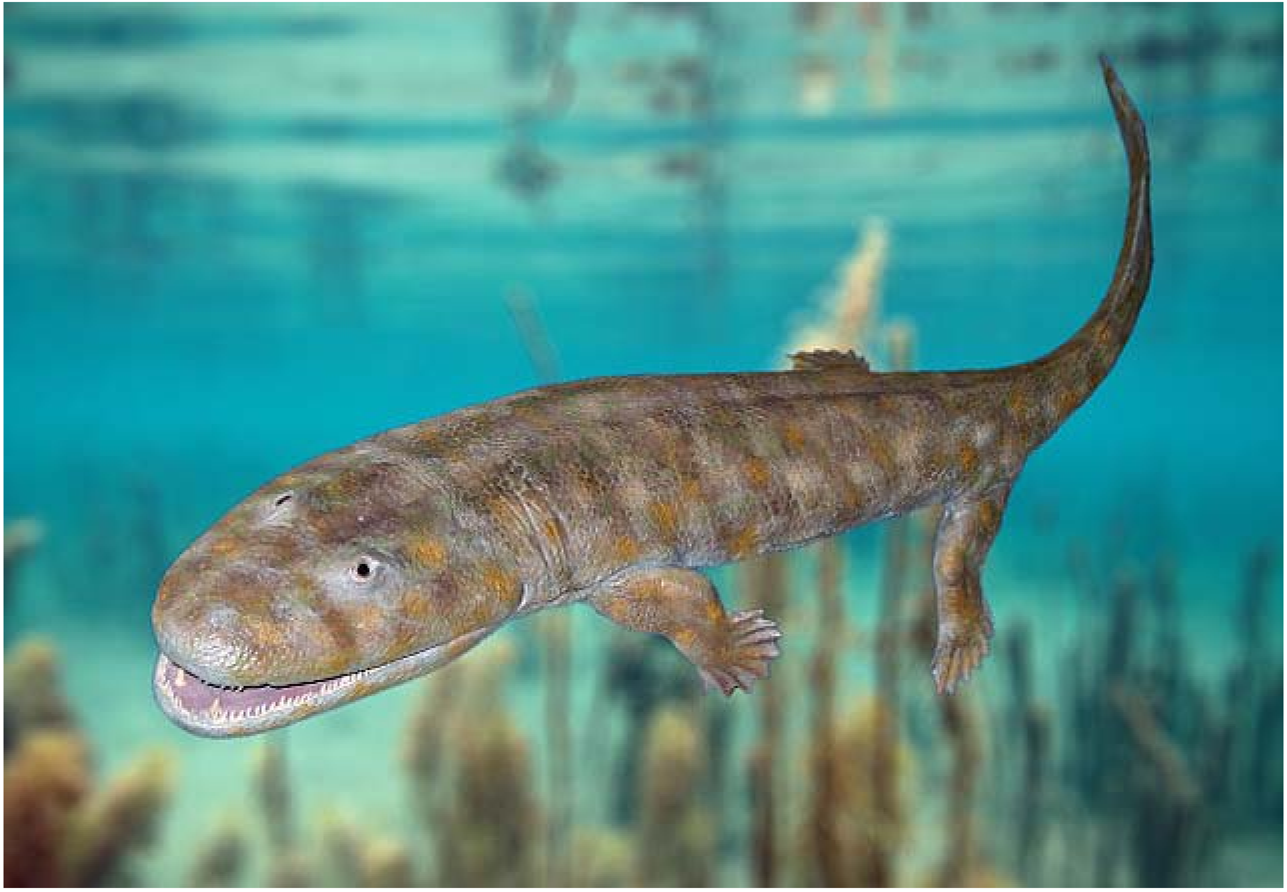
Page Back	Unit Home	Unit Dendrogram	Unit References	Taxon Index	Page Next
Unit Back	Vertebrates Home	Vertebrate Dendrograms	Vertebrate References	Glossary	Unit Next

Tetrapoda: Overview

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Ichthyostega
`--+--Tulerpeton
   `--+--Crassigyrinus
      `--+--Colosteidae
         `--+--Baphetidae
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents



Model of the very early tetrapod Acanthostega gunnneri at State Museum of Natural History in Stuttgart.
Photo by Dr. Günter Bechly, Wikipedia, Creative Commons Attribution-Share Alike 3.0 Unported

This unit is about the first animals on land, the first tetrapods or four-legged (as opposed to finned) animals. These were the first primitive amphibians, evolutionary groundbreakers, in more ways than one. Nevertheless, they were still mostly aquatic or semi-aquatic; legs evolved long before a life on dry land did. The first types, like the 60 cm long *Acanthostega*, shown above, and its slightly larger contemporaries and close relatives such as *Ichthyostega* and *Hynerpeton*, had not evolved far beyond being fish with legs, although from their wide distribution they were clearly still capable animals for all that. These ancestral types quickly radiated out into forms as diverse in appearance as eels and crocodiles. These sinuous creatures were among the top preditors of the rich and murky Carboniferous swamps. Nome lived past the end of the Carboniferous, victims perhaps to the drying out of the swamp lands that was part of the transition to the Permian and the start of the Age of Reptiles. But for as long as conditions allowed, these pioneering creatures were masters of their world. MAK111122

Page Back | **Unit Home** | **Page Top** | **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

New page MAK111122

Tetrapoda

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Tulerpeton
      `--+--Crassigyrinus
         `--+--Colosteidae
            |  `--Greererpeton
            `--+--Baphetidae
               `--Tetrapoda*
                  |--TEMNOSPONDYLI
                  `--+--LEPOSPONDYLI
                     `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. Tetrapoda

A Lot of Rot: the World of the Tetrapods

1. An Introduction to

Tetrapod Environments of the Late Devonian

Health Warning and Disclaimer

We have hinted in various other places that rot may be the key to Late Devonian and Mississippian (Early Carboniferous) environments. It is now time to develop that thesis, since we will never understand the evolution of tetrapods without understanding the environment in which they evolved. It's a very long story, full of chemistry and mostly concerned with the evolution of plant tissues and fungi. The prospect of explaining this stuff is so utterly discouraging that we feel compelled to recommend that you skip the whole thing. Furthermore, we expressly disclaim any and all liability for nausea, vomiting, cerebral atrophy, sleep disturbances, uncontrollable ophthalmic tremors, progressive neuronal putrification, acute mental atrophy, or any other physical or psychiatric side effects which readers may experience. You have been warned.

Geology

Braided river (left) and meandering river (right).

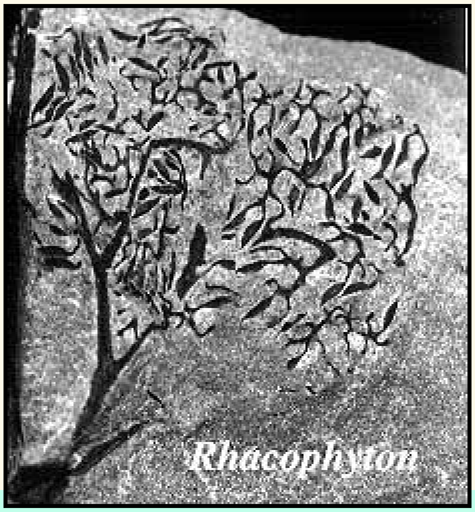
What do we know about the environments at the actual sites in which Devonian tetrapods are found? Not a great deal, as it turns out. If we ignore *Tulerpeton*, it makes things more comprehensible. *Tulerpeton* was found in what is supposed to be a completely marine environment, but with other possibly terrestrial or near-shore remains. Lebedev & Clack (1993); Lebedev & Coates (1995). Its rather hard to explain, except as a rafting accident, or some other weird one-off, and we won't even try to make sense of it.

The others, to the extent anything is known about their depositional environment at all, share two features. They are **all** associated with meandering rivers, and they come with salad. That is, they are also associated with plant material (usually unidentifiable). *Densignathus* and *Hynerpeton*: Red Hill, usually interpreted as an oxbow lake near a meandering river, with shrub-like lycopsids and *Archaeopteris* trees in the neighborhood. Daeschler *et al.* (1994); Clack (1997); Daeschler (2000); Shubin *et al*. (2004). *Ichthyostega* and *Acanthostega*: Aina Dal and Britta Dal Formations with meandering rivers, point bars and unidentified plants. Coates (1996); Clack (1997); Blom (2005). Genoa River tracksite with meandering streams. Clack (1997). *Sinolepis*: plant materials, nearshore or fresh water vertebrate remains, possibly deltaic. Zhu *et al.* (2002).

The existence of meandering rivers is significant. In the absence of well-established terrestrial plants, rivers don't form gently curved meandering river beds. They cut deep, narrow channels or spread out into a maze of braided streams. The implication of meandering rivers is that land plants weren't just a marginal element of these systems. By the Late Devonian, land plants covered substantial areas, and tetrapods lived in the waters in or near these areas.

Plant Life

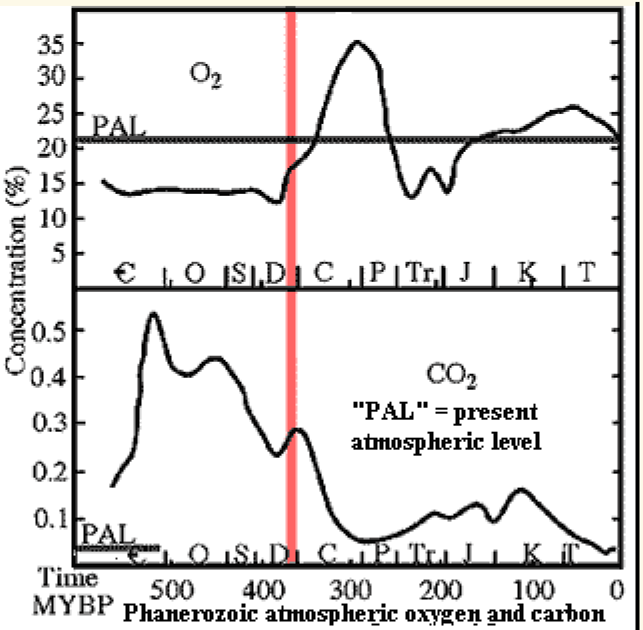
The identities of the plants themselves are reasonably known only at the latest Famennian Red Hill tetrapod site. As mentioned, this site is generally interpreted as an ox bow lake near a large river. Here, fragments of *Archaeopteris* are plentiful; and we can be certain that the lake, like much of the Devonian landscape, was surrounded by a forest of these huge seed ferns (progymnosperms). Shear & Selden (2001). *Archaeopteris* was a true tree, with a woody trunk, xylem, secondary cambium, and leaves. DuBuisson *et al*. (2002). See images and additional discussion at Devonian, Late Devonian and Frasnian. Below the *Archaeopteris* canopy, we would see a ground cover of *Protolepidodendron* (up to 30 cm in height), with stands of various lycopsids. Shear & Selden (2001). The shallows of the lake itself were choked with dense, bushy *Rhacophyton*, growing as tall as 2 m. Additional information on the flora of Red Hill (and much else besides) can be found at Dennis Murphy's Devonian Times site.



For our purposes, we should also note that Red Hill, and all other tetrapod sites about which we have detailed knowledge, shows signs of periodic flooding -- perhaps seasonal, perhaps not. The taphonomy is also important. Plant remains are found as dense mats of poorly (or only secondarily) oxidized litter. Shear & Selden (2001). It seems likely that these two observations are connected, although it is not a certainty. But, whether the forest litter was washed into the lake or accumulated in some other way, it seems almost certain that the lake was weed-choked and generally anoxic.

A More Congenial Atmosphere -- and the introduction of our thesis

While these shallow water environments may have been low in oxygen, the air above them was not. On the right, we show the usual Phanerozoic oxygen and carbon dioxide trends. The graph is from Dudley (1998), but it is largely based on the work of Robert Berner of Yale and his colleagues. As a preliminary matter, note that atmospheric carbon dioxide levels begin to drop long before oxygen begins to accumulate. This is a bit hard to explain. Fortunately, more recent studies tell a more reasonable tale of a modest, gradual decline in carbon dioxide levels from the beginning of the Cambrian, followed by an abrupt and precipitous fall beginning in the Frasnian or thereabouts. Berner & Kothavala (2001). As an independent check on the overall oxygen trend, it is notable that *fusain* is found for the first time in the Late Devonian. This strongly



Phanerozoic atmospheric oxygen and carbon dioxide levels. From Dudley (1998).

implies that (a) oxygen levels had reached the point at which fires could occur (~15%) **[1]** and (b) that there were plants to burn. Berner *et al*. (2003).

No one seems to doubt that the spread of terrestrial plant life in the Late Devonian was the principal cause of the rise in atmospheric oxygen. But why the preceding gradual reduction, and why the concomitant free fall in carbon dioxide? That, in fact, is what this essay is all about. Our thesis, somewhat over-simply stated, is that the evolution of wood resulted in a runaway positive feedback loop towards the end of the Devonian. The problem was that plants are very good at making wood, and they do it even better when oxygen levels are high. However, recycling wood is an extraordinarily difficult, dangerous, and slow job. Wood was, in fact, the plastic waste of the Late Paleozoic: indigestible, often toxic, physically dangerous and sometimes environmentally devastating. It took almost 50 My for a group of fungi, the Basidiomycota, to evolve the complex array of metabolic tools necessary to save the planet from -- yes -- tree pollution.

This speculation has also been advanced by Dudley (1998), and probably by others. Our particular take on it still leaves the matter as a speculation. However, we believe that there is much more to say on the topic, particularly about the biochemistry which drove this near-catastrophe and its environmental effects -- effects which, in turn, seem to have driven the evolution of the early tetrapods. The biochemical foundations of the crisis were laid deep in Archean time, and that is where we will pick up the tale on the next page. ATW050624.

GO TO PART 2. Hazardous Waste & Inefficiency: A Short History of Rubisco

---

[1] One might suppose that the critical parameter is pO_2, the partial pressure of oxygen, not the mole percent O_2. For reasons which are entirely unclear to us, all writers on Paleozoic atmosphere assume (a) that total atmospheric pressure was constant throughout the Phanerozoic and (b) that pN_2, the partial pressure of nitrogen, was also approximately constant. We can think of no reason why this would necessarily be the case, and several reasons why it might not be. However, our sample of the literature was small, and we leave the problem for another day.

Descriptions

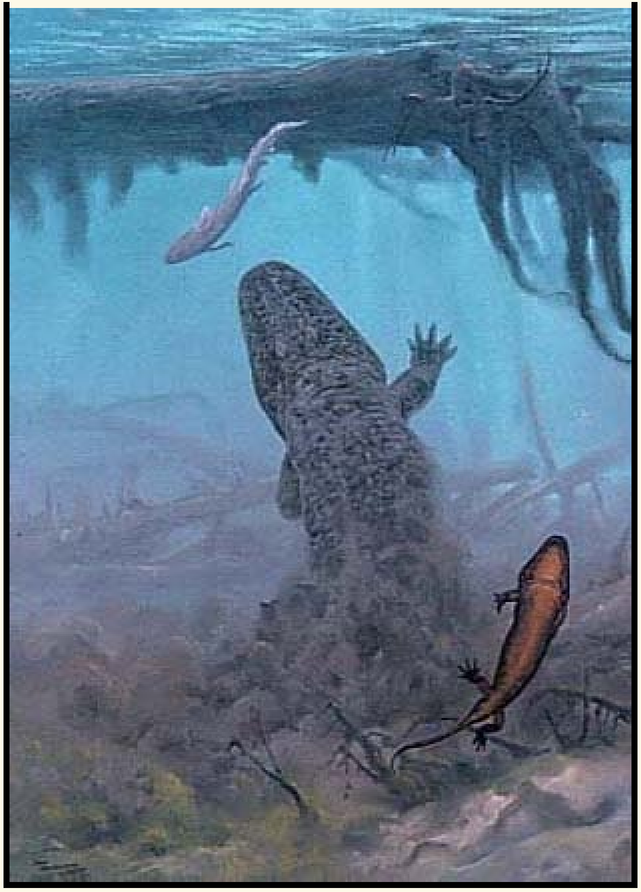
Tetrapoda (= Stegocephalia)

Range: from the Late Devonian (Famennian).

Phylogeny: Elpistostegalia ::: (*Metaxygnathus* + *Ventastega*) + * : *Acanthostega* + (*Ichthyostega* + (*Sinostega* + (*Densignathus* + (*Hynerpeton* + (*Tulerpeton* + (*Ossinodus* + (Whatcheeriidae + (*Crassigyrinus* + (Colosteidae + (*Spathicephalus* + (Baphetidae +

Tetrapoda*))))))))))).

Characters: Dermal skull solidifies, loses complex kinesis and becomes more closely associated with braincase; sphenethmoid and otic-occipital units of braincase become more integrated; snout is longer, post-orbital region shorter; palate changes little; palatoquadrate gradually reduced; supratemporal stiffens former parietal-postparietal hinge; gills and opercular series (including extrascapulars) lost; dermal skull not attached to pectoral girdle; primitively, notochord still prominent and extends into midbrain; atlas-axis complex originally absent & evolved convergently in several later lineages; primitively, retain large, crescent-shaped intercentra connected to neural arches by short ribs, small paired pleurocentra; zygapophyses on vertebrae; cleithrum freed from scapulocoracoid; more-or-less fused sacrum with sacral rib; pelvic girdle from three, enlarged centers and sutured together; iliac blade attached to vertebral column; glenoid and acetabulum significantly reoriented to face ventrolaterally; limbs with well-defined joints, carpals, tarsals & digits; dermal fin rays lost. Stem tetrapods now believed to be aquatic based on groove for aortic arch on ceratobranchials in *Acanthostega*.



The temnospondyl *Eryops* lunges after the shark *Orthacanthus*. Another, smaller temnospondyl (*Trimerorhachis*) swims in the foreground. Painting © Doug Henderson, reproduced with permission

Links: Introduction to the Tetrapoda; Terrestrial vertebrates; Definition of Tetrapoda; Fossil tetrapods; Tetrapoda -- The Dinosauricon; Lecture 8 - Tetrapods; Literature - Tetrapoda; Linking fish to the land; Devonian Times - More about Lobe-Fin Fishes; Re- tetrapoda. ATW030127.

Page Back | Unit Home | Page Top | Page Next

checked ATW040813

Tetrapoda: Overview

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Ichthyostega
`--+--Tulerpeton
   `--+--Crassigyrinus
      `--+--Colosteidae
         `--+--Baphetidae
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

What's a "Tetrapod"?

```
SARCOPTERYGII
|--Lungfishes
`--Tetrapoda #1
   |--Rhizodontiformes
   `--+--Tristichopteridae
      |  |--Eusthenopteron
      |  `--Mandageria
      `--+--Panderichthys
         `--Tetrapoda #2
            |--Livoniana
            `--+--Elginerpeton
               `--+--Obruchevichthys
                  `--Tetrapoda #3 & TETRAPODA
                     |--Acanthostega
                     `--Tetrapoda #4 & TETRAPODA*
                        |--Temnospondyls
                        |  |--salamanders
                        |  `--frogs
                        `--+--snakes
                           `--Pander, princes,
                              professors, etc.
```

Abbreviated cladogram showing relative position of taxa mentioned in the text.

The short answer is that we don't know. There are *at least* four definitions current in the scientific literature. These are (from most to least inclusive):

1) Lizards > Lungfish. This is the "total group" definition, which aims to include the crown group and the entire stem. Coates *et al*. (2002). This definition has two major problems. First, this taxon already has a perfectly good name: Tetrapodomorpha. Second, it's a bit awkward to call something that is obviously a fish and has *no* feet -- *Eusthenopteron* for example -- a "tetrapod." Worse, this definition includes animals such as the more derived rhizodonts and tristichopterids. These forms scarcely have four paired fins, much less four feet.

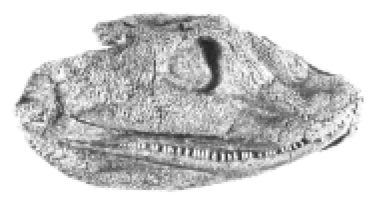
2) Christian Pander > *Panderichthys*. This is a slightly obsolete attempt at a compromise position. We like it, except

for (as usual) two reasons. First, *Panderichthys* is a very tetrapod-like fish. However, the definition assumes that *Panderichthys* is more or less on the direct line to conventional tetrapods. This is quite likely, but not quite as likely as it seemed a few years ago. Second, there is a growing gap between *Panderichthys* and the folks with four feet. Paleontologists are all constitutionally incapable of leaving a good thing alone. Now we have *Livoniana*, *Elginerpeton*, *Obruchevichthys*, and whatever comes out of the Baltics next year, to somehow cram in between *Panderichthys* and "conventional" tetrapods.

3) Animals with four feet and other characters. This is the historical or conventional definition. It suffers from the same problem as all apomorphy-based definitions. What if feet evolved more than once? When, exactly, does a fin become a foot? What about snakes or microsaurs? Finally, it is an arbitrary box. *See* discussion at **Dendrograms**.

4) frogs + princes. This is the crown group Tetrapoda, the last common ancestor of Lissamphibia and Amniota and all of its descendants. We like this one, too, but it's borders are extremely unclear, and it probably leaves far too many "labyrinthodont" forms homeless. As a practical matter, this definition is unuseful because it *really* irritates certain people, notably, Dr. Jenny Clack Similarly it seems to inspire an equal measure of tenacious defense from others, notably Prof. Clack's former coworker in the study of *Acanthostega*, Prof. Michael Coates **[1]**.

