991) the temnospondyl amphibian *Doliserpeton* might be a common ancestor of modern amphibians since it has, among other features establishing this connection, bicuspid, pedicellate teeth.

3. 2. Relationships of Aïstopoda to other Lepospondlys

The relationships of aïstopods to other lepospondyli is not yet clear, as they share features with each of the other orders among lepospondyli, yet no specific relationship could be established. CARROLL (1995) and REISZ (1997) grouped aïstopods close to adelospondylids, although this is a classification based mainly on the reduction of limbs. According to ANDERSON (2001) aïstopods are most closely related to the order lysorophia, a clade of the superorder microsauria. Further researches have also suggested a close relationship of aïstopods with nectrideans (THOMPSON and BOSSY (1970), SMITHSON (1985) cited in ANDERSON (2001)).

Due to the complete reduction of limbs, aïstopods are the most divergent lepospondyl order.

3. 3. Relationships within the Order Aïstopoda

The relationships within the order aïstopoda have lately been throughly revised. The classification of taxons may be difficult due to the extremely small bones, which can make a distinguation of critical features problematical. Therefore new analysation methods have been introduced by ANDERSON 2003,

who revised the taxonomy of the aïstopods using high-resolution computed tomography scans:

Tetrapoda GOODRICH 1930
Lepospondyli ZITTEL 1888
Aïstopoda MIALL 1875
Lethiscidae WELLSTEAD 1982
Lethiscus stocki WELLSTEAD 1982
Ophiderpetontidae SCHWARTZ 1980
Ophiderpeton brownriggi WRIGHT and HUXLEY 1866
Ophiderpeton kirktonense MILNER 1994
Oestocephalidae ANDERSON 2003b
Oestocephalus amphiuminum COPE 1868
Oestocephalus nanum HANCOCK and ATTHEY 1868
Coloraderpeton brilli VAUGHN 1969
Phlegethontioidea ANDERSON 2003
Pseudeophlegethontiidae ANDERSON, CARROLL & ROWE 2003a
Pseudophlegethontia turnbullorum ANDERSON 2003a
Phlegethontiidae COPE 1875
Phlegethontia linearis COPE 1871
Phlegethontia longissima FRITSCH 1875
Sillerpeton permianum LUND 1978
Phlegethontiidae incertae sedis
Phlegethontia "phanerhapha" THAYER 1985
Aïstopoda incertae sedis
"Ophiderpeton" swisshelmense THAYER 1985

This taxonomy is based on a wide range of different morphological features. While the order Aïstopoda is defined as animals showing an elogante body with a loss of limbs as well as a reduction of girdles, the evolutionary trends within the order Aïstopoda are mainly characterized by the loss of dermal ossification. Furthermore, an evolutionary trend towards the

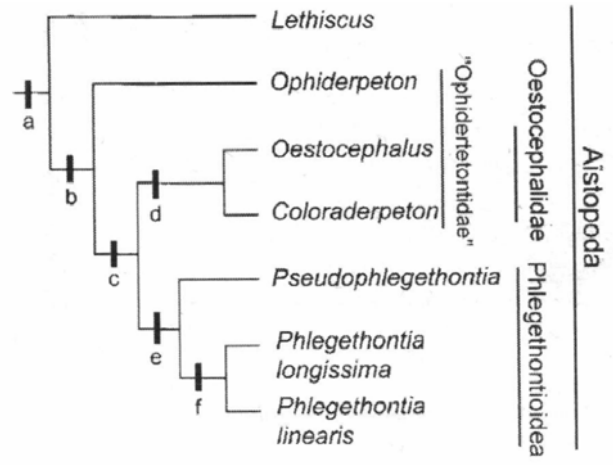

Fig. 7. Hypothesis of aïstopod relationships. Mapped onto the tree are several characters suggesting a trend towards loss of dermal ossification. (a) body elongate, loss of limbs, reduction of girdles. (b) loss of separate palatal ossifications (vomers, palatines). (c) loss of postorbital. (d) elongation of skull in parietal region. (e) loss of dorsal oestoderms, reduction of extent of gastrialia ossification, rostrum becomes pointed. (f) loss of most skull table elements, hyper ossification of the braincase. Modified from ANDERSON (2003)

development of larger fenestrae within the skull can be observed (compare fig. 7 for taxonomy, fig. 4-6 for morphological features of the skull).