So, in a really pathetic and sycophantic attempt to please everyone, this is what we're going to do:

TETRAPODA = Dr. Clack  **+ *Acanthostega***  **.**

TETRAPODA* = Prof. Coates  **+ frogs**  **.**

In Tetrapoda*, the asterisk is supposed to suggest a crown, since this is the crown group. Of course it suggests nothing of the sort, but life is full of these little disappointments. If one prefers, Tetrapoda* can be pronounced "crown tetrapods." Under this regime, the unornamented Tetrapoda is more or less the same as the colloquial "tetrapod." However, if we ever find the feet/fins of *Livoniana* and it has toes, that will be just too bad. It still won't be a tetrapod. If one prefers, Tetrapoda can be pronounced "stem tetrapods." ATW030921.

Note added in disproof: since the original posting of this essay, Prof. Coates has decamped from his previous position on the issue, slipping away without so much as a postcard to Palaeos. Doubtless he hoped to be relieved of the onerous responsibilities of anchoring the Crown Tetrapoda*. Prof. Coates now seems to favor the "total group" concept ("Tetrapoda #1"). Ruta *et al*. (2003). We are unsure precisely where Prof. Clack currently stands, but she still stands on someone's feet. That is, she yet maintains that tetrapods may be defined as sarcopterygians with hands and feet. Clack (2002). However, the ground has shifted under those feet a bit, since it is now quite likely that, for example, *Ventastega* and *Elginerpeton* would qualify as tetrapods by this definition. Thus, she has been moved a few feet down the phylogenetic tree. Nonetheless, while our anchor taxa may have have abandoned their posts and turned their backs on their plain phylogenetic duty, we are unmoved. Like Horatius Cocles at the Pons Sublicius, we will stand our ground until the whole phylogenetic structure gives way and we, with our harness on our back, plunge headlong in the tide **[2]**. ATW050520.

---

[1] and our own colleague, the normally steady and convivial Mikko Haaramo, who has strongly protested our former use of "Tetrapodomorpha" to mean four-footed stem tetrapods.

[2] Lord Macauley's *Horatius* is only average poetry, but still a hell of a story.

Auntie Stega's Condition

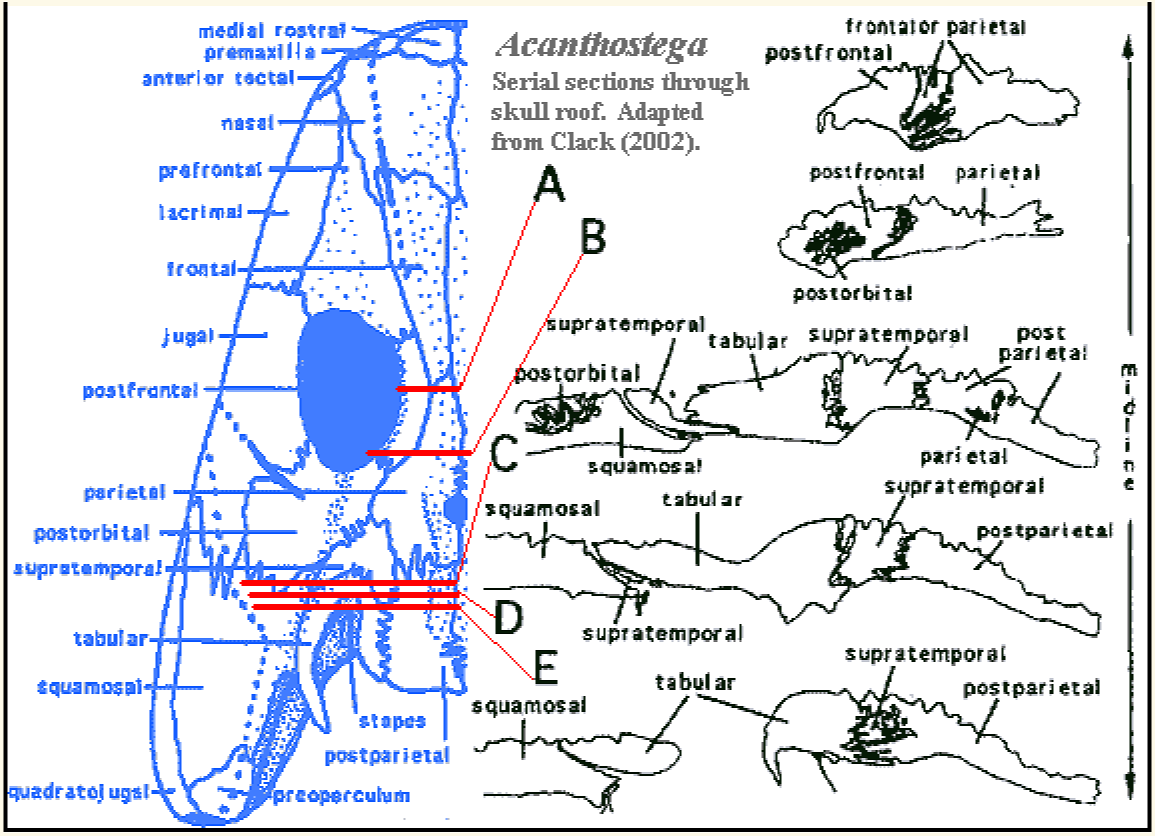
We usually leave this sort of anatomical survey for the "Characters" section of the main entries. However, so many stray bits and pieces have been added to our knowledge of early tetrapods over the last 15 years that we thought it might be interesting and convenient to sort them out here. That is, of course, interesting and convenient *for us*. We reluctantly concede that it may not be interesting (much less convenient) for the reader. Fortunately, one of the compensations of Palaeos is that, like a small chorus of demented bullfrogs shrouded in the fetid mists of some starless midnight bog, we enjoy a certain freedom to emit loud, coarse noises for the manifest satisfaction of doing so. Such is our response to the conjectural disapprobation of our equally conjectural readers.

Having disposed of all opposition with the irrefutable logic of this batrachian simile, we will turn to the question of the day: why is Prof. Clack like *Acanthostega*? Or, to be more precise, what did their last common ancestor look like? To address *this* matter, we need no longer resort to batrachian simile. It is no longer necessary to invent an ancestor based on some ill-conceived analogy to frogs. The growing legion of Late Devonian *'stegas* and *'petons* -- particularly *Acanthostega* -- has yielded enough data that we can be quite specific.

The Dermal Skull & Branchial Apparatus

In order to illustrate the tetrapod condition, we will need to make the close acquaintance of Auntie Stega, the last common ancestor of *Acanthostega* and ourselves. Auntie lived about 365 Mya, quite possibly in Baltica. We will suppose (for no particular reason) that she was Irish.

Auntie was a headstrong creature. That is, she had a heavily armored skull. The dermal bones locked together through complex, interdigitating sutures [C02a]. The word "interdigitating"



Acanthostega
Serial sections through skull roof. Adapted from Clack (2002).

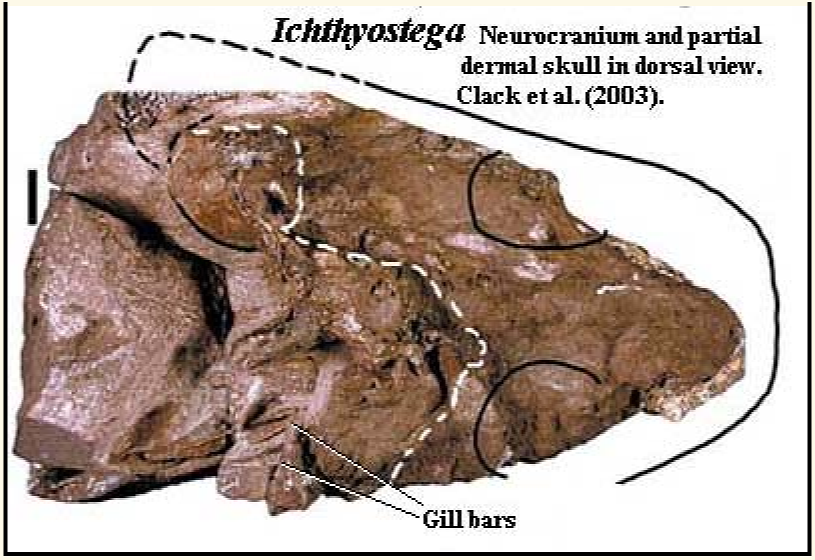
doesn't really do justice to these structures. The word brings to mind interlocked fingers. This is a fair description of the skull sutures in many living amniotes, but it understates the weirdly complex, intertwined curves of Paleozoic forms. Auntie Stega thus surely had a hard head, but was somewhat inflexible by today's standards. In addition to being rigid, Auntie Stega was probably somewhat thin-skinned. Auntie had already evolved the characteristic tetrapod ornament of irregular pits and ridges, radiating from presumed growth centers [LC93] [A95]. Then again, she was perhaps a bit less ornamented than her Carboniferous descendants, which suggests a thicker and/or looser skin covering. However, the whole issue of skin covering is speculative, and many reconstructions seem to assume an absence of integument on the skull.

Auntie Stega's snout was probably broad, certainly low, and relatively long [LC93]. Her external nostrils were set very low, near the edge of the upper jaw bones. *Id.* These bones were probably rather narrow. We may imagine her as viewing the approaching close of the Devonian with pursed lips, nostrils flaring slightly with stern disapproval.

Despite her very modest intellectual attainments, Auntie had a well-developed skull table, generally of the conventional tetrapod sort, with successive pairs of nasals, frontals, parietals and postparietals. At theanterior end, Auntie Stega may have had paired rostrals in addition to the usual premaxillae. The nasals were a simple paired set, elongate and rather large [Co96]. However, she had a soft spot between them, an internasal fontanelle [C02a] [AL04]. This region was not bone- covered, and may have served to relieve some of the stresses of Irish Devonian life on her otherwise rigid skull. She had a few more bones than the usual amniote might have on the top of her head, but nothing flashy. These were just the traditional Paleozoic complement of intertemporals, supratemporals and the like -- all of the old-fashioned bones that became obsolete when the skull table later separated from the cheek.

Auntie Stega's postorbital skull was markedly shorter than the skulls of her ancestors [C02a]. In part, this was due to the separation of the shoulder girdle from the skull and the reduction of the branchial (gill) region. This separation of head and shoulders may not have been complete in Auntie's day. She was a stiff-necked sort, atthe very least. Nevertheless, the operculogular series was absent, with only a small preopercular remnant [Co96]. Thus, Auntie Stega could likely move her jaw without making an unseemly show of flapping her gill chambers or waving her arms. Yet she had functional internal gills, which she would use when she thought no one was looking. Indeed, her branchial apparatus included a large ceratohyal and three or more deeply grooved, ossified branchial arches [CoC91] [Co96] [C+03]. Quite likely she also had a functional spiracle, and may have sported a small tabular "horn" supporting the soft tissue of a spiracular notch [CoC91] [LC93].

Auntie had large eyes, or, at least, her orbits were large. Likely, the orbits faced dorsally, although it isn't really possible to tell what her range of vision may have been. It is difficult to imagine Auntie Stega with great, adoring eyes cast ever heavenward, like a plaster saint. In addition to the


Ichthyostega Neurocranium and partial dermal skull in dorsal view. Clack et al. (2003).

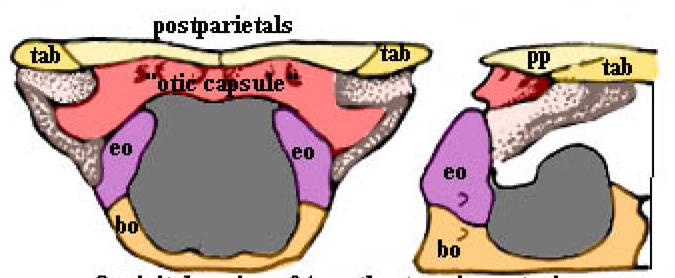
practical difficulties of this pose, it seems entirely out of character.

Not only was Auntie Stega's postorbital skull short, it was also much simplified. The postorbital and jugal were large and formed the entire posterior margin of the orbit [C02a] [A98]. The jugal also dominated the cheek region. Having finally established contact with the quadratojugal at the level of *Ventastega*, the jugal thereafter strictly forbade any contact between the squamosal and maxilla [Co96]. Thus the basic four-part organization of the tetrapod cheek was established: with postorbital and squamosal above, jugal and quadratojugal below.

Braincase & Occiput

We know remarkably little about Auntie Stega's occiput. As mentioned elsewhere, the formation of her neck was far from complete. The notochord still penetrated well into the skull [C98] and must yet have borne a considerable fraction of the task of holding up the head. We might assume that the occipital region looked like the occiput of *Acanthostega*. However, the posterior skull in the closely related *Ichthyostega* is so weirdly different [J96] [C+03] that such an assumption would be risky. Auntie Stega could not stick her neck out, and neither shall we.

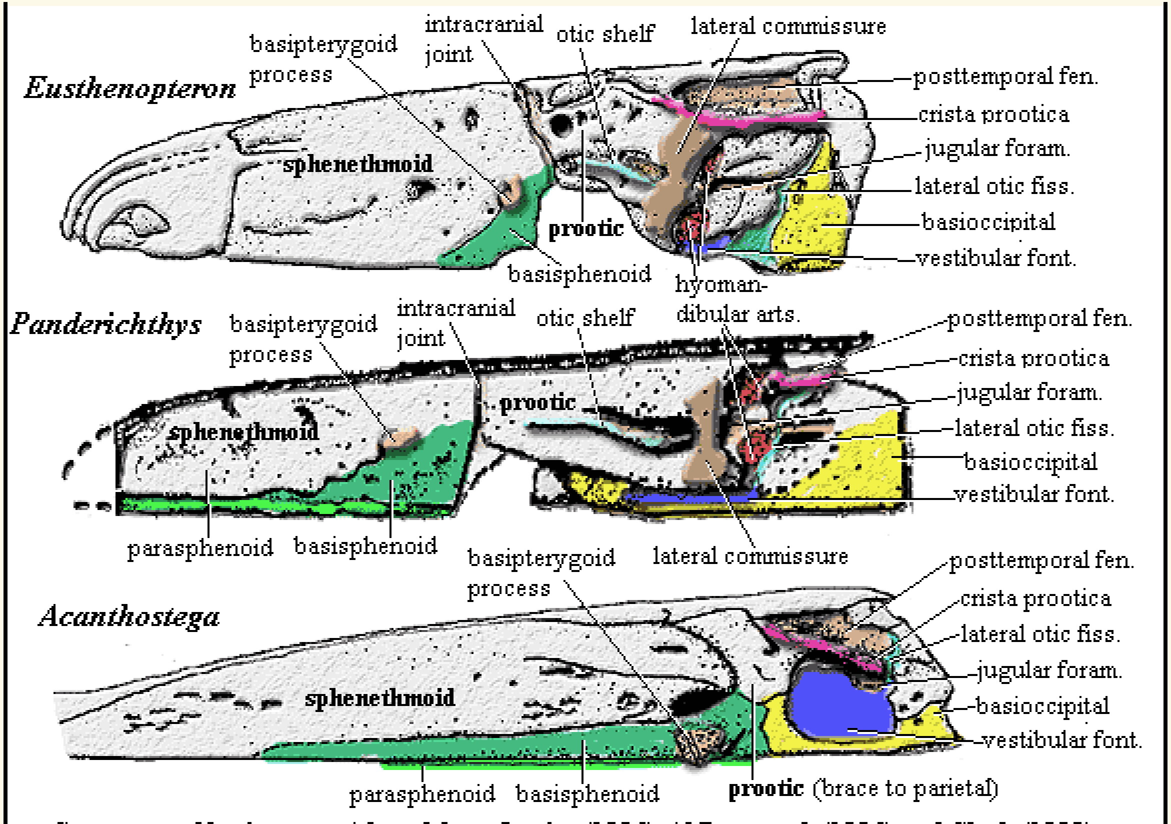
Auntie Stega's immediate ancestors were of two minds, with the *sphenethmoid* (anterior) and *otoccipital* (posterior) regions separated by a fissure, *the intracranial joint*. Auntie had a more integrated personality. That is to say, her mind was made up, with the various parts of the braincase firmly sutured, or even fused, together. In particular, the sphenethmoid and the otic capsules were co-ossified [C98]. Except in *Ichthyostega*, the basisphenoid was sutured both to the basioccipital and to the prootic portion of the otic capsule [C98]. In turn, a prootic process braced the braincase on the parietal, and (except in *Acanthostega*) the opisthotic met a facet of the tabular [C98]. Auntie did not have one final piece of stapling that her descendants soon acquired, a parasphenoid which extended onto the otoccipital region [C94].



Occipital region of Acanthostega in posterior and right lateral views. From Berman (2000).

As we might expect from the short postorbital skull, the entire otic region was relatively short, front-to-back [C+03]. In fact, this region shows a remarkable degree of reorganization over a rather small region of phylospace [A+96]. The *lateral commisure*, *otic shelf*, and jugular canal -- standard features of *Panderichthys* and other osteolepiforms -- were all lost in Auntie's generation [C98]. The *vestibular fontanelle* was reorganized as a space that would eventually become the inner ear [Co96]. It opened to the outer world through what is presumed to be a *fenestra ovalis*. Despite all this talk of ears, Auntie Stega herself was probably quite deaf. The lateral otic fissure (embryonic *metotic fissure* of amniotes) was continuous with the inner ear, as it still is. However, the elaborate systems which allow amniotes to use this connection to sort and analyze sound waves did not yet exist [MC04].

Perhaps because Auntie Stega was a single-minded sort, her mind had fewer facets. Specifically, she lacked the usual facets for the hyomandibula to attach



Stem tetrapod braincases. Adapted from Janvier (1996), Ahlberg et al. (1996), and Clack (1998)

to the braincase. Fortunately, she really didn't have much use for the hyomandibula anyway, since the whole branchial apparatus was of decreasing importance to her way of life. Neurocrania lack closets, umbrella stands, or other receptacles for elongate objects of no immediate utility, so the hyomandibula was more or less wadded up and thrown in a corner. One end came to rest blocking the vestibular fontanelle (or fenestra ovalis), while the distal end was jammed up against the tabular (or in that general vicinity), where it spread out, like a candle in holder which has fallen over and half melted on the table [C89]. This crude and unsightly condition is obviously a long way from the graceful double-headed arc of a proper hyomandibula. Perhaps for that reason, this bone is referred to, from Auntie's time onward, as the *stapes*.

If the stapes didn't look much like a hyomandibula, it also bore little resemblance to the stapes of amniotes, among whom the stapes eventually became a tiny, gracile hearing ossicle for conducting sound from the tympanic membrane and through the middle ear. There is no indication that Auntie or any of her immediate descendants possessed a tympanic membrane [C89] [MC04]. Auntie Stega's stapes was thick, massive, and incapable of transmitting high frequency sound [C89] [MC04]. Perhaps the only resemblance to the future hearing ossicle was the stapedial foramen. Both heads of the old hyomandibula participated in blocking the fenestra ovalis, and the stapedial foramen appears to have been a relic of the former space between the two heads [C94]. Functionally, the stapes of Auntie's day was simply a mechanical brace between the braincase and the dermal skull.

Auntie Stega minded her mouth. Auntie's basipterygoid process was huge, bulbous, and anchored her braincase to her palate in an authoritative fashion by fitting into a socket formed by the epipterygoid and pterygoid [C98] [C02]. Originally, this may have been a moveable *synovial joint* [C89]. However, it was only used on holidays and eventually became an immoveable bolt in almost all of Auntie's descendants [LCo95]. The sphenethmoid region was already losing bone in Auntie Stega, and (to judge from *Acanthostega*) was also becoming quite thin and less massive. In all of Auntie's Carboniferous descendants, the sphenethmoid is largely unossified and thus unknown. Fortunately, *Acanthostega* retained enough bone in the sphenethmoid region to demonstrate that it was already acquiring the eye musculature of tetrapods, quite likely an adaptation to vision above the surface of the water.

Before biting into on the palate and jaw, we pause for some thoughts on the brain. What's going on here? The braincase has become suddenly *much* more compact, unitary and tightly braced. The front part is stripped to its sensory core, losing bone and mass. The relative length of the otic region is cut by about half. Two massive braces are added, and a line of weakness between the two halves is completely obliterated -- all in about 10 My and possibly much less. This is evolution on steroids. Like the skull bones -- but even more so – the braincase has become somewhat simplified, tightly interlinked, and vastly stronger. We can think of only two factors that would be sufficient to explain this evolutionary sprint, and suggest that both were true. First, the skull was far more active because it was used in very active locomotion as the primary control surface, as argued elsewhere. Second, the skull was frequently uncushioned by water and was required to bear the more severe shocks of rapid momentum changes in air. [Recall -- if recollecting physics is not too painful an exercise -- that F = dp/dt. Force is rate change of momentum.] We don't mean to suggest that Auntie Stega was terrestrial; but she may well have kept her chin up and, perhaps aware of her status as the Mother of all Tetrapods, her nose in the air.

CONTINUED ON NEXT PAGE

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW031011

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Tetrapoda: Overview (2)

Contents

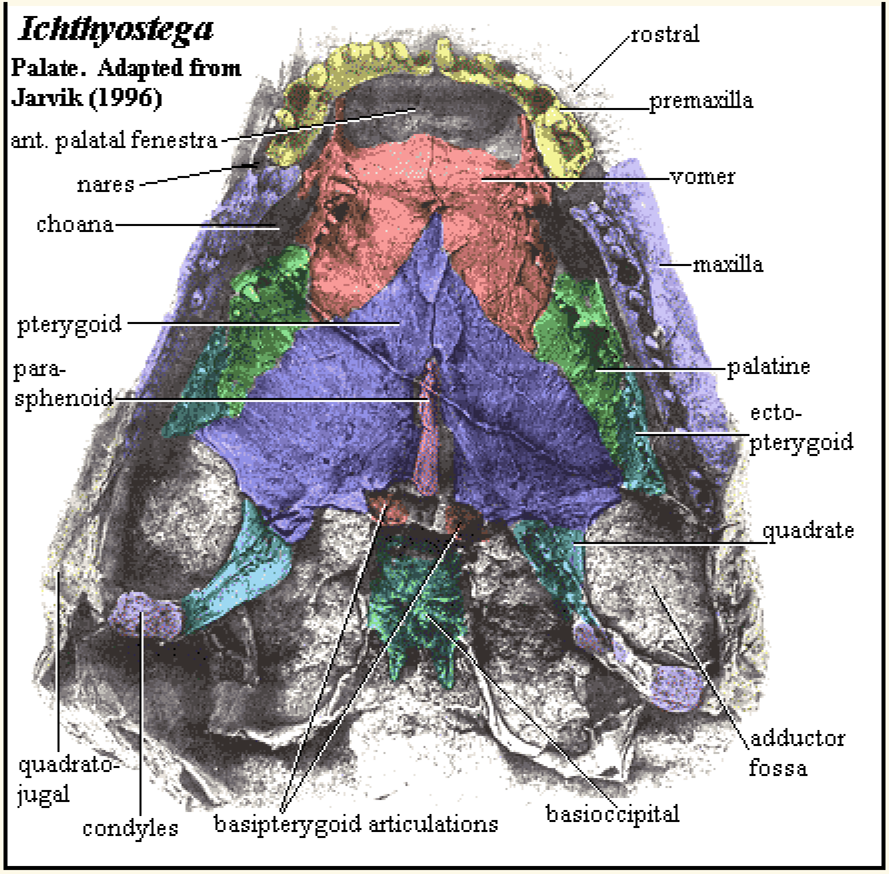
Abbreviated Dendrogram

```
SARCOPTERYGII
|
Tetrapoda
|--Ichthyostega
`--+--Tulerpeton
   `--+--Crassigyrinus
      `--+--Colosteidae
         `--+--Baphetidae
            `--Tetrapoda*
               |--Temnospondyli
               `--+--Lepospondyli
                  `--Reptiliomorpha
```

CONTINUED FROM PREVIOUS PAGE

Palate and Jaw

We have hinted that Auntie Stega was not an individual of refined or adventurous tastes; and, indeed, her palate was of a rather conservative type. As mentioned elsewhere, parasymphysial fangs had become increasingly popular in her day. To accommodate these appliances, a number of early tetrapods developed anterior palatal fenestrae [LC93]. Likewise, the vomer exhibited some tendency to expand and develop denticle fields [LC93], and ultimately its own dentition. Certainly, a number of individual adaptations appeared. However, there are no distinctively tetrapod innovations of the


Ichthyostega

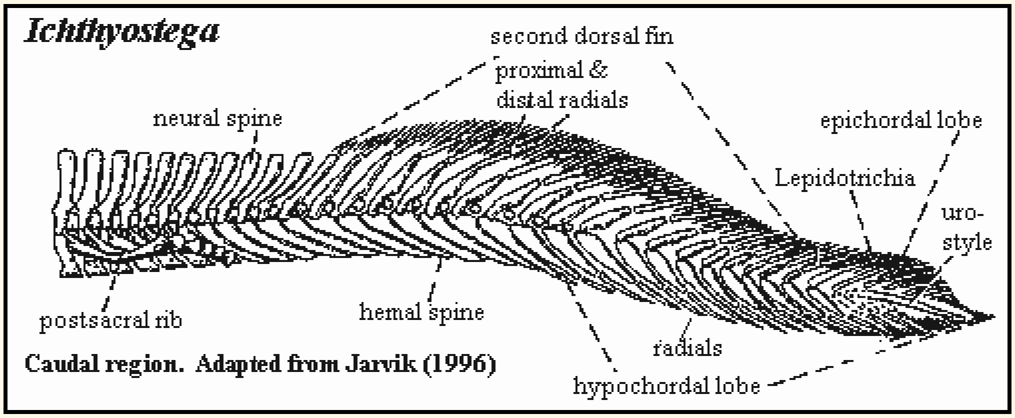
Palate. Adapted from Jarvik (1996)

palate.

Much the same can be said of the jaw. Auntie Stega was the beneficiary of 20 My of elpistostegalian jaw evolution, which had produced the advanced jaw design discussed in connection with *Ventastega*. Auntie conserved this legacy but did little more than refine some details. So, for example, the tetrapod splenial developed a medially-directed twist of the ventral margin, exposing the splenial ventrally and mesially [D00]. In other words, the jaw tended toward a sharper keel anteriorly and a more smoothly curved and hydrodynamic ventral surface. Tetrapod jaw adductors were larger, and pulled more vertically. This required reorientation of the articular, but was otherwise compatible with the existing design [D00]. The process of de-ossifying the Meckelian and zippering up the Meckelian fossa continued [AC98].

Axial Skeleton

We have seen that Auntie Stega inherited a well-developed palate and jaw. Sadly, like many a learnèd professional, she was all mouth and no backbone. Granted, the parts were all there. She probablyhad a *rhachitomous* vertebral column with 30 or more presacral segments [Co96]. However, the intercentra were paired, not fully fused [Co96]. Zygapophyses were present, but poorly developed [A98] [Co96]. Transverse processes were absent or rudimentary [A98]. The neural arches were well-developed, but the two halves were only partially fused [A98] [Co96]. Auntie Stega did have ribs; and, for the first time, their length generally exceeded the combined height of the centrum, neural arch and spine [Co96]. However, it is unlikely that they were much longer, or that they had developed the curvature needed to support the gut against gravity. Auntie did have a single pair of sacral ribs [Co96], and the pelvic girdle (as we will see) was quite substantial. Thus, on the whole, the old girl had all the parts to be a terrestrial type, but they were not yet configured for strolling about.


Ichthyostega

Caudal region. Adapted from Jarvik (1996)

Auntie *also* had all the axial equipment, and *properly* configured, to be a fish. However, almost all of these accessories were located on the tail. All of the unpaired fins had coalesced into a single structure which wrapped around the end of the tail. This general arrangement is found in many fishes which live in unstable, shallow, fresh water environments, typically with strong seasonal changes, *e.g.*, bichirs, *Amia*, aruana, and lungfishes **[1]**. All of these fishes are, like Auntie Stega, predators, and all have additional tetrapod-like behaviors in various combinations:

e.g., obligate air-breathing, surface feeding, surface basking, unusual adaptations of the eye, and station-holding using forelimbs. Thus, Auntie and her near-tetrapod kin were not unique in their suite of axial characters. However, for the same reason, these adaptations make very strong statements about Auntie Stega's environment and mode of life, which we may take up in more detail later.

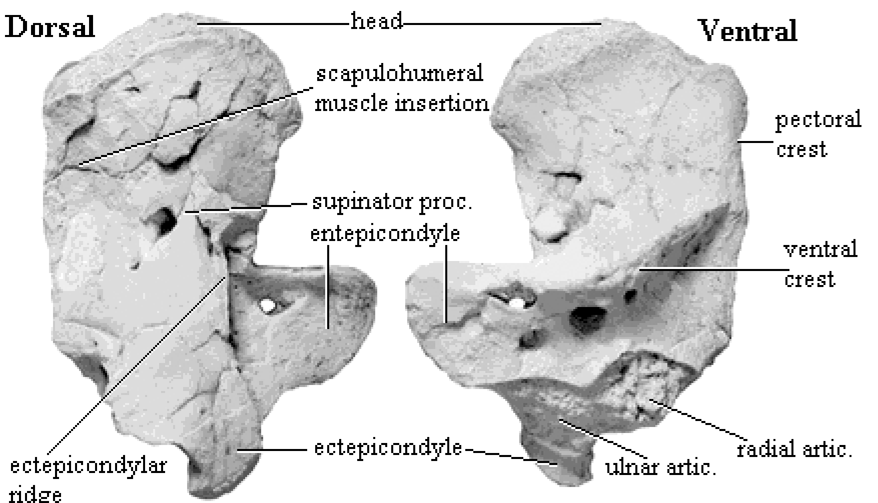

Ichthyostega Cast of digits on left pes. Adapted from Jarvik (1996)

Appendicular Skeleton

[2]

A brief description of the pectoral (forelimb) girdle in *Eusthenopteron* can be found at this link. Much more basic anatomy of the shoulder girdle in Elpistostegalia can be found here, together with an explanation of the nomenclature used on this page.

As we've mentioned, Auntie's shoulders were almost certainly not part of her head [Co96]. Most of the bones responsible for the head-shoulder connection in *Eusthenopteron* had been discarded: the supracleithra, posttemporals, and all of the extrascapulars [Co96]. However, the cleithrum retained a *postbranchial lamina* [Co96], suggesting a strong (or perhaps weak to absent – [D+94]), residual ligament connection, as well as functional gills. Auntie's cleithrum probably had a rakish posterior slant to it [D+94], perhaps to allow for some remaining degree of coordinated gill-girdle motion through this ligamentous connection [**]. However, in her descendants, the cleithrum assumes a more vertical orientation [**]. Auntie's cleithra, like those of her immediate ancestors, remained fused to the scapulocoracoid [D+94].



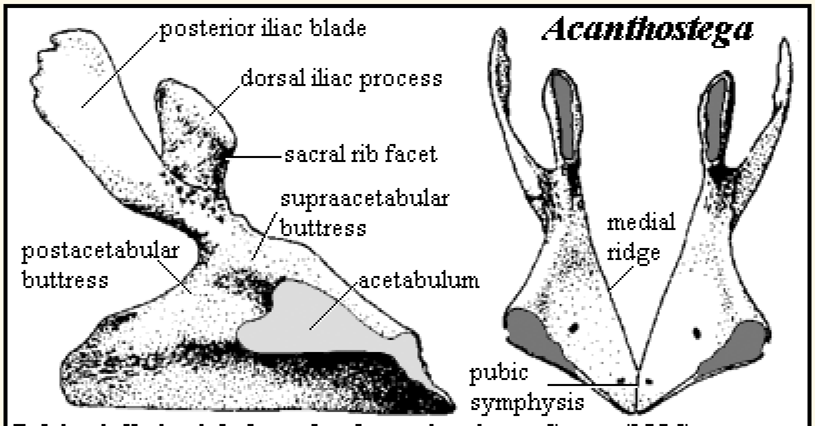
ANSP 21350 Shubin et al. (2004)

Humerus of unnamed Famennian tetrapod in dorsal & ventral views. Although not obvious, there appears to be an area of significant abrasion on the dorsal face which has nearly obliterated the supinator process. The latissimus dorsi processs, if present, cannot be located, perhaps for the same reason.

While Auntie was not yet ready to shoulder her way onto land, she was evolving in that general direction. The fossa *Tonya* was deep, and various scattered scapulocoracoid foramina were beginning to consolidate in that location [**]. The infraglenoid and lateral scapulocoracoid buttresses were becoming more pronounced [**], and the supracoracoid buttress more robust [D+94]; although the coracoid remained a very thin sheet of bone ventrally [D+94]. The glenoid (shoulder joint) itself continued its slow evolutionary movement to increasingly lateral positions [**]. The glenoid cavity was strap-like, suggesting a range of arm motion strongly limited to simple dorsoventral movements [A98] [Co95]. However, the glenoid retained an odd, possibly bimodal curvature hinting at more complex activities -- or perhaps just the ability to fold her arms to the side when not needed [**]. Auntie's clavicles had a broad ventral plate and narrow ascending processes [C97], and they articulated with an elongate, diamond-shaped interclavicle.

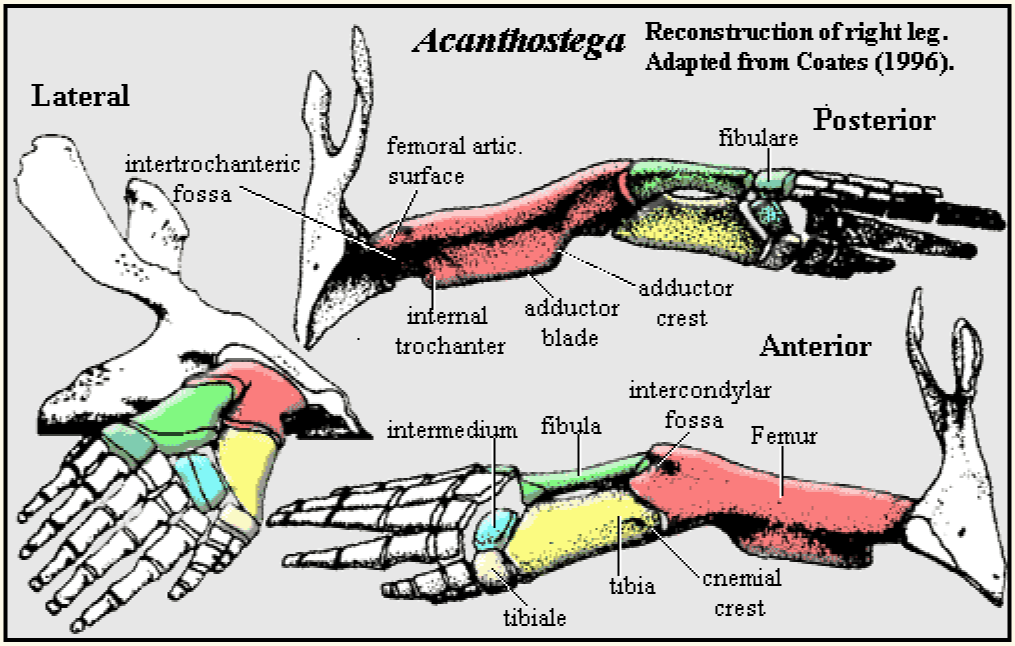
Auntie Stega's humerus was flat and L-shaped [A98] [Co96]. It had become "a broad platform for the insertion of extensor and flexor muscles that [was] less mobile than the humeri of *Eusthenopteron* and other basal tetrapodomorphs" [S+04]. The anterior margin was sharp, bearing a strong pectoral process [A98]. The *supinator ridge or process* also lay close to anterior margin [A98]. The *entepicondyle* was very large and probably rectangular [Co96] The tall, slender *ectepicondyle* arose from a strong ectepicondylar ridge and extended well below the distal end of the humeral shaft [Co96] [A98] [S+04]. Where the ectepicondyle and entepicondyle nearly meet, we see a deep recess [S+04]. In her descendants, a *latissimus dorsi ridge* was present there, generally continuous with the ectepicondylar ridge [S+04]. The ventral, or "oblique" ridge remained a dominant feature of the ventral surface, pierced by large foramina. This ridge ran nearly perpendicular to the long axis of the humeral shaft and was confluent with the posteromedial rim of the entepicondylar process [S+04]. The *epipodial* facets (*i.e.* the articulations for ulna and radius) were probably separated [Co96].

The epipodials themselves remained quite primitive. Auntie's radius was distally quite flat and broad [Co96]. The ulna was short and lacked an *olecranon process* [Co96]. The *intermedium* articulated only proximally and distally -- that is, it did not articulate with other wrist bones [Co+02]. Auntie had no *distal carpals* [Co+02]. In fact there was little specialization of the wrist or ankle bones, although they were soon to develop [LCo95]. On the other hand, so to speak, Auntie's had fingers -- in fact she probably had 6-8 fingers on each hand.



Pelvic girdle in right lateral and anterior views. Coates (1996).

Generally speaking, Auntie Stega's arms weren't all that different from the forelimbs of *Eusthenopteron*, except that they bore fingers instead of fin rays. However, Auntie had great legs. Compare the pelvis of *Acanthostega* with the pelvic girdle of *Eusthenopteron*. It's difficult even to recognize them as the same structure. Each side of Auntie's pelvic girdle was still composed of a single bone [Co96]. To that extent, the structure was still fish-like. But the two halves of the pelvic girdle were sutured together all along the ventral margin to form a single, smoothly curved ventral surface. Dorsally, the hips were attached to the spine by small sacral area involving a specialized sacral rib [Co96]. The pelvic girdle had two iliac processes (albeit oddly constructed), an anteroventral pubic symphysis, a laterally-facing *acetabulum*, and a *supraacetabular buttress*. Auntie's hips were, therefore definitively tetrapod hips -- not fundamentally different from the hips of an early archosaur, for example.



Reconstruction of right leg. Adapted from Coates (1996).

Auntie's femur looked strikingly like the femur of a very early synapsid [Co96]. To some degree this is coincidence, since the legs of many of Auntie's more immediate descendants look less like those of a "pelycosaur." Nevertheless, it is indisputably a tetrapod leg. None of the limb elements is measurably twisted [Co96]. The femoral adductor blade and crest are well-developed [A98] [Co96]. A rugose fourth trochanter is present and restricted to adductor blade [Co96]. Between the distal condyles of the femur we can clearly see an intercondylar fossa, presumably the precursor of the *popliteal fossa* [A98]. The epipodials are parallel, and both articulate with identifiable *tarsal* elements. The tibia has an L-shaped distal articular surface (since it articulates with two tarsals) and a cnemial crest [Co96]. At least some of the tarsal elements may articulate laterally as well as proximodistally [Co96], although that development may post-date Auntie. Typically for an early tetrapod, the fibulare and intermedium are large and each articulates with several digits. Finally, Auntie Stega's toes were much longer than her fingers.

Auntie Stega's Condition

This concludes our head-to-toe survey of the Mother of All Tetrapods. As usual, we have had to deduce her characteristics by triangulating through her immediate neighbors in phylospace. However, as it turns out, those characteristics are consistent enough that we can draw a very detailed picture of the old girl. What we see is a very mixed bag: a few startling innovations, such as the otic region of the brain, a few parts that hardly changed at all, like the palate -- but mostly the continuous, if slightly irregular, ticking of time and evolution, constantly remodeling anatomy in small increments.

References: Ahlberg (1995) [A95]; Ahlberg (1998) [A98]; Ahlberg & Clack (1998) [AC98]; Ahlberg & Luksevics (2004) [AL04]; Ahlberg, *et al*. (1996) [A+96]; Clack (1989) [C89]; Clack (1994) [C94]; Clack (1997) [C97]; Clack (1998a) [C98]; Clack (2002) [C02]; Clack (2002a) [C02a]; Clack, *et al*. (2003) [C+03]; Coates (1996) [Co96]; Coates & Clack (1991) [CoC91]; Coates, *et al*. (2002) [Co+02]; Daeschler (2000) [D00]; Daeschler, *et al*. (1994) [D+94]; Jarvik (1996) [J96]; Lebedev & Clack (1993) [LC93]; Lebedev & Coates (1995) [LCo95]; Manley & Clack (2004) [MC04]; Shubin, *et al*. (2004) [S+04].

---

[1] For some reason, the early tetrapods are frequently compared to a totally different ecomorph, the short-range ambush predators exemplified by pike. We have discussed elsewhere the many reasons why these body forms are mechanically dissimilar.

[2] In the process of working up materials on the elpistostegalian shoulder girdle, we noticed some minor patterns that weren't expressly stated by others in the articles we reviewed. To avoid confusing these speculations with reliable information, we've marked them with a double asterisk [**].

Page Back | Unit Home | Page Top | Page Next

Amphibians, Systematics, and Cladistics

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Ichthyostega
`--+--Tulerpeton
   `--+--Crassigyrinus
      `--+--Colosteidae
         `--+--Baphetidae
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

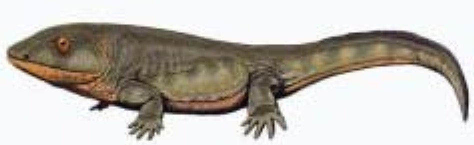
This unit begins with not one but two taxonomic controversies. The first of these (see quizz, *right*) comes about through a clash of paradigms (scientific methodologies and perspectives) and the other through how best to define things within a single methodology. Each revolve around a question, the first, what is an amphibian? and the second (considered on the following page), what is a tetrapod? If you find such taxonomic quibbling unintersting (and if you do we certainly don't blame you) feel free to skip ahead to *Ichthyostega*, where we return to a consideration of the procession of life through deep time (via *Beowulf*)

Quick quizz. Which of these is an amphibian?