4. Palaeoecology of Aïstopod Amphibians

4. 1. General Palaeocology

Aïstopods are typically found in coal swamp localities in Noth America as well as Europe. Yielding sites are located in North America and Europe, the most prominent areas beeing Nýřany, Czech Republic (Pennsylvanian); Linton, Ohio; Jarrow, Ireland; Newsham, England; Edinburgh and East Kirkton, Scotland (lower Carboniferous); central France; Mazon Creek, Illinois (Pennsylvanian); Fort Sill, Oklahoma; Fremont County, Colorado and the Swisshelm Mountains, Arizona (BENTON et al. 1998):

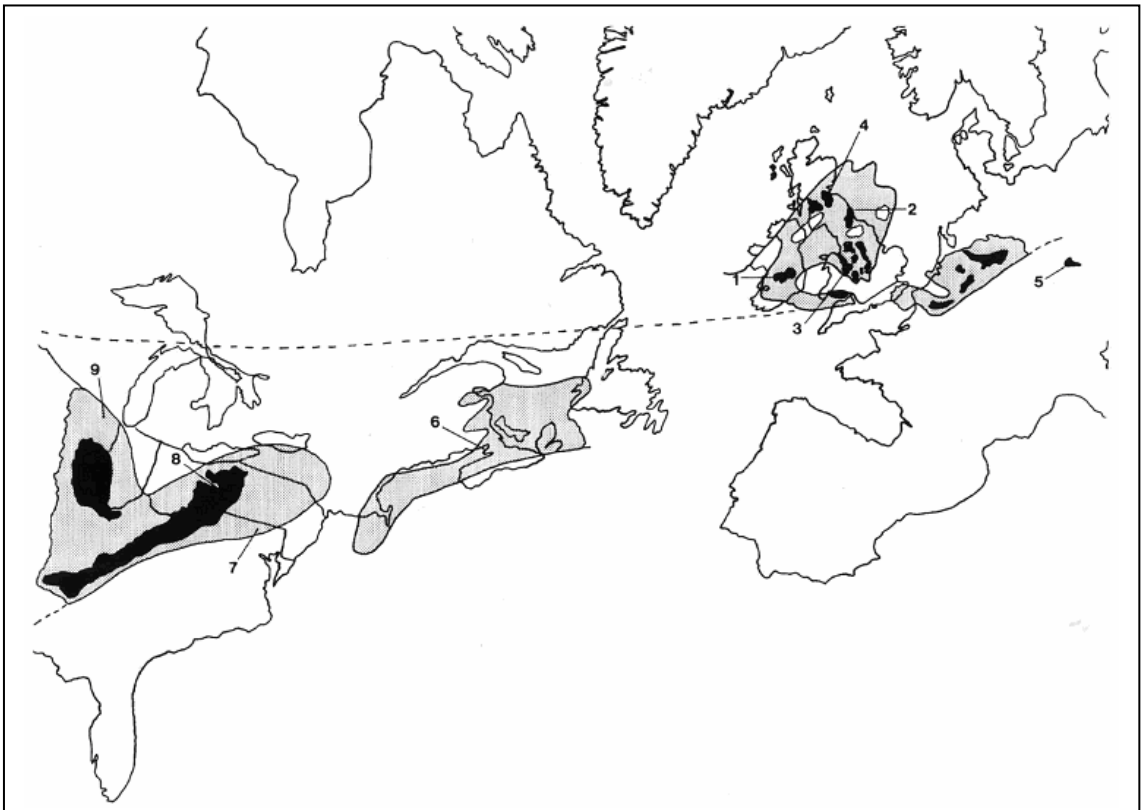

Fig. 8. The extent of terrestrial Carboniferous deposits in North America and Europe, showing the approximate position of the equator in the late Paleozoic and the localities from which major lepospondyl faunas are known. Stripple = areas of continental deposition during the Carboniferous, black = coalfields. Localities as numbered: 1. Jarrow, 2. Newsham, 3. Longton, 4. Wardie and East Kirkton, 5. Nýřany and Tremosna, 6. Joggins, 7. Dunkard, 8. Linton, 9. Mazon Creek. From CARROLL et al. (1998)

Although none of the aïstopod remains show a lateral line, which is typically distinguishable in primarily aquatic animals, an aquatic way of life is suggested. This is chiefly based on the fauna assemblage, that shows well articulated skeletons of aïstopods together with aquatic amphibians as well as fishes (Carroll et al. 1998). Apart from this, a terrestrial habitat has been

suggested (ibid.), similar to modern snakes, although it has to be taken in acount that amphibians rely on an aquatic environment for reproduction.