(a) *Pederpes* (top) and *Rana* (center)

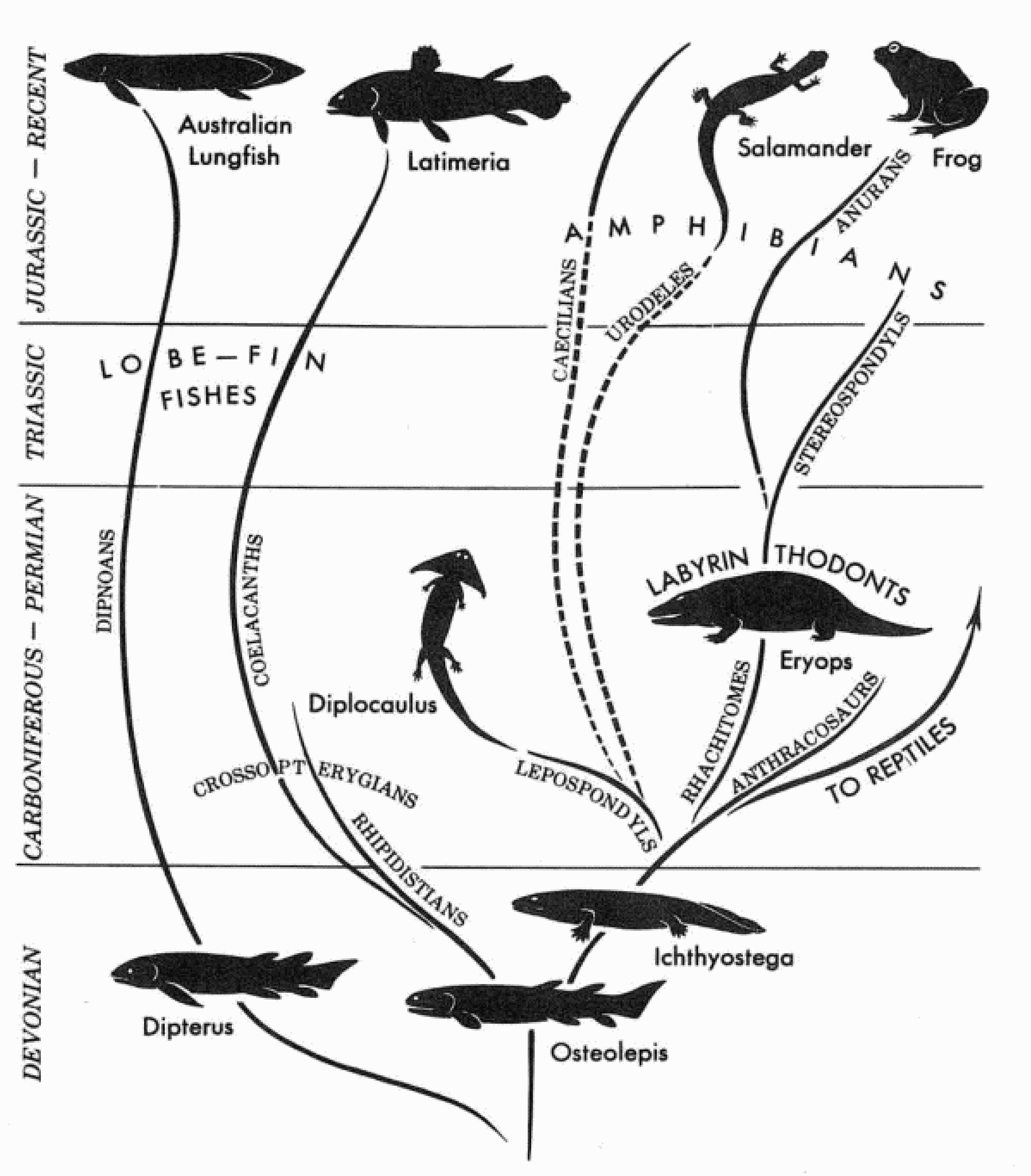
(b) *Rana* but not *Pederpes*

(c) *Catalina* (bottom) but not *Pederpes* or *Rana*



Hello to those folks still here. Now, in any biology textbook, Amphibians, Class Amphibia, are generally defined as vertebrate animals that lay their eggs in water and undergo a metamorphosis from a juvenile water-breathing tadpole or larval aquatic form to an adult air-breathing terrestrial form [1]. They include frogs and toads, newts and salamanders, and little known animals called caecilians, limbless amphibians that resemble snakes or large earth worms), as well as a number of extinct palaeozic forms, labyrinthodonts and lepospndyls. Simple? Well, as it turns out, not really.

Class Amphibia - Evolutionary Systematics



In the first comprehensive systematic and scientific classification of the natural world, the 18th century *Systema Naturae* of the Swedish botonist Linnaeus, amphibians and reptiles were grouped together in a single category. By the way, defining "Reptiles" is another taxonomic headache, which we've devoted an entire page to it as well. This is because amphibians and reptiles are pretty interesting creatures, and *prehistoric* [2] amphibians and reptiles more interesting again, especially to palaeo geeks like ourselves. But because of changing paradigms, according to which emphasis switches from one methodology to another, amphibians and reptiles don't mean the same now as they used to. Normally a bit of historical background would be in order. But we'll skip the intro and go straight to the chase. By the start of the 20th century, the main lines of the the evolutionary tree of life had been sketched out. Although many details have changed since then, and will continue to do so, we had a pretty good general idea of which group evolved from which. So in the early to mid 20th century, vertebrate paleontologists such as A.S. Romer (for reptiles) and G.G. Simpson (for mammals) had developed an understanding of vertebrate evolution and phylogeny based on a system that for the sake of convenience we refer to as Evolutionary Systematics (at the time, this term was rarely used). Others such as Raymond Moore developed similar arrangements for invertebrates, and paleobotoanists did the same for plants. The books of these authors can still be read and hold their own as classic reference works today.

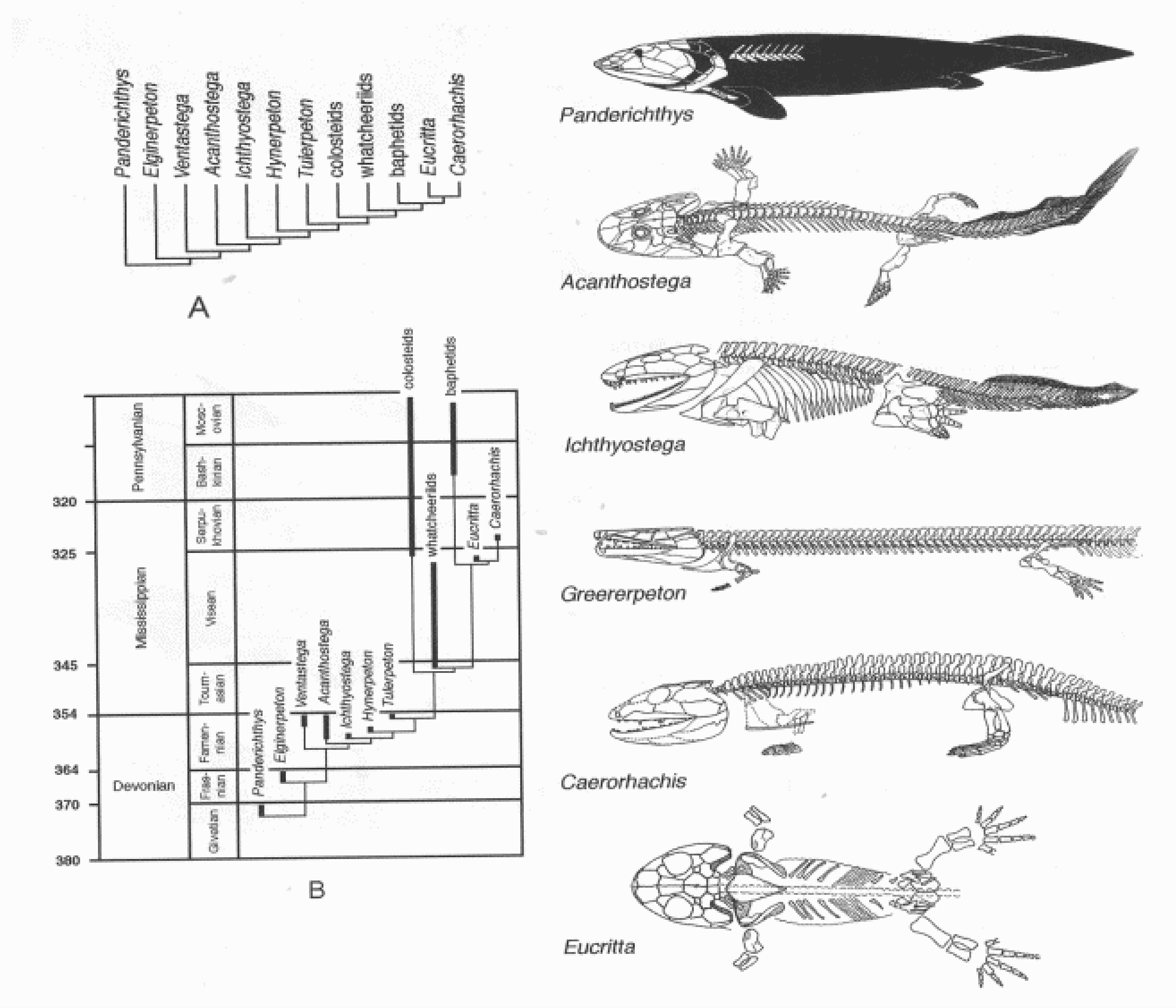
The diagram at the left is from Edwin Colbert's *Evolution of the Vertebrates* (Colbert 1969, p.90), and gives the consensus view of amphibian evolkution in the mid 20th century. This is still very much how we see the relations between the different groups now. The lungfish are a somewhat more distant branch than the rhipidistians like *Osteolepis*, which were ancestral to the first amphibians like *Ichthyostega*. From an Ichthyostega-like ancestor, or rather something a bit more advanced, there was a Carboniferous adaptive radiation not only of various Paleozoic amphibians but also of the ancestors of both reptiles and modern amphibians (Lissamphibia). Two main Palaeozoic groups (given, like Lissamphibia, the Linnaean rank of subclass) stand out, the large and diverse Labyrinthodonts (represented by the well known early Permian genus *Eryops*) and the small Lepospondyls (represented by the distinctive *Diplocaulus*). The Lepospondyls are a motley assemblage that has nothing in common other than small size and associated loss of primitive characteristics (the fact that they are considered a natural group today is in the opinion of the present author the result of confusing convergences associated with minaturisation (Carroll 2009, pp.155-6) with shared ancestral features). The Labyrinthodonts or "maze teeth", are named after the complex pattern of infolding of the dentin and enamel of the teeth, a characteristic they inherited from their fishy, rhipidistian ancestors (*right*) and basically include all Paleozoic amphibians apart from Leposondyls, and all Mesozoic ones not included under the Lissamphibia. This was a very diverse and indeed vaguely defined group; other than the structure of their teeth they are defined by complex vertebrae (as distinguished from the simple spool-like vertebrae of the leposondyls) and and a soild and heavily armoured and skull roof, another feature inherited from their lobe fin fish ancestors, and in turn inherited by early reptiles (captorhinomorphs and anapsids). This gives them their alternative, 19th century, name, Stegocephalia - "plated heads".

Traditionally (e.g. Romer 1933, 1954, and 1966; Colbert 1969; Carroll 1988) the Labyrinthodonts are divided into three smaller groups or orders. The Devonian *Ichthyostegalia* are the ancestral forms, in keeping with the evolutionary systematic tendency to posit a short-lived stem group (e.g. cotylosaurs, thecodonts, condylarths...) from which all the other lineages evolved. The *Temnospondyli* are the main line of labyrinthodont evolution, including both large and small types. They developed progressively more simplified vertebrae through time as they reverted to an increasingly aquatic existence, hence the distinction between the earlier, more terrestrial types, like *Eyrops*, who belong to the suborder Rachitomi, and the Triassic aquatic capitosaurs and metoposaurs, suborderStereospondyli, in which the vertebrae only consist of two elements., Finally, the *Anthracosauria* are another diverse group that include both aquatic and terrestrial forms, and were considered somewhat more closely related to reptiles.

Clade Tetrapoda - Phylogenetic Systematics (Cladistics)

The problem with all these sorts of definitions is that they can be somewhat vague and arbitrary. For example, modern amphibians (Lissamphibia) are probably just as distinct and specialised in relation to the heavy skulled Permo-Carboniferous labyrinthodonts as modern reptiles are. Both these groups *evolved from* labyrinthodonts, that is an objective phylogenetic fact, but apart from one needing to return to water to lay eggs and the other not, is there a reason why one should be included with them in the same category (Class Amphibia) and the other placed in a different category (Class Reptilia).

The cladistic revolution of the 70s and 80s was an attempt to introduce greater rigour into biological classification. It was pointed out that because the definition of Subclass Labyrinthodontia, and for that matter of class Amphibia, is simply based on primitive characteristics inherited from lobefin fish, and because Labyrinthodonts/Amphibians gave rise to creatures that are not Labyrinthodonts (to wit, Reptiles, Lepospondyls, and Lissamphians) or Amphibians (to wit, Reptiles), neither constitutes a natural group, and therefore in the interests of greater precision such terms - as well as others such as Protista, invertebrates, Reptiles, Thecodonts, Condylarths etc - should be discarded. That is why most *vertebrate paleontologists* now no longer say amphibian but "tetrapod", the group that includes both amphibians and their descendents; and not reptile but amniote (reptiles and their descendents). They restrict the word "amphibian" to a more limited grouping, either the last common ancestor of all recent amphibians and its descendents, or all animals more closely related to (insert here any recent species of amphibian) than to (insert here any recent species of reptile, mammal, or bird). Creatures that previously were referred to as amphibians but fall outsuide these definitions (some labyrinthodonts for example) are no simply called "tetrapods". On the other hand, *zoologists*, who deal with recent amphibains (a well recognisable group) happily continue to use the old Linnaean terminology and find no reason to change.



For cladistics what is important is not the taxonomic ranking (order, subclass, whatever), or the stratigraphic range in deep time, or which groups *evolve into* which (ancestors and decsendents), but what characters to use to define a group of organisms, and how choice of characters effects the statistical outcome of the phylogenetic relationships between these different organisms, represented diagramatically as a phylogenetic tree, or cladogram. Thus, with amphibians (or tetrapods) the question is not how did fish evolve into amphibains, but what traits do we select to define tetrapod, and also, at what point can one of the nested clades (groups nade up of a common ancestor and all its descendents) be called a tetrapod? This is shown by the following diagram, from a pdf by Dr Stuart Sumida (Biology 680 - Advanced Topics in Evolution - Evolution of the Vertebrate Limbs - *left*). This whole diagram could be cosnidered a zooming in or higher resolution focus on the drawing of *Ichthyostega* in the previous diagram. Here *A* constitutes the actual cladogram itself, which is a hypothesis on phylogenetic relationships, not an actual evolutionary tree (it is easy to get these two ideas confused). Note that this is only one possible cladogram out of many. *B* is a dendrogram, or chronogram, an evolutionary tree, based on cladogram A, but plotted against geological time. Incidentally one could reverse the position of Colosteidae and Whatcheeriidae, and even make the latter a grade - that would get rid of some of that excessive ghost lineage (the dotted lines not represented by the fossil record). The six drawings on the righta re representative early tetrapods, with the most basal (in this case the advanced sarcgopterygian fish *Panderichthys*) and the most derived or advanced at the bottom. Not only is it difficult to decide at what point a fish becomes a tetrapod, perhaps because the fossils may be incomplete, or there could be disagreement on interpretation, but even where there is agreement on the fossils, there is still a difference of opinion on where tetrapoda starts, according to one's preferred method of phylogenetic nomenclature.

Which is best?

Choice of particular methodology gives certain advantages, but also comes with disadvantages. Evolutionary systematic definitions of amphibia or reptilia may tend to vagueness or ambiguity, but cladistics can be detrimental for the oipposite reason: its formalism can be excessively restrictive. Whether having a group of animals or plants (like, say, reptiles, or gymnosperms) rendered invalid because it has descendents that are different to it, is a good or a bad thing, is up to the individual to decide. There is an interesting comment regarding this on the Wikipedia page devoted to phylogenetic nomenclature. The editors there have provided an article that does not take sides or polemically push one position as best (an attitude the present author finds all too prevalant on discussions on phylogeny, evolution, nomenclature etc). They give an analogy with chemistry. To quote:

> Proponents of phylogenetic nomenclature claim that, as rank-based nomenclature does not delimit taxa precisely, its definitions will need to change as the science of biology advances. They see their approach as preferable in that their definitions are not susceptible to this kind of instability. It is a disputed matter whether such changes are characteristic of sciences outside of biology and whether, if so, biology should follow the example of such sciences. Chemistry has been used as an example.
>
> Michel Laurin, one of the foremost advocates of phylogenetic nomenclature, considers that the concept of a chemical element has been stable ever since Dmitri Mendeleev put forth the periodic table in 1869. Biology should, on Laurin's view, follow the example of chemistry and define its terms as precisely as possible. (Laurin 2008)
>
> The historian and philosopher Thomas Kuhn argued that changing the meaning of established concepts is central to significant advances in science (Kuhn 1962). Prior to John Dalton's work, he pointed out, the criteria for something's being a chemical compound were such as to include salt water; by new criteria adopted afterwards, this fluid was excluded. (Kuhn 1962)
>
> Michael Benton, a prominent defender of rank-based nomenclature, regards biology as an endeavor very different from chemistry. Chemical classification, as he sees it, circumscribes entities in terms of properties that enter into knowable laws; biology, lacking such laws, must look to the usefulness of classifications. From this perspective, he argues, it is less important that the definition of a term classifying organisms remain constant than it is that the term continue to apply to most of the same organisms. As he views phylogenetic nomenclature as seeking the former kind of stability and rank-based nomenclature as seeking the latter, he considers rank-based nomenclature to be preferable (Benton 2000)

- Wikipedia

Because of these two different definitions, we can still refer to linnaean-evolutionary taxa and concepts, including similarity, evolution through deep time, supra-specific ranks, and groups that evolve into totally different groups, when the emphasis is on classification applying to particular group of organisms (in this case, Class Amphibia [3]). At the same time, we can also avail ourselves of the statistical and methodological rigour that cladistics provides, when emphasise is on the precise phylogenetic definition of a particular clade (in this case, Clade Tetrapoda). Even though the two systems of classifying life are incompatible, that does not mean that one is wrong and the other right. They can both be right, but in different ways

The problem with relying only on one particular methodology and paradigm can be illustrated with a simple example.

In cladistic nomenclature, because of the prohibition against recognition of paraphyletic groups, there is literally *no term* for the group of transitional forms (*Ichthyostega*, *Acanthostega*, etc) intermediate between "fishapod" (very tetrapod-like lobe-finned fish, like *Panderichthyes* and *Tiktilaak*) and amphibian-proper (four-legged semi-aquatic animals). Sure, you can say "tetrapod", but that refers to reptiles, birds and mammals as well. The term "basal" is often used by paleo enthusiasts in a vague way to mean the same as "primitive" did under evolutionary systematics. Which is fair enough, but it has nothing to do with the precision of definition that otherwise comes with cladistics. So "basal tetrapod" does not work here either; properly speaking it refers either the node at the bottom of the tetrapod cladogram, or the first terminal to branch off. Normally stem taxon would be the right choice, but because of the ambiguity around the use of the word tetrapod, "stem tetrapod" can mean anything - fishapods, bapheitids, even (in some phylogenetic trees) temnosondyls, ... Because science is about classification, this is a curious, and indeed irritating, lack. That is why there is no simple replacement for Ichthyostegalia (link, link), which can be used to cover all these early transitional forms (not only *Acanthostega* and *Ichthyostega*, but also *Sinostega*, *Hynerpeton*, and (if it does not belong in a more advanced category) *Tulerpeton*.

Apart from this, and differing methodological perspectives aside, it doesn't really matter, as Shakespeare informs us, if we refer to primitive amphibians as class Amphibia or basal or stem group tetrapods. In the following pages we will consider more about these ancestors of all land-living animals (as well as of animals that returned to the sea). And here we leave Linnaean ranking in favour of cladistic trees and definitions, beginning with the rather sticky point of the definition of clade Tetrapoda. MAK111110

Images: *Upper left*: Evolution of lobe-fin fish and amphibians, from E.H. Colbert, *Evolution of the Vertebrates*, 2nd ed., 1969, copyright John Wiley & Sons. *Middle right*: Cross section of Labyrinthodont tooth (from the Triassic genus *Mastodonsaurus*), from St. George Mivart, F.R.S. *On The Genesis of Species* London: Macmillan and Co. 1871, public domain, Wikipedia. MAK111110

Quizz results

If you answered (a) you are a linnanean/evolutionary systematist

If you answered (b) you are a cladist

If you answered(c) you like flying boats

Notes

[1] Like all such statements, this is something of a generalisation. Some amphibians, like the mexican walking fish (axotl) retain gills in adulthood, others like the Plethodontid salamanders lay eggs on land that hatch into miniature adults (Carroll 2009, p.200) but still require moist envirnments.

[2] Using the word prehistoric in the colloquial sense - before history, before man, millions of years ago, in deep time. Ffor example the present writer as a child a collection of those wonderful How and Why Wonder Books; one of which was called *Prehistoric Mammals*. In the more technically correct archeological sense however, prehistoric refers to the human period before recorded history, for example the neolithic, or the late palaeolithic. While this is a long time ago, it's not yet in the millions of years (see for example our tabulation of orders of ten gradations of time)

[3] Although the earlier classification of subclasses and orders given above no longer can accommodate modern discoveries, with only Temnospondyli (the topic of the next unit) being retained; see Benton 2005 for an updated version.

Page Back | Unit Home | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page by MAK111113

Page Back | Unit Home | Unit References | Unit Dendrogram | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Tetrapoda: *Acanthostega*

Abbreviated Dendrogram

```
SARCOPTERYGII
|
Tetrapoda
|--Acanthostega
`--+--Ichthyostega
   `--+--Hynerpeton
      `--+--Tulerpeton
         `--+--Whatcheeriidae
            `--+--Crassigyrinus
               `--+--Colosteidae
                  |  `--Greererpeton
                  `--+--Baphetidae
                     `--Tetrapoda*
                        |--TEMNOSPONDYLI
                        `--+--LEPOSPONDYLI
                           `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Acanthostega*

A Lot of Rot: the World of the Tetrapods

2. Hazardous Waste & Inefficiency: A Short History of Rubisco

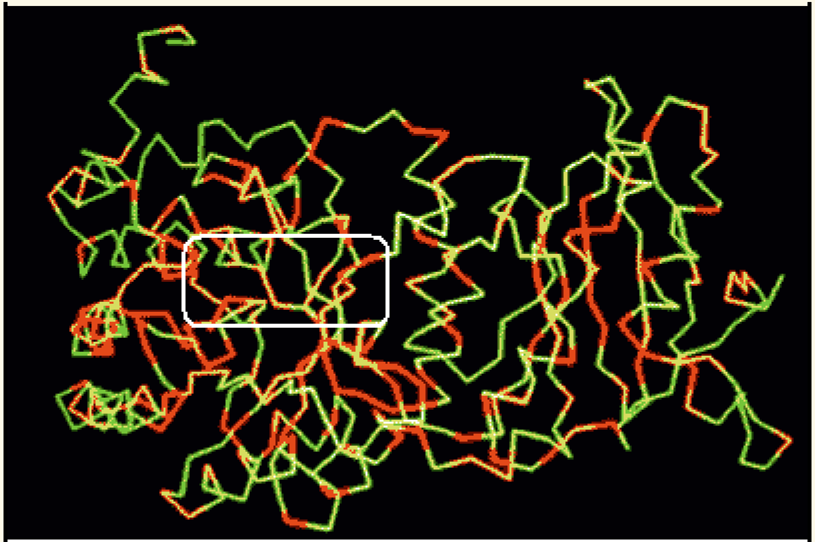
[GO TO PART 1. An Introduction to Tetrapod Environments of the Late Devonian]

It really isn't necessary to our plot line to explain the ultimate origins of the Late Devonian wood crisis, but the explanation makes rather compelling sense, to us at least. If we are correct, the Late Devonian wood problem was an almost inevitable result of evolutionary developments at the dawn of life.

As mentioned, the story begins deep in the Archean, even before the time of LUCA, the last universal common ancestor of all present life. At that time, all organisms were single cells, living in the sea, feeding on primordial soup, or by chemautotrophy, or by means of various other bizarre biochemical schemes which are found today, if at all, only in weird and extreme environments. However, all of these wildly varied cells, we are told, shared one common problem. They all faced death from a particularly noxious poison -- oxygen. Worse, in the high energy world of 2-3 Gy ago, oxygen would sometimes occur in highly reactive forms such as ozone (O_3), hydrogen peroxide (H_2O_2), or even as some hideous epoxide or superoxide (O_2^-) radical. These nasty substances were virtually guaranteed to crosslink and denature proteins and cause all manner of metabolic and genetic havoc. Fortunately oxygen was, at the time, a very small component of the atmosphere. Still, it was found nearly everywhere in low concentration and had to be dealt with routinely. Consequently, one early development in the history of life was the evolution of a variety of enzymes whose basic function was to capture and destroy oxygen, and particularly reactive oxygen species, such as peroxides. These enzymes, not too much altered by evolution, are still common today. Examples include catalase and other peroxidases, such as those used to detoxify aberrant organic compounds in the tetrapod liver.

The material in the last paragraph is all standard textbook stuff with which we have taken no significant liberties. What we *speculate* is that, not long after LUCA, one group of bacteria developed an interesting variant on this system. Perhaps the whole thing started with one of those simple ion-exchange pumps so common in bacteria. The protein might let H^+ into the cell down a concentration gradient, while pumping Mg^{++} out. Under appropriate conditions, magnesium ions can coordinate with oxygen, which would then be cotransported through the membrane and out of the cell. But, however it began, our supposition is that these cells evolved an enzyme which could use magnesium ions to coordinate free oxygen *and* a phosphorylated 5-carbon sugar (ribulose-1,5-biphosphate or RBP). Rather than transport the oxygen out of the cell, this enzyme could then *react* the oxygen with the RBP to yield (a) 3-phosphoglycerate (3PG) and (b) phosphoglycolate.

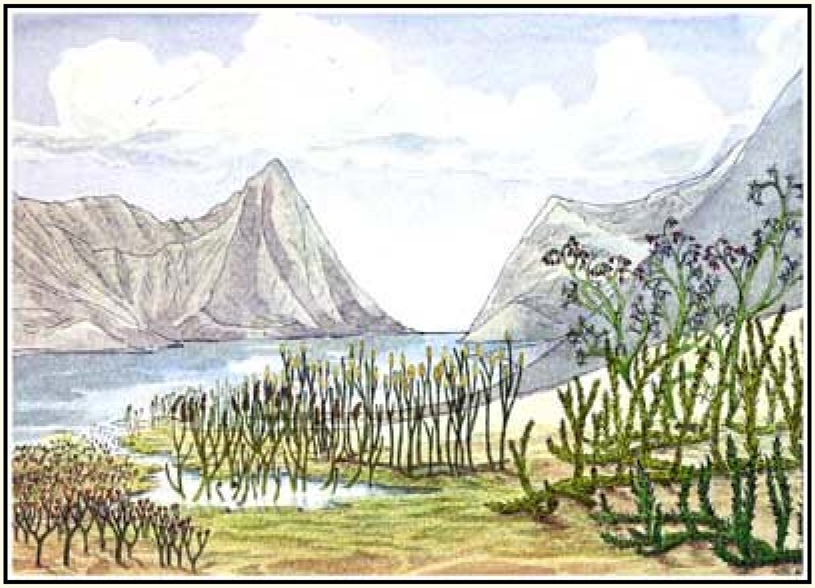
You don't need to know what these molecules are at this point. It's enough to recognize that 3PG falls neatly into the routine metabolic pathways of the cell, a useful intermediate which can either be broken down for energy through glycolysis, or used as a brick to build glucose (*e.g.* for cell walls) or other complex sugars. Phosphoglycolate, on the other hand, is recycled to the amino acid glycine through a process which generates hazardous hydrogen peroxide. However, the glycolate is safe enough by itself. It can be transported to specialized peroxisomes by a sort of cellular bomb squad, for detonation under controlled conditions. Interestingly for us, the "explosive" reactivity of this peroxide is harnessed in the peroxisomes to degrade other toxic compounds, including aromatics (ring compounds with double bonds).



Backbone diagram of Rubisco. Red regions are invariant, yellow highly conserved. White rectangle indicates region of active site. Adapted from Kellogg & Juliano (1997).

Peroxide can detoxify these materials by derivatizing and cross-linking them for (a) disposal outside the cell, (b) transformation into "friendly" aromatics like DNA bases and certain amino acids, or (c) degradation into digestible small molecules.

Now, supposing all this to be true, we can see that this useful enzyme needn't be overly efficient, since oxygen was only present in small quantities. However, it did need to be relatively ubiquitous, since oxygen could turn up anywhere. A few of you, who have studied the right biochemistry, will see where we're going. Such an enzyme, evolved to react with oxygen, might well also react with carbon dioxide, in which case the reaction would become: RBP + CO_2 => 2(3PG). And, in such a case, we would recognize the enzyme to be ribulose-1,5-biphosphate carboxylase, or **Rubisco** -- the most common enzyme on earth today. *See also Eukarya glossary entry*. Rubisco is the key enzyme in photosynthesis. It is this enzyme which actually takes atmospheric carbon dioxide and incorporates it into sugars. Thus, our speculation is not really so arbitrary after all. We have simply postulated that rubisco began life with a different function. (Nor are we the first to make guesses of this sort! *See, e.g.*, Introduction)



Why do we think so? Rubisco has two characteristics which have puzzled biochemists for years. First, it is one of life's least efficient enzymes. It works so slowly that enormous quantities are needed to get the job done in today's atmosphere. Second, it is incredibly sloppy and reacts with oxygen as well as CO_2, forming messy glycoylate which has to be recycled at some expense and danger to the cell, as described above. Frankly, this *only* makes sense if the original function were to dispose of oxygen, carbon dioxide being tolerated as an alternate substrate because it did no harm. It bears emphasis that atmospheric oxygen was very low, and carbon dioxide very high, for a *very* long time. From an evolutionary point of view, oxidative metabolism is relatively recent. Even after the evolution of photosynthesis, rubisco may have had *both* functions, since the newly evolved cyanobacteria needed to have a method for disposing of the waste oxygen generated by photosynthesis, before it reached dangerous intracellular levels. Thus, it is unsurprising that rubisco still reacts with both oxygen and carbon dioxide. It evolved under selective pressure to perfect this dual ability for two or three *billion* years, without much selection for efficiency. There are strong experimental indications that rubisco is, by now, under very tight genetic constraint, and has little freedom to evolve into some hypothetical faster or more selective form more consistent with Cenozoic requirements. *See*, e.g., Kellogg & Juliano (1997); Leebens-Mack & dePamphilis (2002).

During the Archean and Early Proterozoic, continental iron deposits and reduced sulfur species acted as a gigantic sink, sopping up excess oxygen and keeping things almost balanced. Oxygen levels increased only slowly, incrementally. That gave life time to develop oxidative metabolic pathways. Eventually, oxygen was no longer a poison, and became an indispensible metabolite. But, fast forward to the Devonian. Plants were now moving onto land in a big way. This had been happening, very slowly, since the Late Ordovician. Refer to the *atmosphere graph* on the previous page. The early downward drift of carbon dioxide levels may be explained as the gradual accumulation of a standing crop of plant biomass in and around fresh waters and tidal regions. However,full terrestriality was achieved in the Devonian; and, with it, a sudden rise in atmospheric oxygen. What would (or wood) happen then? ATW050703.

Images: The Archean scene is from NASA. I'm uncertain where the Devonian scene is from. I found it here.

Acanthostega

Acanthostega, were it not already extinct, would have been beaten to death over the last 15 years or so by three of paleontology's best minds and pens, and we will not attempt to improve on the excellent state of the literature. From time to time we comment on science in the manner of art critics; and from that point of view, it's a real treat to read and compare the styles of Clack, Ahlberg and Coates. We have already commented on Ahlberg's style, a cross between Baron Cuvier and David Copperfield. Coates is very different. He publishes relatively little, but his principal papers are each massive, thorough, and intricately detailed. Coates (1996) is still probably the best single paper on any early tetrapod ever published. It is now a little dated in some areas. However, there is yet unexploited material for any number of follow-up studies based on the insights he generated through exhaustive comparative analysis of the early tetrapod material.

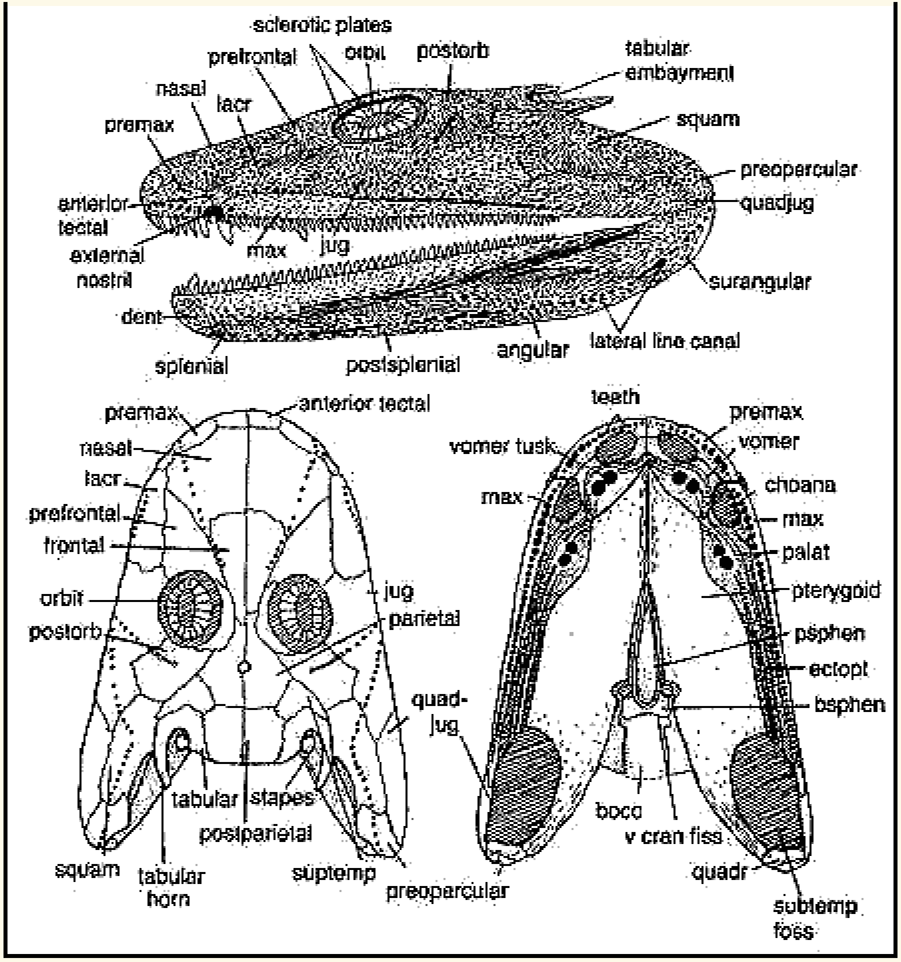
If we had to pick, Clack might have the most athletic mind of the three. One gets the impression that she has to force herself to quit working long enough to write things down. Each paper is a work in progress -- "we're still working on this," "we look forward to getting the results of that project." She changes her mind more often than most scientists and delights in explaining where she went wrong last time and how much progress is being made. She isalso the most likely of the three to go shooting off in some new direction to develop a new angle, *e.g.*, the neuroanatomy of hearing, the mechanics of underwater locomotion, or the physiology of respiration.

They make a remarkable group, and seem to be attracting an equally talented new generation. Ofthese, we take particularly unmerited pleasure in mentioning Dr. Henning Blom, now in Per Ahlberg's lab. Our unearned satisfaction is derived solely from the fact that we spotted Blom as a name to watch, based on his thelodont work, in the late 1990's. If we could only spot new basketball talent in the same manner ... . Inany event, and despite Prof. Clack's frustrating inability to muscle in a lay-up past the likes of Yao Ming, we are extremely lucky have these folks on hand to deal with *Acanthostega*. We nearly did not -- but we will deal with some of that history, very briefly, when we get to *Ichthyostega*. ATW050704.

Descriptions

Acanthostega: *A. gunnari* Jarvik, 1952.

Range: Late Devonian (Famennian) of East Greenland (Aina Dal Fm. & *Britta Dal Fm*.) Possibly very early Famennian, based on co-occurrence of *Phyllolepis* and *Remigolepis*. Long & Gordon (2004).

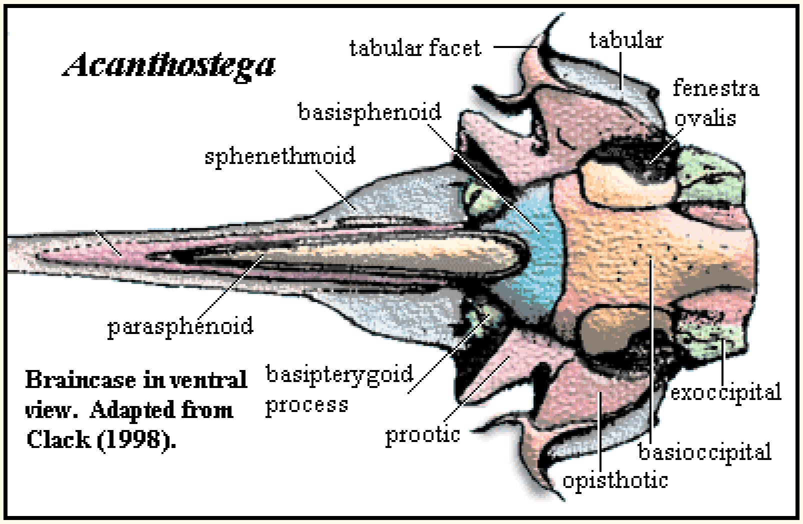


Phylogeny: Tetrapoda **:** (*Ichthyostega* + (*Sinostega* + (*Densignathus* + (*Hynerpeton* + (*Tulerpeton* + (*Ossinodus* + (Whatcheeriidae + (*Crassigyrinus* + (Colosteidae + (*Spathicephalus* + (Baphetidae + Tetrapoda*)))))))))) + *.

Characters: *image of life reconstruction*;

dermal skull: *additional image of skull* [Cl02] and discussion; paired median rostrals [Cl98a]; superficial anterior tectal above nares [Cl98a]; external nostrils small & close to jaw margin; naris and choana may have been used for chemosensation (as osteolepiforms?); premaxilla not sutured to maxilla [LCl93] and loosely sutured to nasals [Cl98a]; spade-shaped snout with enlarged bilateral nasals [Co96]; nasal bones do not suture together in the midline, leaving internasal fontanelle as in *Ventastega* [Cl03]; additional gap between nasals and median rostrals [Cl03]; prefrontal-jugal contact excludes lacrimal from orbit [Cl02a] [R+03]; prefrontal elongate & triangular [Cl02a]; postfrontal large, very thick [Cl02a]; "arrow-shaped supratemporal spanning skull table-cheek junction" [$Co96] [$Cl02a]; intertemporal absent [LCl93] [R+03]; postparietals forming square, but weakly sutured together [Cl02a]; tabular with both a posteriorly directed horn & embayment with possible spiracle [$Co96] [$Cl98a] [R+03]; eyes supported by ring of *sclerotic plates*; orbits enlarged relative to osteolepiforms [A98]; deep postorbital participating in orbit [A98] [LG04]; jugal large and extends anterior to orbit, underlapping all surrounding bones except maxilla [Cl02a] [R+03]; squamosal large, with hook-like process clasping tabular [Cl02a]; possible soft operculum attached to squamosal [LG04]; quadratojugal elongate triangle with narrow tapering process separating jugal from jaw margin [Cl02a];

branchial: preoperculars present [Co96]; large ceratohyal & 3+ well-developed & deeply grooved branchial region (*i.e.* functional gills) [CoCl91] [Co96] [Cl+03]; operculogular series absent [Co96];

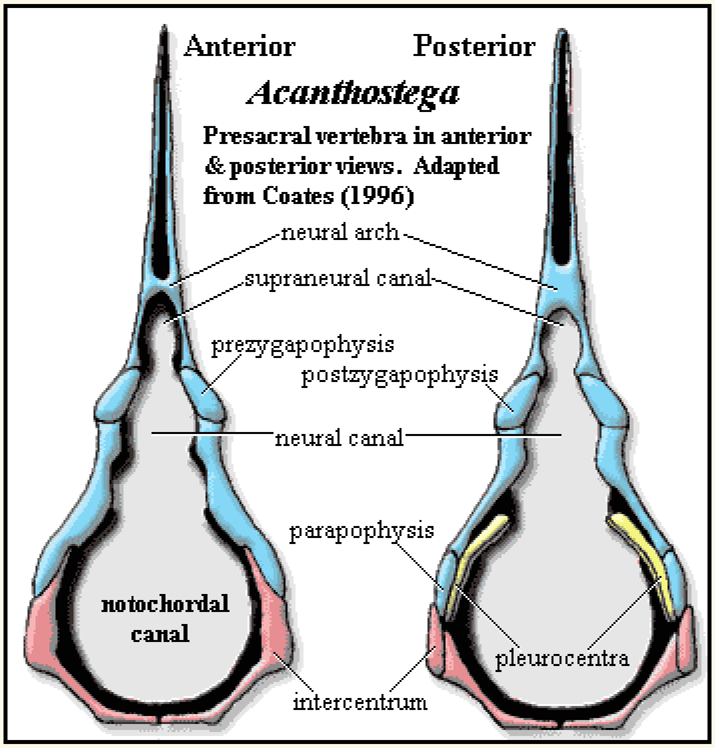


Braincase in ventral view. Adapted from Clack (1998).

Occiput & braincase: exoccipitals small; braincase enclosing notochord; otic region short, dorsally flat & square [Cl+03]; otic region, ventral part unossified [Cl98a]; opisthotic and prootic fused [Cl]98; opisthotic forms *crista parotica* laterally, probable unossified posterior facet for exoccipital, and ventrally forms anterior wall of *lateral otic fissure* [Cl98a]; lateral otic fissure continuous with fenestra vestibulae [Co96]; opisthotic posterolateral corner with slight groove for lateral head vein and probably part of *jugular foramen* [Cl98a]; crista parotica shelf forms posterodorsal margin of fenestra vestibuli [Cl98a]; stapes strongly attached to *fenestra ovalis* [Cl98a]; *fenestra vestibulae* large, accommodating stapedial head; *stapes* short & stout [LG04]; stapes with large proximal footplate & flared distal end; *image of lateral braincase* [Cl98a] and discussion; stapes incorporating both heads of former hyomandibula, visible as two closely appressed semicircles [Cl94]; margins of *fenestra vestibuli* formed by basioccipital & otic capsule, excluding basisphenoid and parasphenoid [Cl94] [Co96]; *lateral commisure* absent [Co96]; prootic robust, with sidewalls enclosing *semicircular canals* [Cl98a]; anterior prootic forming possible spiracular groove continuous with spiracular notch in tabular [Cl98a]; basisphenoid without notochordal pit [Cl98a]; basisphenoid with dorsally directed *dorsum sellae* "wings" weakly sutured to prootic & basioccipital [Cl98a]; *ventral cranial fissure* sutured, but traceable [R+03]; parasphenoid not contacting basisphenoid or prootic [Cl98a]; epipterygoid not contacting otic capsule [Cl94]; *basipterygoid processes* "bifaceted, cartilage-finished, apparently [with] synovial surfaces [and] approximately semicircular and slightly concave. The processes project a little below the parasphenoid. They are large, conspicuous, bulbous structures in ventral view, unlike those of any non-tetrapod osteichthyan, [and] were large and bifaceted." [Cl98a]; *sphenethmoid* region weakly attached to *otoccipital* [Cl98a]; sphenethmoid very lightly ossified, with nasal capsules unossified or not recovered [Cl98a]; sphenethmoid fused with basisphenoid [Cl98a]; sphenethmoid with muscle scar for orbital retractors [Cl98a]; sphenethmoid narrows abruptly anteriorly (primitive), with pineal foramen on broader posterior part (derived) [Cl98a];

palate: anterior palatal vacuity paired [R+03]; pterygoids covered with shagreen [Cl02a]; ectopterygoid forms significant part of adductor fossa [Cl02a]; parasphenoid terminates anterior to *ventral cranial fissure* [Co96];

jaw: lower jaw slender, long & low, with shallow ventral curvature [ACl98]; dentary narrow and tapers to a point posteriorly, not reaching articular [ACl98]; dentary weakly sutured to rest of jaw [ACl98]; dentary crest present, but without accessory tooth row [ACl98]; infradentaries with broad lateral exposure and sharp ventral margin [ACl98]; dorsal angular crest absent [ACl98]; angular contacts prearticular [R+03$] surangular rhomboidal & plate-like [ACl98]; surangular almost covers articular laterally and posteriorly [ACl98]; surangular participates in adductor fossa [ACl98]; *Meckelian* unossified between prearticular and dentaries [ACl98]; "foraminal" parasymphysial dental plate present [Co96]; medial parasymphysial foramen present, but lateral foramen absent (compare *Obruchevichthys*) [ACl98]; splenial, mesial lamina well-developed as strong buttress below parasymphysial plate [ACl98]; splenial with posterior process overlapping prearticular [ACl98]; muscle attachment striations on buttress & posterior process [ACl98]; splenial ventral edge forming deep concave space on medial face [ACl98]; "The hollow tube formed by the splenial, dentary and parasymphysial plate is occupied in part by remnants of Meckelian bone" [ACl98]; splenial not sutured to anterior coronoid [R+03]; prearticular very large, extending from articular almost to symphysis, with dorsal ridge bearing band of *shagreen* [ACl98]; prearticular not sutured ventrally to surangular, angular or postsplenial; prearticular lower margin with small Meckelian fossae; prearticular forms medial margin of adductor fossa [ACl98]; prearticular with tight suture to all coronoids and parasymphysial plate [ACl98];

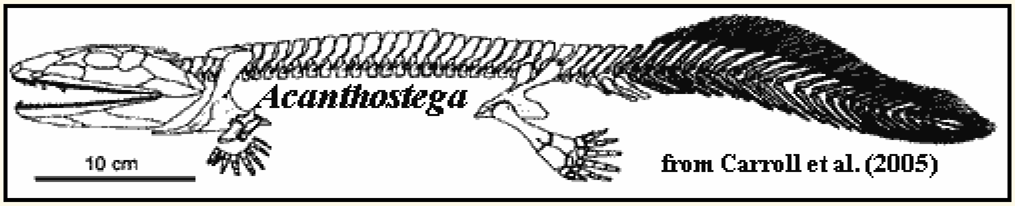


Acanthostega

Presacral vertebra in anterior & posterior views. Adapted from Coates (1996)

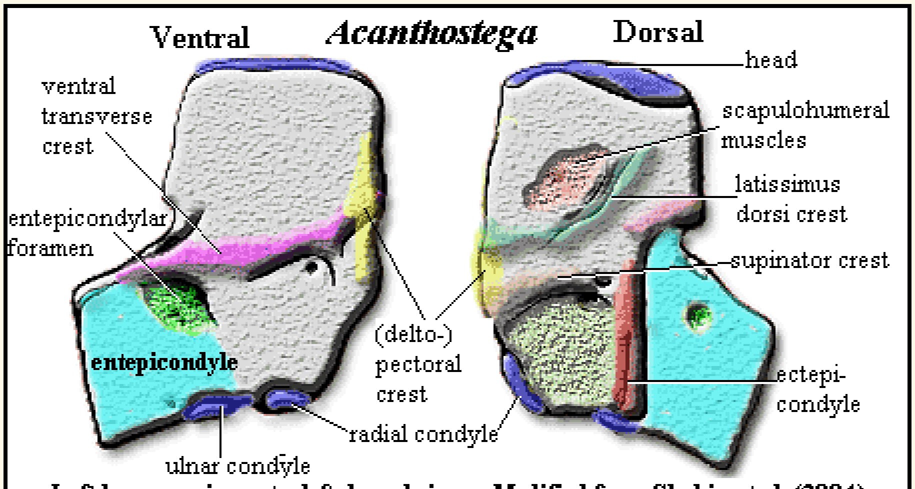
dentition: vomer with large fang-pairs; palatines & ectopterygoids with marginal row of smaller teeth & denticles; all coronoids with reduced dentition consisting of row of small teeth and denticles similar to palatal bones, but fang-pairs absent lCl02a]; anterior coronoid fang pair offset from tooth row [LCl93]; maxilla with ~40 teeth, premaxilla with ~13 [Co96]; dentary with smaller and more numerous teeth (about 75 [Co96: ~70] than upper jaw (about 60) and anterior fang pair [ACl98]; well-ossified gill arches;

axial skeleton: 28 to 30 notochordal, rhachitomous presacral vertebrae, with neural arches sometimes remaining as paired structures [A98] [*compare* Co96: 30+ *presacrals*]; little regional specialization in presacral vertebrae [Co96]; *intercentra* paired, with complete ventral fusion only in atlas & sacral intercentra [Co96]; pleurocentra not well ossified (unlike *Ichthyostega*) [Co96]; neural arches with canals for both nerve cord and a (more ventral?) supraneural ligament [A98]; small *atlas* arches set over large atlantal intercentrum; post-atlas arches little differentiated; narrow *zygapophyses* present but poorly developed [Co96] [Ca+05]; transverse processes & *diapophyses* only very slightly developed [Co96]; arches weakly bound to centra [Co96]; neural spines squared off [Co96]; accessory articulations present between some neural spines; ribs relatively short, straight, & slight, present from atlas to caudal #4 [Co96]; anterior thoracic & posterior cervical ribs *uncinate* [Co96]; rib articulations directed posterolaterally, dorsally continuous with posterior intercentral rim [Co96]; ribs with broadly spatulate proximal end, not conspicuously bifurcated [Co96]; anterior thoracic ribs distally expanded [Co96]; pelvis attached to vertebral column via single pair of elongate *sacral* ribs [Co96] [Ca+05]; sacral centrum not strongly differentiated [Co96]; deep tail supported by fin rays and accessory internal supports; about 35 caudal vertebrae [Co96]; caudal fin more extensive than in *Ichthyostega* [Co96]; caudal intercentra fused from caudal #4 [Co96]; caudals 1-4 with ribs [Co96]; hemal arches, fused to intercentra, begin at caudal #4 [Co96]; "first three complete hemal arches (caudal intercentra 5-7) are specialized and fit closely together" [Co96] **[3]**; caudal #6 with anteriorly serrated hemal arch plus spine [$Co96]; supraneural canal absent in the caudal region [Co96]; caudal fin lepidotrichia present, elongate, unsegmented, and unbranched [Co96]; first neural radial from 8th caudal vertebra, and first hemal radial 15th caudal vertebra [$Co96]; caudal supraneural spines articulated with some arches dorsally, to support the tailfin;



from Carroll et al. (2005)

appendicular skeleton: shoulder girdle detached from skull [Co96], with loss of *posttemporals* and *supracleithra* [LG04]; *pectoral girdle image* [Co96] [Co+02] & further discussion; cleithrum & scapulocoracoid co-ossified (as *Ichthyostega* and *Hynerpeton*); dorsal anocleithrum retained (as *Tulerpeton*) [Co96] [R+03]; an incurved flange (= *postbranchial lamina*) of cleithrum runs down leading edge of shoulder girdle (in fishes this lamina forms the back of the opercular chamber and helps direct water out of it) [CoCl91] [Co96] [L+00]; anteroventral process of cleithrum wraps around scapulocoracoid [A98]; numerous scapulocoracoid foramina [LCo95]; endochondral bone in coracoid region very thin [Co96]; *See* Atlas & Gazetteer for further details on the scapulocoracoid and cleithrum; clavicles with "broad, rounded subtriangular ventral plate and a rod-like ascending, dorsal process" [Co96]; clavicles do not meet anteriorly [R+03]; posterior margin of interclavicle drawn out into parasternal process [R+03]; large glenoid foramen [R+03]; glenoid posterolaterally oriented, with strap-shaped, strongly concave fossa slightly helical ('screw-shaped') [Co96]; humerus L-shaped and very flat, with accessory foramina as in *Ichthyostega* [S+04]; *latissimus dorsi process* offset anteriorly [LCo95] **[2]** [R+03]; humerus, anterior edge with near-vertical *deltopectoral crest* [LCo95] **[4]**; "recess and incipient crest at the proximal union of ectepicondylar and entepicondylar processes" [S+04]; humerus with transverse ventral ridge [S+04]; *entepicondyle* somewhat rectangular [Co96]; distally extended ectepicondylar process [S+04]; extensive extensor muscle scars on posterior side of ectepicondyle extending onto entepicondyle [Co96]; epipodial facets face laterally (distally) [Co96]; radial & ulnar facets face distally (not ventrally as in later tetrapods) [S+04]; convex facets well-separated [LCo95]; radial facet bimodal (lateral and anteriorly directed surfaces) [Co96]; epipodials shaped as triangular prism, with distinct, straight anterior surface, and sharp, convex posterior edge [Co96]; radius much longer than triangular ulna (as in *Eusthenopteron*); radius distally spatulate and flat [Co96]; *olecranon process* absent [Co96]; 'elbow' joint held more or less straight; 'wrist' diffuse structure formed around arc encompassing the long radius and short ulna [Ca+05]; distinct carpal (intermedium) & tarsals [Co96] [Ca+05]; intermedium articulates only proximally & distally [Co+02]; eight manual digits [Ca+05]; manus with phalangeal formula of 33334443 [$Co96]; paddle-like limbs; individual phalanges cylindrical and slightly constricted in the middle [Co96]; dermal fin rays absent [Co+02];



Left humerus in ventral & dorsal views. Modified from Shubin et al. (2004)

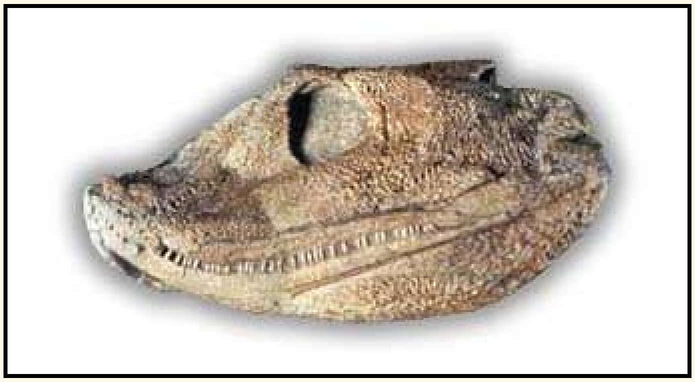
pelvic: *image of pelvis* [Co96] and discussion; pelvis attached to vertebral column via sacral rib [Ca+05]; no distinct facet for sacral rib [Co96]; pelvis is single ossification with no sutures [Co96]; pelvic blades all smooth except extensive ventromedial "striations extending onto the base of the dorsal iliac process" (probably =*iliofemoralis* insertion) [Co96]; *biramous* ilium [Co96]; pelvic post-iliac process long & posterodorsally directed with upright-oval cross-section [A98]; iliac neck attached to pelvis posterior to acetabulum [Co96] [A98]; postacetabular buttress more prominent than *supra-acetabular buttress* [Co96]; pubo-ischial pelvic symphysis [Co96] [Co+02]; pelvic plate posterior to acetabulum thinly ossified [Co96]; *image of hindlimb* [Co96]; hindlimb was paddle-like similar to

Ichthyostega; femur 25% longer than humerus [Co96] (*compare* [R+03]: femur approximately same length as humerus); femur relatively slender with large rectangular *adductor blade* placed midway along its length [LCo95] [Co96]; "internal trochanter is separated from the femoral head and projects proximally above a short smooth groove" [LCo95]; femur with ~75° anterior tortion [LCo95] [Co96] [A98**$?**]; "proximodorsal (extensor) surface is convex and smooth" [Co96]; tibial facet on anterior condyle only & fibular facet on posterior condyle [Co96]; tibia 25% longer than fibula [Co96]; tibia blocky & rectangular [A98]; tibia and fibula flattened and overlapped each other slightly in life in a manner suitable for twisting in a swimming stroke but not for bending at the ‘knee’; tibia with "well-developed cnemial crest, flanked anteriorly by a series of muscle scars" [LCo95]; ridge present near posterior edge of flexor surface of fibula [R+03]; fibulare articulates directly with digits [Co96]; ‘ankle’ consisted of a few flattened tarsals, with no obvious ankle joint; 8+ pedal digits with formula probably 1,2,3,3,3.3,3,2 [Co96] [L+00];

integument: ventral scales and gastralia, but no evidence of dorsal scales [Co96]; thinly ossified scutes associated with undetermined limb elements [Co96]; lateral line contained in tubes running through dermal bones, opening by series of pores;

other: perhaps an entirely aquatic organism [Cl02] or perhaps not [Ca+05].

Images: Skull reconstructions from Clack (2002). Photograph from Prof. Clack's website. Images elsewhere on this site include *life reconstruction*, *additional image of skull* [Cl02], *occipital region* [B00]; *image of lateral braincase* [Cl98a], *pectoral girdle image* [Co96] [Co+02], *image of pelvis* [Co96], *image of hindlimb* [Co96].



Notes: [1] Clack, on the Tree of Life page, notes that stapes formed the only bony link between the braincase and the palate, apart from the basal articulation, and may have acted as a brace between the two. It may also have provided an origin for spiracle-operating muscles. **[2]** "(misidentified as a deltoid process in Coates & Clack, 1990)" [LCo95: 315]. **[3]** The details are complex, but the point is that there is a "break" in the tail here, probably permitting the tail to move without jerking the entire spine around. Whales, for example have a group of specialized, highly mobile vertebrae just anterior to the fluke. **[4]** Coates [Co96] notes that his identification of the *latissimus dorsi* process is at odds with the Andrews & Westoll (1970) interpretation of *Eusthenopteron*. [AW70] identify the analogous structure in *Eusthenopteron* as a deltoid process. For what it may be worth, we strongly favor the Coates interpretation. Coates also sounds an apt note of warning that, although the various humeral structures are likely homologous to the attachment sites for the muscles for which they are named, "[i]nterpretations of musculature for extremely primitive limb skeletons need to be treated with caution, because the degree of muscular differentiation which had evolved from that of paired sarcopterygian fins is most uncertain." [Co96: 383-85].

Links: Acanthostega gunnari; Devonian Times - about Acanthostega; \Acanthostega\ by Janice McCafferty; Québec Science - L’acanthostega, notre nouvel ancêtre; Acanthostega; Acanthostega: fossil. . .; acanthostega.htm; Acanthostega gunnari; NOVA Online | The Missing Link | Diva of the Devonian (3) | PBS; 256.htm; Zimmer Chapter Four; Fall'96Syllabus; Biology 356; DEVONIANO Tetrápodes 1; Devoniano (Portuguese); Biology 356.

References: Ahlberg (1998) [A98]; Ahlberg & Clack (1998) [ACl98]; Andrews & Westoll (1970) [AW70]; Berman (2000) [B00]; Carroll *et al*. (2005) [Ca+05]; Clack (1994) [Cl94]; Clack (1998a) [Cl98a]; Clack (2002) [Cl02]; Clack (2002a) [Cl02a]; Clack (2003) [Cl03]; Clack *et al*. (2003) [Cl+03]; Coates (1996) [Co96]; Coates & Clack (1991) [CoCl91]; Coates *et al*. (2002) [Co+02]; Laurin *et al*. (2000) [L+00]; Lebedev & Coates (1995) [LCo95]; Long & Gordon (2004) [LG04]; Ruta *et al*. (2003) [R+03]; Shubin *et al*. (2004) [S+04]. ATW050702.

Page Back | **Unit Home** | **Page Top** | **Page Next**

Tetrapoda: *Ichthyostega*

Abbreviated Dendrogram