Furthermore, the extremely fragmentary fossil record needs to be considered. While some known Carboniferous localities, such as Nýřany, Czech Republic and Mazon Creek, Illinois show a very rich preservation of taxa, only 20 sites representing lepospondyl amphibians are known. These are mostly reduced to swamplike stream channel deposits showing only a very short timespan for accumulation, namely 1,000 to 10,000 years. (ibid.) Due to the limited inventory of both fossils and locations, a lot of data containing additional information on palaeoecology might be missing.

4. 2. The Nýřany Community

As shown in fig. 8, all known localities yielding aïstopod remains are located close to the palaeoequator. Thus, a tropical warm, humid climate can be assumed. Most sites represent swamplike environments. A throughly studied area with a very rich fauna and flora preservation are the coal deposits of Nýřany, Czech Republic. It dates to the Westphalian D (Late Carboninferous C, ca. 300 Myr). Preserved are lake sediments showing a poor aeration as well as a fairly rapid accumulation of sediments. Fossils show an excellent preservation, including soft tissue as well as little decomposition. About 700 speciamen are known. Floral elements preserved are, amongst others, calamites. Faunal elements range from aquatic arthropods and terrestrial millepedes to sharks (acanthodians, actinopterygians) and 20 species of basal tetrapods:

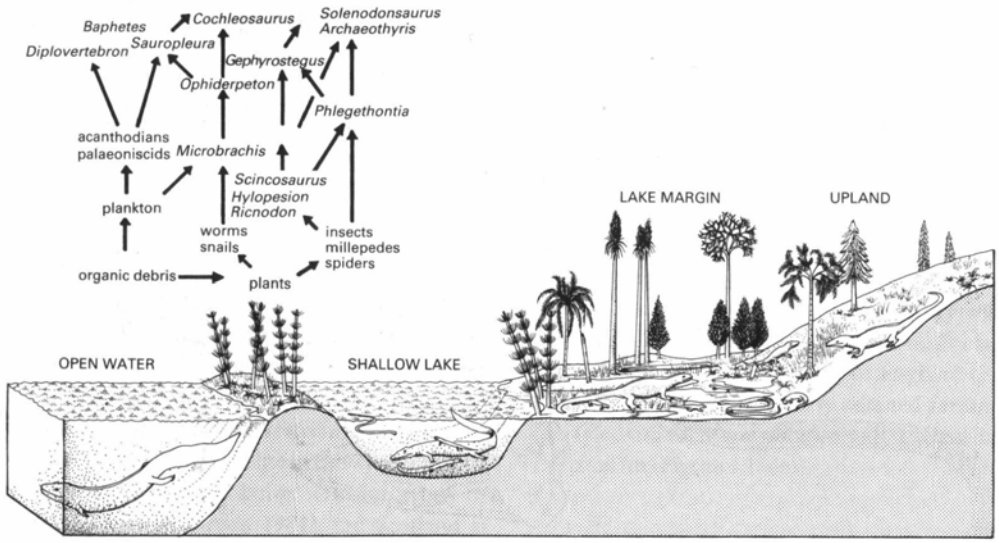

Fig. 9.. A late Carboniferous community, based on the Nýřany locality, Czech Republic. Four main habitats are indicated, with representative vegetation and tetrapods, from left to right: open water (eogyrinid, *Baphetes*); shallow lake (***Ophiderpeton***, *Sauropleura*, *Microbrachis*, *Scincosaurus*); lake margin (*Gephyrostegus*, *Amphibamus*, ***Aornerpeton***, *Ricnodon*, etc.); possibly upland (*Scincosaurus*). The food web on the left shows what eats what (the arrows run from the base of the food chains – the plants – through various invertebrates and fishes to the predatory tetrapods, and terminating at the top of the diagram with the 'top' carnivores that feed on other tetrapods). From BENTON (2004)

Here, aïstopods occur both as terrestrial animals, living close to the shores of the lake (*Phlegethontia* feeding on small tetrapods, insects, millepedes and spiders) as well as in the shallow water/swamp lake association as partly aquatic animals (*Ophiderpeton* feeding on *Microbrachis* and other lepospondyl amphibians).

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