```
SARCOPTERYGII
|
Tetrapoda
|--Ichthyostega
`--+--Hynerpeton
   `--+--Tulerpeton
      `--+--Whatcheeriidae
         `--+--Crassigyrinus
             `--+--Colosteidae
                 |  `--Greererpeton
                 `--+--Baphetidae
                    `--Tetrapoda*
                       |--TEMNOSPONDYLI
                       `--+--LEPOSPONDYLI
                           `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Ichthyostega*

... Þá gén sylf cyning Geweóld his gewitte· / wællseaxe gebraéd Biter ond beaduscearp / þæt hé on byrnan wæg· Forwrát Wedra helm / wyrm on middan. Féond gefyldan / -- ferh ellen wræc -- Ond hí hyne þá bégen / ábroten hæfdon, Sibæðelingas· / swylc sceolde secg wesan Þegn æt ðearfe. / Þæt ðám þéodne wæs Síðas sigehwíle / sylfes daédum, Worlde geweorces. / ...	... Once more the old king, Drew deep on his Will, drew out the death dagger, Steel sharpened by battle, on iron mail lashed. Struck Lord of the Wederas! Knife gutting dragon! Cut demon down dead - for courage breeds strength -- And so both together created destruction, As brothers in arms, as each man should stand For the other in troubles. That was the Chief's way, His high road to triumph, to the last of his Deeds, Of his work in this world. ...
Beowulf XXXVII, ll 2702-2711	Transl. ATW050806

Erik Jarvik and *Ichthyostega*

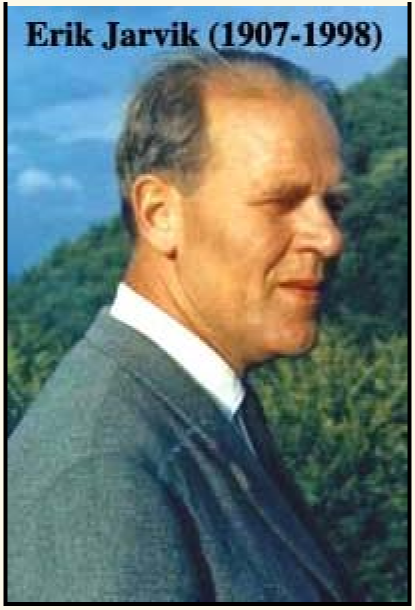
Below is the usual compressed summary of the characteristics of *Ichthyostega*. In preparing this summary, we have done our usual incomplete survey of the descriptive literature; and, like a blackbird, we have probably picked up shiny facts more for their intrinsic attraction than for their significance. However, in the case of *Ichthyostega* we've made an important exception. We have read, but have included nothing from, Jarvik (1996). Jarvik (1996) is the only monograph on *Ichthyostega*, a very important early tetrapod; and it was written by a scientist whom we have frequently praised for his work on *Eusthenopteron* and other osteolepiform fishes. The reason for this deliberate omission is simply that Jarvik (1996) is not a reliable source. Here we will first justify that statement and then examine some of the historical background of the paper, with an eye toward some of the odd effects this state of affairs has had on the study of early tetrapods.

The problems with Jarvik's study of *Ichthyostega* seem to be well known in the small community of early tetrapod workers. A brief, and by no means exhaustive, summary of the literature reveals the following. Säve-Söderberg originally named and identified about five different species of *Ichthyostega*, together with a supposed sister genus, *Ichthyostegopsis*. However, "Jarvik never really attempted to recognize or verify the presence of the different species" and simply lumped all of the material under *I. stensioei* without significant discussion of either morphology or geological setting [B05]. The dermal bones of the skull were described using a rather bizarre and certainly unique system of nomenclature drawn in part from supposed resemblances to the skulls of humans and frogs [J96]. Ahlberg & Clack [ACl98] concluded that Jarvik had misinterpreted the medial face of the inner jaw in various significant details, including the course of the oral sensory canal. In the palate, he ignored the presence of an ectopterygoid [B05].

Although Jarvik was the custodian of most known remains of *Ichthyostega* for fifty years, he never really attempted to explore, compare or understand its strange braincase [B05]. What little work he did on the braincase included misidentification of both the stapes and inner ear [Cl02a] [Cl+03]. Jarvik's description of the spine was at least partially "idealized" and inaccurate, and he misidentified both the sacral rib and its attachment point on the pelvis [Co96]. Blom bluntly states that "the braincase and the vertebral column, still remain to be explored." [B05] Jarvik's reconstruction of the pectoral girdle exaggerates the post-branchial lamina and includes a large supraglenoid process which appears to be an artifact [LCo95]. He plainly found 7-8 digits, but insisted that *Ichthyostega* had only five. Other, vaguer, grumblings in the literature suggest that this by no means exhausts the list of problem areas.

Jarvik was 89 years old when the article finally went to press. Not all of us will reach the age of 89, and few of us indeed are likely to be inclined or inspired to write a massive monograph on a unique tetrapod at that age -- even assuming we were capable of doing so at some earlier point. So, perhaps Jarvik's work does not reflect failure. It only suggests lack of complete success at a task which almost no one else would even have attempted in the first place. But, how did it happen that Jarvik took on this immense challenge at such an unlikely point in his career? The story has some odd resonances with the epic of another aging Scandinavian who struggled to lift a curse and obtain the treasure of another unique creature -- the saga of Beowulf and the Fire Dragon with which we began this section.

In the saga, the aging Beowulf attacks the red dragon. He is helped only by a very young warrior named Wiglaf. Beowulf's sword breaks, and he is terribly wounded. But Wiglaf comes in under Beowulf's shield (his own having been



reduced to charcoal) and delivers a huge blow which snuffs the dragon's flame. Beowulf seizes the chance to pull out his small *wællseaxe* -- normally used for routine camp chores, such as butchering game and dispatching wounded enemies. With a last, huge effort, Beowulf disembowels [1] the dragon; but he dies a few minutes later, after a suitably dramatic speech to Wiglaf. Jarvik's story is more complex and multi-generational – actually more like a traditional Norse epic than *Beowulf* in some ways -- and he was both Wiglaf and Beowulf at various points.

The first Late Devonian tetrapods were found in 1929 in rocks dating from the upper Famennian stage of East Greenland (on the north slope of Celsius Berg) by Oskar Kulling of Sweden. He sent his material to Erik Stensiö (1891-1984) at the Swedish Museum, who was intrigued, recognizing them to be scales of a fishlike vertebrate of uncertain identity. Stensiö had two serious students at the time: Erik Jarvik and an even younger man (who may have been an undergraduate at the time), Gunnar Säve-Söderberg. To judge by Jarvik's later reputation, he was thorough and brilliantly analytical, but he lacked flair or intuition. He tended to be dogmatic [J96] and somewhat unimaginative, at least by comparison to Säve-Söderberg. Säve-Söderberg seems to have been a golden boy -- charming, articulate, creative, and blessed with legendary energy [Jk96]. Thus Stensiö sent Säve-Söderberg to Greenland in 1930 and 1931 [LG04], rather than Jarvik. Consequently, it was Säve-Söderberg who found the first good tetrapod material from the region and published quickly, identifying two genera (*Ichthyostega* and *Ichthyostegopsis*) and several species [LG04] [B05]. Jarvik was finally allowed to accompany Säve-Söderberg in 1932 or 1933. He found limited material of a new genus, which he later named *Acanthostega* [LG04] [B05].

Säve-Söderberg continued collecting for several more years, but apparently put off monographic treatment until after his thesis was completed. As might be expected, Säve-Söderberg finished quickly and brilliantly, and he was immediately offered a professorship in 1937 [Jk96]. Unfortunately, that same year, Säve-Söderberg was struck by a mysterious wasting lung disease. Between his illness and the problems created by World War II, nothing was done about *Ichthyostega*. Eventually, Jarvik was ready to defend his own thesis in 1942 (he was 35 that year). Although Jarvik would continue to work in Stensiö's orbit for most of his life, Jarvik remained close to Säve-Söderberg, who was on his thesis Committee. Jarvik's thesis defense, however, was Säve-Söderberg's last public appearance. He died in 1948, and bequeathed the task of describing *Ichthyostega* to Jarvik [B05] [Jk96].

Thus, at the age of 41, after Jarvik was well-launched on his exhaustive studies of *Eusthenopteron* and other osteolepiforms, he was suddenly burdened with the responsibility for writing a definitive monograph on the most famous early tetrapod in the world, a creature wildly different from anything that had evolved before it -- and almost as different from the tetrapods which came after it. He was expected to do all this with Stensiö looking over his shoulder. Jarvik also knew (we may suppose) that (a) he was definitely not Stensiö's first choice, and (b) that he was supposed to fill the shoes of Säve-Söderberg, who had become the tragic hero of Swedish paleontology. Despite all this, Jarvik tried. He published a well-regarded paper on the post-cranial skeleton in 1952, and went on to lead at least one more collecting trip to Greenland. He also published a study of the limbs and limb girdles in 1980 [LG04]

[B05]. However, all things considered, it isn't too surprising that he was less than eager to discharge this unwanted obligation. Unlike Wiglaf, Jarvik lacked the protection of Beowulf's shield -- nor did Wiglaf have the acerbic Stensiö [J96] offering helpful suggestions **[2]**.

As a result, Jarvik was left to face the dragon alone, when he was in his eighties and without a Wiglaf of his own. One might argue that he ought to have let Clack and her students come in under his shield. Yet, from Jarvik's point of view, why would he want to pass the curse down to another generation? It was his *wirgþu* (curse, doom, punishment). But the saga-like irony of this course of action is that the curse *has* passed to one more generation. Ahlberg, Clack and co-workers are even now attempting the task of *re*-describing *Ichthyostega* because the current situation is untenable. Early tetrapod paleontology cannot continue with this key genus described with incomprehensible terminology, with many erroneous details, and with some parts never completed, almost 80 years after its discovery. Then, will the *wirgþu* continue? Who knows? But we hope Ahlberg *et al*. have fireproof shields this time, bring all their Wiglafs along -- and keep that *wællseaxe* handy. ATW050808.

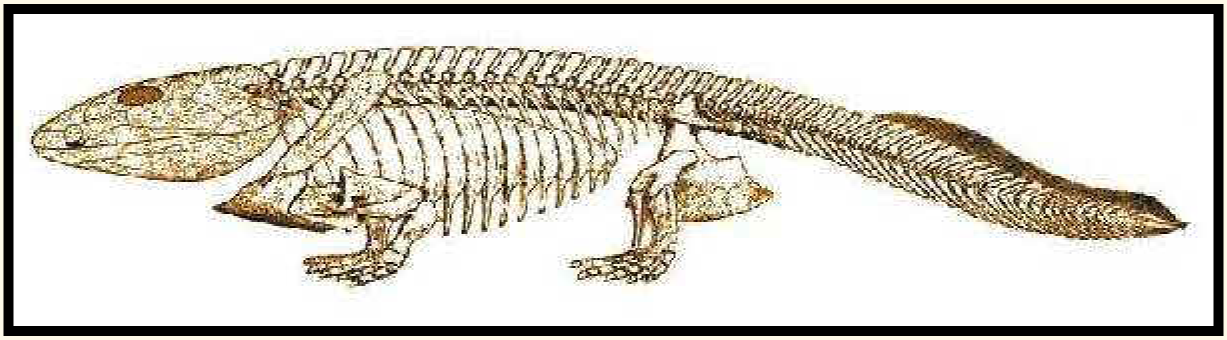
---

[1] The phrase *Forwrát ... wyrm on middan*. Is usually rendered as "cut the dragon in two." For a variety of poetic, logical, cultural, and linguistic reasons, I'm convinced this is simply wrong.

[2] Our take on Stensiö's role is influenced by timing and the fact that Stensio was best known for his descriptive and theoretical work on the vertebrate skull, particularly the braincase [J96]. Although Jarvik attacked the axial skeleton of *Ichthyostega* with dispatch, he delayed his paper on limb girdles (recall that the pectoral girdle is part of the skull in fishes) until 1980, when Stensio was finally phasing out of active Museum work. Jarvik did not begin work on the skull proper until after Stensio's death in 1984, and *never* did much with the neurocranium.

Descriptions

Ichthyostega: Säve-Söderberg, 1932. *I. stensioei (stensiöi)* Säve-Söderberg, 1932; *I. eigili* Säve-Söderberg, 1932; *I. watsoni* Säve-Söderberg, 1932 [B05].



Range: Late Devonian (Famennian) of East Greenland, *Aina Dal* & *Britta Dal Fms*. Possibly also Famennian of Scotland [A98] and France [Cle+04].

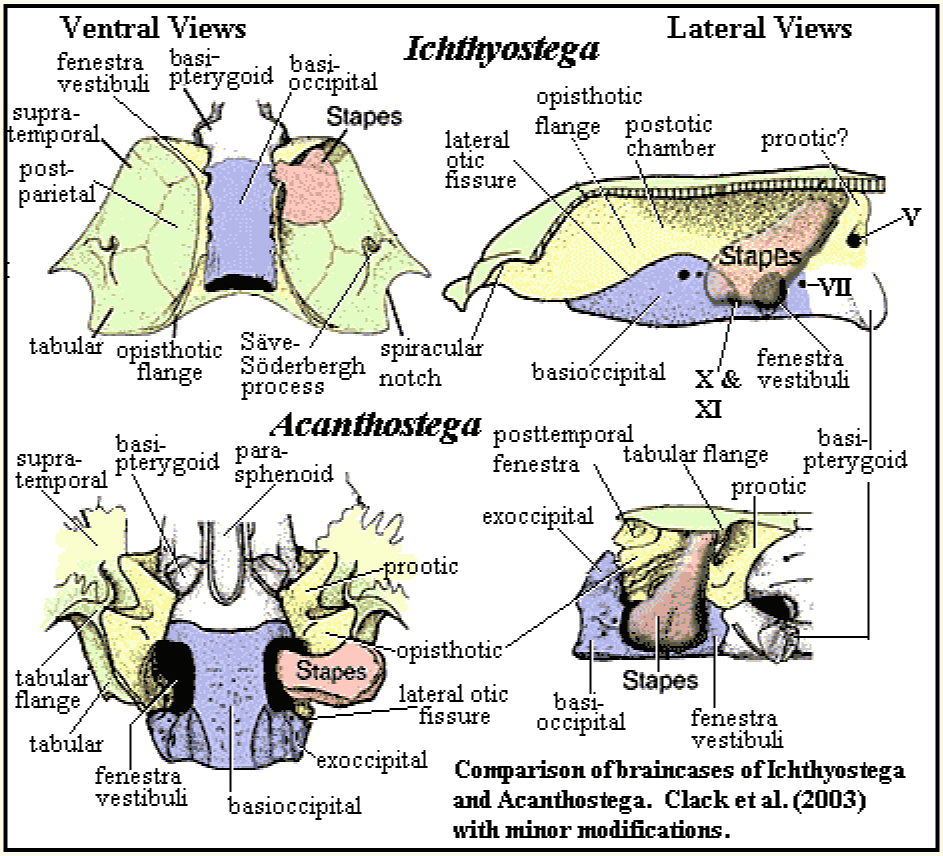
Phylogeny: Tetrapoda **::** (*Sinostega* + (*Densignathus* + (*Hynerpeton* + (*Tulerpeton* + (Crassigyrinus + (Colosteidae + (*Spathicephalus* + (Baphetidae + Tetrapoda*)))))))) + *.

Characters: a robust Famennian tetrapod 1+ m long.

dermal skull: snout large & rounded; skull roof flat; unpaired median rostral [B05]; paired lateral rostrals present [R+03]; robust maxilla with anteriorly high portion forming triangle pointing towards jugal- lacrimal suture [B05]; nares between anterior tectal and lateral rostral; septomaxilla absent (or = anterior tectal) [R+03]; prefrontal & jugal exclude lacrimal from orbit [R+03]; supratemporal pentagonal; intertemporal absent [Cl02a]; unpaired median postparietal [B05]; tabulars with posteroventral notch and deep ventrally projecting flanges attaching to the braincase; tabular suture with squamosal deeply interdigitated [R+03]; supratemporal & postparietal with large flanges extending downwards to receive braincase [Cl02a]; squamosal located relatively posteriorly (relative to parietal mid-length) [R+03]; .

branchial: preopercular present [R+03]; deeply grooved gill bars for functional gills [Cl+03].

occiput: posttemporal fenestra absent [R+03] **[2]**; basioccipital was long and notochordal [R+03], with no occipital condyle;



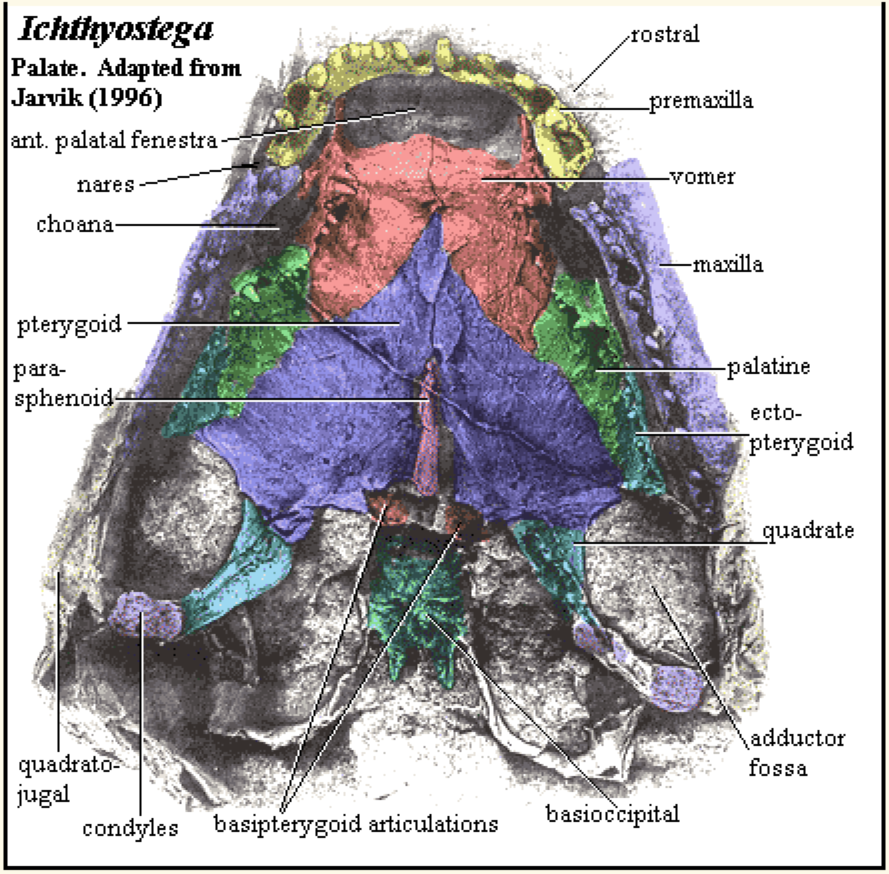
Comparison of braincases of Ichthyostega and Acanthostega. Clack et al. (2003) with minor modifications.

braincase: [1] notochord penetrates well into skull, as in *Acanthostega* [J+03]; otoccipital forming narrow crest suturing to median postparietal [Cl+03]; rounded sac-like structures flanking basioccipital; braincase long and narrow [$B05]; posterior stem of otic region very long and narrow [Cl+03]; opisthotics with large posterior "flanges suturing to down-turned extensions of the skull table margin" [$Cl+03]; prootics with strong transverse buttresses [Cl+03]; "On either side of the otoccipital braincase block is a large chamber, defined by solid walls formed of several different but closely sutured bones (proötic, opisthotic, epipterygoid and skull table ...). The chamber extends above the otic capsules to the midline crest. ... Projecting into the chamber from the undersurface of the skull table is a finger-like scrolled structure named 'Säve-Söderberg's process'" [$Cl+03]; otic chamber homologous to middle ear [Cl+03]; *stapes* very "thin and leaflike, almost circular in outline and anterodorsally curved" [$B05]; *sacculus* chambers very small and anterior [Cl+03]; stapes with "'shaft' [] a very thin, almost circular, anterodorsally curved lamina of bone, projecting dorsolaterally into the otic chamber." [$Cl+03]; stapes with two heads, in contact but unfused, separated by large stapedial foramen [$Cl+03]; ventral cranial fissure not sutured [R+03]; basisphenoid does not suture to prootic or basioccipital [Cl98a]; basal articulation immobile [LCo95].

palate: palate closed; maxilla excludes premaxilla from choana [B05]; maxilla and premaxilla form shelf lingual to tooth row [R+03]; vomer sutures to maxilla anterior to choana [R+03]; vomer without anterior crest [R+03]; mesial margin of pterygoid, quadrate ramus, strongly anteriorly concave, forming large space lateral to braincase [$B05].

jaw: lower jaw robust with long dentary reaching articular [B05]; dentary loosely attached to surangular & angular, but firmly sutured to postsplenial & splenial [ACl98]; unique & complex symphysis formed of Meckelian bone [$ACl98]; parasymphysial plate present [R+03]; suture between prearticular and splenial deeply interdigitated [B05]; parasymphysial foramen on suture line with splenial [ACl98]; lateral parasymphysial foramen absent [ACl98]; coronoids large & wide [B05]; circular Meckelian foramina piercing wide strip of Meckelian bone [B05]; prearticular long & without shagreen; contact between prearticular angular + surangular not sutured [ACl98].

dentition: ~30 uniform dentary teeth [ACl98]; dentary teeth significantly larger than coronoid teeth, with very large symphysial fangs on dentary [B05]; dentary teeth widely separated [Cle+04]; no accessory dentary tooth row [ACl98]; parasymphysial fangs [R+03]; only one other tooth on parasymphysial plate [ACl98]; substantial gap between parasymphysial plate teeth and coronoid teeth [ACl98]; all coronoids with single marginal tooth row & without fang pairs, accessory tooth row, or denticle field [ACl98] [B05]; ~27 much larger teeth in upper jaw; maxillary tooth



Ichthyostega
Palate. Adapted from Jarvik (1996)

count 17-22 [B05]; maxillary teeth strongly curved, with posterior crest [B05]; vomerine, palatine & ectopterygoid fangs absent [R+03] **[3]**; weak posterior denticle fields on pterygoid [B05]; denticle fields generally absent from both upper & lower jaws [$ACl98].

axial skeleton: vertebrae notochordal, but neural arches bore zygapophyses; neural spines squared off dorsally [Co96]; ribs long, blade-like, expanded & overlapping [B05]; cervical ribs distally expanded [R+03]; sacral rib present [Ca+05]; caudal fin with supraneurals & lepidotrichia (fewer & shorter than *Acanthostega*) [Co96] [Cl02a].

appendicular: cleithrum clavicle fused; anocleithrum absent [LCo95]; postbranchial lamina present [LCo95] [R+03]; clavicles do not meet anteriorly [R+03]; "posterior margin of interclavicle drawn out into parasternal process" [R+03]; large supraglenoid & supracoracoid foramina; moderately sized supraglenoid foramen within the triangular area [LCo95]; scapulocoracoid extends ventral to glenoid [R+03]; humerus L-shaped & flat; humerus without torsion [LCo95]; latissimus dorsi process weak or absent [LCo95]; humerus with prominent ectepicondylar buttress; ulnar & radial condyles well separated [LCo95]; ulnar condyle terminal; radial condyle ventral [A98] [R+03] (*contra* [Co+04], artifactual, citing unpublished recent work of others); forelimb with "permanently flexed elbow" [A98]; radius & ulna of equal length [Co+02]; ulna with conspicuous, forked olecranon [B05]; radius short & blunt [Co96]; manus unknown [Co+02]

pelvic: hindlimb flat and paddle- like [Co+02]; pelvic girdle large & unitary [Co+02]; pelvis with horizontal post-iliac process [A98]; & dorsally orientated iliac blade with unfinished facet for sacral rib attachment; extensive puboischiadic plate [Ca+05]; pubis sometimes separate from other elements [Co96]; acetabulum continuous with anterior edge of pelvis in most specimens [Co96]; supraacetabular buttress more prominent than postacetabular buttresses [Co96]; femur expanded proximally & distally [LCo95]; femur bearing large adductor blade [LCo95]; & deep intercondylar fossa; tibia large, quadrangular, with longitudinal ridge down medial surface [B05]; tibia & fibula both broad & flattened [LCo95] [Co+02]; tibia & fibula without well-defined shafts [Co96]; tibia significantly longer than fibula [Co96]; tibia with "well-developed cnemial crest, flanked anteriorly by a series of muscle scars, extends along the entire anterior edge of the lateral (extensor) surface" [LCo95]; fibula not waisted [R+03]; tarsus almost completely ossified [Ca+05]; large intermedium & fibulare present; fibulare large, articulating with two or more digits, as in *Acanthostega* [LCo95]; single? centrale [LCo95]; intermedium pentagonal [LCo95]; seven digits on pes [B05]; three small at leading edge & four stout digits more posteriorly [Co+02].

integument: ventral scales present [Ca+05].

Notes: [1] The braincase image requires explanation, since we have taken unusal liberties with the original in [Cl+03]. In addition to our usual complete relabelling, we have made the following modifications: (a) The *Ichthyostega* prootic is not identified in the original, and we've made our best stab at identifying it. (b) We've added a suture line between the tabular and supratemporal in the lateral view of *Ichthyostega*. (c) In the ventral view of *Acanthostega*, we've changed some lines and coloring to clarify the shape and position of the tabular flange. (d) In the lateral view of *Acanthostega* we've added a complete stapes, including the presumed course of the unossified distal region, to conform to Clack's speculation that it connected with the spiracular notch. (e) In the same image, we've changed the shape of the tabular to reflect the tabular flange. Even with these changes, we still have concerns that the position and extent of the stapes is inconsistent between the two views of *Ichthyostega*. Finally, the anterior braincase of *Ichthyostega* is not shown, since it is largely unossified and unknown. **[2]** This part of the skull is so aberrant in *Ichthyostega* that it is not a simple matter to state whether a posttemporal fenestra exists or not. **[3]** !? see image.

Links: Ichthyostega; Devonian Times - about Ichthyostega; ICHTYOSTEGA AS A TRANSITIONAL FOSSIL; RE-Ichthyostega digits; ICHTHYOSTEGA; Ichthyostega stensioei; Palaeozoic puzzle; J17 Did labyrinthodonts evolve from lung fish or crossopterygians ... ; Biology 356.

References: Ahlberg (1998) [A98]; Ahlberg & Clack (1998) [ACl98]; Blom (2005) [B05]; Carroll *et al*. (2005) [Ca+05]; Clack (1998a) [Cl98a]; Clack (2002) [Cl02]; Clack (2002a) [Cl02a]; Clack *et al*. (2003) [Cl+03]; Clement *et al*. (2004) [Cle+04]; Coates (1996) [Co96]; Coates *et al*. (2002) [Co+02]; Coates *et al.* (2004) [Co+04]; Janvier (1996) [J96]; Jarvik (1996) [Jk96]; Johanson *et al.* (2003) [J+03]; Lebedev & Coates (1995) [LCo95]; Long & Gordon (2004) [LG04]; Ruta *et al*. (2003) [R+03]. ATW031004.

Page Back | **Unit Home** | **Page Top** | **Page Next**

checked ATW040813

Hynerpeton

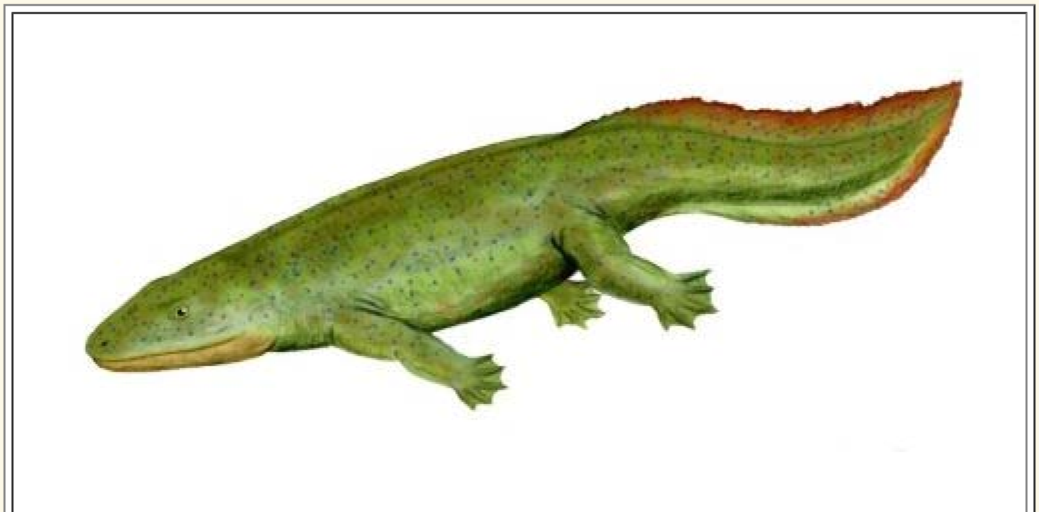
Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Hynerpeton
      `--+--Tulerpeton
         `--+--Whatcheeriidae
               `--+--Crassigyrinus
                  `--+--Colosteidae
                      |  `--Greererpeton
                      `--+--Spathicephalus
                          `--+--Baphetidae
                              |--Eucritta
                              `--Tetrapoda*
                                 |-
-TEMNOSPONDYLI
                                 `--+-
-LEPOSPONDYLI
                                     `-
-REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Hynerpeton* X



Hynerpeton bassetti, life reconstruction, by Nobu Tamura
Wikipedia, GNU Free Documentation/Creative Commons Attribution

Editor's note: due to lack of time and the need to fuill out missing pages, this page has been copied verbatum (apart from the last sentence, which I added) from Wikipedia. Soem generic material has been excluded MAK111112

Hynerpeton

Hynerpeton was a basal carnivorous tetrapod that lived in the lakes and estuaries of the Late Devonian period around 360 million years ago. Like many primitive tetrapods, it is sometimes referred to as an "amphibian" . The Late Devonian saw the evolution of plants into trees and growing into vast forests pumping oxygen into the air, possibly giving Hynerpeton an edge because it evolved complex lungs to exploit it. Its lungs probably consisted of sacs like modern terrestrial vertebrates. In 1993, the paleontologists Ted Daeschler and Neil Shubin found the first Hynerpeton fossil, a shoulder bone, near Hyner, Pennsylvania. They were surveying the Devonian rocks of Pennsylvania in search of fossil evidence for the origin of animal limbs. The animal had a very robust shoulder, which indicated that it had powerful appendages. Only a few bones have been found from Hynerpeton, in Red Hill, Pennsylvania, U.S.A.. The known fossils include two shoulder girdles, two lower jaws, a jugal bone and some gastralia.

The structure of the shoulder girdle indicates this animal may have been one of the earlier, more primitive tetrapods to evolve during the Devonian. Information on the relationship of the known fossils of Hynerpeton to other Devonian tetrapods can be found in *Gaining Ground The Origin and Evolution of Tetrapods* by Jennifer A. Clack.

It is thought that that these early amphibians are descended from lobe-finned fish, such as *Hyneria*, whose stout fins evolved into legs and their swim bladder into lungs. It is still not known whether *Hynerpeton* is the direct ancestor to all later backboned land animals (including humans), but the fact that it had eight fingers, not five, suggests that it is simply our evolutionary cousin. However, that may not be relevant, as polydactly was standard among all early tetrapods

References:

Shubin, Neil (2009). *Your Inner Fish: A Journey Into the 3.5-Billion-Year History of the Human Body.* New York: Vintage. p. 13. ISBN 9780307277459.

Haines, Tim, and Paul Chambers. *The Complete Guide to Prehistoric Life*. Pg. 30-31. Canada: Firefly Books Ltd., 2006.

Descriptions

Hynerpeton: *bassetti* Daeschler et al., 1994

Range: Fammenian (Latest Devonian) of Pennsylvania

Phylogeny: Tetrapoda : *Acanthostega* + (*Ichthyostega* + (*Tulerpeton* + (*Ossinodus* + (Whatcheeriidae + (*Crassigyrinus* ::: Tetrapoda*)))) + *.))

Links: Devonian times

Page Back | Unit Home | Page Top | Page Next

Text content Dnswitzer101104; page MAK111112

Tulerpeton

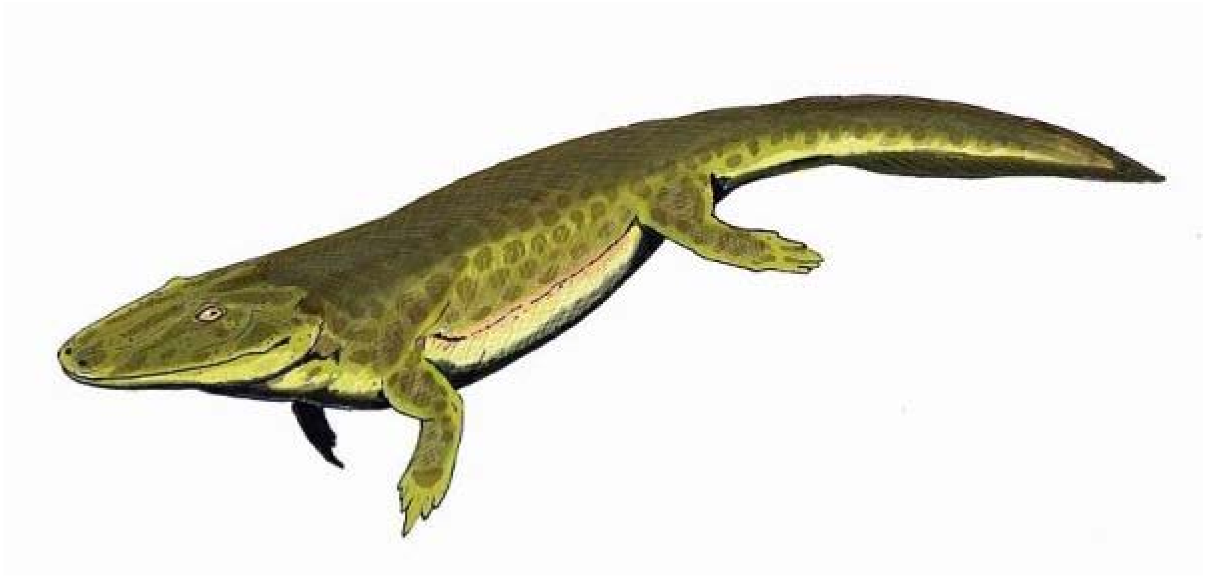
Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Hynerpeton
      `--+--Tulerpeton
         `--+--Whatcheeriidae
               `--+--Crassigyrinus
                  `--+--Colosteidae
                      |   `--Greererpeton
                      `--+--Spathicephalus
                          `--+--Baphetidae
                              |--Eucritta
                              `--Tetrapoda*
                                 |-
-TEMNOSPONDYLI
                                 `--+-
-LEPOSPONDYLI
                                     `-
-REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Tulerpeton* X



Tulerpeton curtum, life reconstruction, by Dmitry Bogdanov.
Wikipedia, GNU Free Documentation/Creative Commons Attribution

Editor's note: due to lack of time and the need to fill out missing pages, this page has been copied with very little modification from Wikipedia. Some generic material has been excluded MAK111112

Tulerpeton

Tulerpeton is a fossil of an extinct genus of Devonian labyrinthodont that was found in the Tula Region of Russia at a site named Andreyevka. This genus and the closely related *Acanthostega* and *Ichthyostega* represent the earliest tetrapods

Tulerpeton is considered one of the first true tetrapods. It is known from a fragmented skull, the left side of the pectoral girdle, and the entire right forelimb and right hindlimb along with a few belly scales. This species is differentiated from the less derived "aquatic tetrapods" (such as *Acanthostega* and *Ichthyostega*) by a strengthened limb structure. These limbs consist of 6 toes and fingers. Additionally, its limbs appear to have evolved for powerful paddling rather than walking.

The fossil fragments also indicate that its head was disconnected from the pectoral girdle. From the absence of the rough postbranchial lamina of the pectoral girdle, it has been determined that*Tulerpeton* had no gills and was therefore entirely dependent on breathing air.

Even though *Tulerpeton* breathed air, it lived mainly in shallow marine water. The Andreyevka fossil bed where it was discovered was at least 200 km from the nearest landmass during this era. The fossils of plants in the area tell us that the salinity of the waters where it lived fluctuated wildly, indicating that the waters were quite shallow. Because the bones of the neck and the pectoral girdle were disconnected, Tulerpeton could lift its head. Therefore, in shallow water, it had a considerable advantage over the other animals whose heads only moved side to side. The later land animals that descended from Tulerpeton’s relatives needed this head flexion on land, but the condition probably evolved because of the advantage that this gave it in shallow marine waters, not for land. In the book “Vertebrate Life”, authors Pough, Janis, and Heiser say that,” The development of a distinct neck, with the loss of the opercular bones and the later gain of a specialized articulation between the skull and the vertebral column (not yet present in the earliest tetrapods), may be related to lifting the snout out of the water to breath air or to snap at prey items.” The six fingered hands and toes were stronger than the fins from which they developed, therefore “tulerpeton” had an advantage in propelling itself through shallow and brackish water, but the limbs do not yet seem strong enough for extensive use on land.

Tulerpeton is one of the early transition tetrapods – a marine animal capable of living on land. The separation of the pectoral-shoulder girdle from the head allowed the head to move up and down, and the strengthening of the legs and arms allowed the early tetrapods to propel themselves on land.

Tulerpeton is important in the study of *dactyly*. The polydactyl (more than 5 toes) condition of *Tulerpeton* caused considerable comment when the fossil was first discovered. Before the discovery, the pentyldactyl, the 5-fingered condition that is ancestral to all living tetrapods, was thought to have developed before the first terrestrial tetrapods appeared. But the discoveries of *Acanthostega* and *Ichthyostega* confirm that the pentyldactyl ancestor came later in the development of tetrapods. Dnswitzer101104

Descriptions

Tulerpeton: *curtum* Lebedeu, 1984

Range: Fammenian (Latest Devonian) of Tula region, Eastern Russia

Phylogeny: Tetrapoda **:** *Acanthostega* + (*Ichthyostega* + (*Hynerpeton* + (*Ossinodus* + (Whatcheeriidae + (*Crassigyrinus* **:::** Tetrapoda*))) + *.)))

Comments: Although *Tulerpeton* has, like *Crassigyrinus*, been placed with, or at the base of, the reptiliomorphs, the consensus now is that it represntes instead the early tetrapod lineage. Generally it is placed between *Hynerpeton* (as a contemporary but more primitive form) and early to mid Carboniferous Whatcheeriids, *Crassigyrines*, and Colosteids. In terms of the old order Ichthyostegalia, *Tulerpeton* represents a good transition form between the other late Devonian tetrapods and the Carboniferous amphibians proper MAK111112

References: Lebedev & Coates 1995, Gordon & Long 2004

Links: Devonian Times, Recent Transitionals, Tree of Life - Stegocephalians: Tetrapods and other digit-bearing vertebrates - Wikipedia 110831)

Text content Dnswitzer101104 (and more recent updates on Wikipedia); page MAK111112

Whatcheeriidae

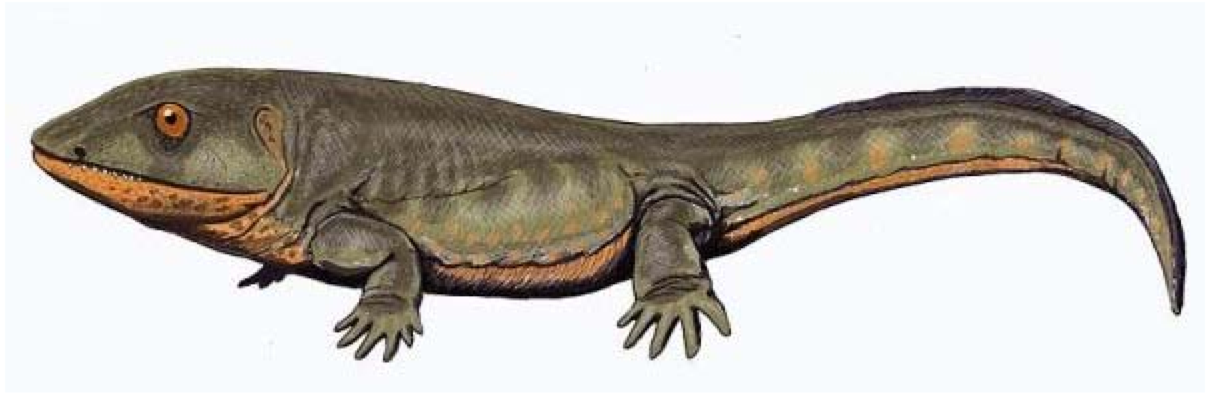
Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Hynerpeton
      `--+--Tulerpeton
         `--+--Ossinodus
            `--+--o Whatcheeriidae
               |    |--Pederpes
               |    `--Whatcheeria
               `--+--Crassigyrinus
                  `--+--Colosteidae
                      |  `--Greererpeton
                      `--+--Spathicephalus
                          `--+--Baphetidae
                              |--Eucritta
                              `--Tetrapoda*
                                 |-
-TEMNOSPONDYLI
                                 `--+-
-LEPOSPONDYLI
                                     `-
-REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Ossinodus* X
2. *Pederpes* X
3. *Whatcheeria* X
4. Whatcheeriidae X



Pederpes finneyae, life reconstruction, by Dmitry Bogdanov.
Wikipedia, GNU Free Documentation/Creative Commons Attribution

Romer's Gap

About twenty million years separate the Late Devonian with its assemblage of fish-like early tetrapod fossils and the amphibian fossils known from the late part of the early Carboniferous (the Viséan). The late Devonian forms were barely more than lobe-fin fish with legs, the middle Carboniferous was populated by a diverse assemblage of small and large amphibains, everything from crocodile to salamnder to snake and eel like forms. there were even animals that may have been the first reptiles. During this mysterious interval, from which for a long time little or no fossil remains were known, the evolution of land animals underwent a sort of Cambrian explosion of its own. The interval has been referred to as *Romer's gap*, after the great vertebrate paleontologist Alfred Sherwood Romer, who first recognised it.

Recently, the analysis of a primitive amphibian (early tetrapod) gave us a glimpse into this lost world.

Pederpes finneyae was originally discovered in 1971 in central Scotland and classified as a lobe-finned fish. Its fossils were found in the Ballagan Formation. The type specimen was a nearly complete, articulated skeleton. Only the tail and some bones of the skull and limbs were missing. It was not until 2002 that Jennifer Clack named and reclassified the fossil as a primitive tetrapod. (Wikipedia). it is the only nearly complete tetrapod known from the Tournaisian age . The only other Tournaisian tetrapods known are disarticulated and fragmentary material from the Horton Bluff Formation of Nova Scotia. These represent several taxa, not much can be known of them, although they can be very speculatively placed in other groups such as Ichthyostegids and Colosteids on the basis of general appearance of isolated leg bones.

Pederpes, the first "modern" tetrapod

Pederpes was a stocky animal about a meter in length, the same size as *Ichthyostega* and other early tetrapods. In contrast to the many toed (polydactyl) paddle-like feet of the late devonian tetrapods, it had (on the fore foot or hand at least) five toed foward-facing feet like that of later land animals. Although it is not known if the hind feet had five toes, the foot has characteristics that resemble the feet of later, more terrestrial Carboniferous forms.

The high, narrow skull was another innovation. it is possible that Pederpes breathed by inhaling with a muscular action like advanced tetrapods, rather than by pumping air into the lungs with a throat pouch the way many modern amphibians do. The shape of the skull and the fact that the feet face forward rather than outward indicate that Pederpes was well adapted to land life. It is currently the earliest known fully terrestrial animal, although the structure of the ear shows that its hearing was still much more functional underwater than on land, and may have spent much of its time in the water and could have hunted there. (Wikipedia)

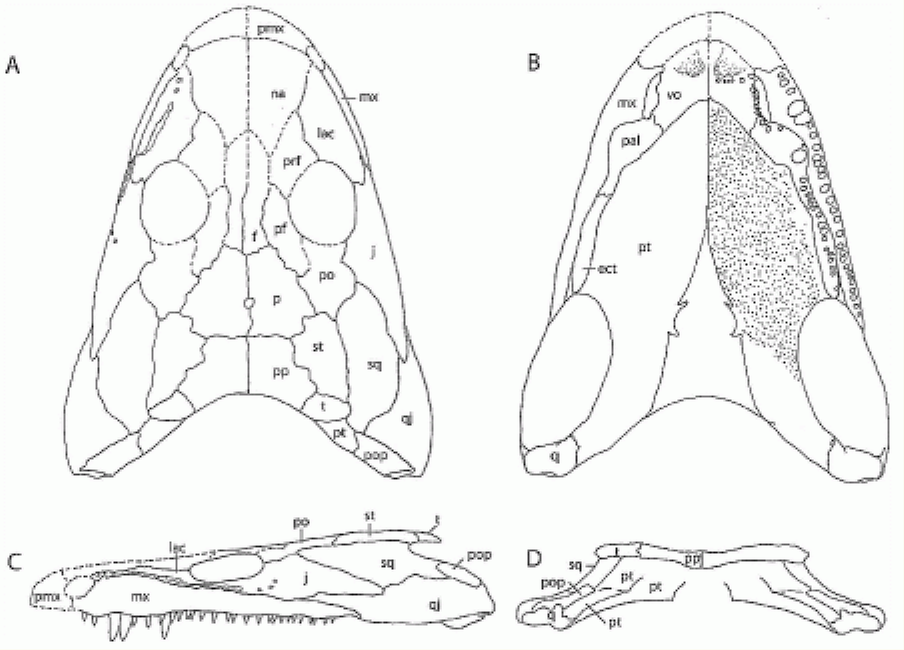
The Whatcheeriidae

Pederpes closely respembles a slightly later (post-Romer's Gap) American form called *Whatcheeria* (during this time

Europe and Northe America were part of a single land mass), and has been placed with it in the family Whatcheeriidae. *Occidens portlocki*, a partial mandible known from the Visean of Northern Ireland may also be whatcheeriid and there are even two tentative whatcheeriid identifications are from below the gap, in the late Devonian of Pennsylvania and Russia (Clack and Finney, 2005, via Warren 2007).

Recently the Australian taxon *Ossinodus pueri* was assigned to this group, as analysis by Warren and Turner (2004) placed it as the sister taxon to *Whatcheeria* and *Pederpes*. A more recent study has given more ambiguous results (Warren 2007), and it is possible that *Ossinodus* represents a more primitive evolutionary grade. Indeed, the whole idea of a monophyletic group of early tetrapods may simply be an artefact resulting from a lack of sufficient material, shared primitive features, and not taking into account convergence, homoplasy, and collective character reversal (for example, groups like the Coelophysoidea and Pistosauridae were previously considered clades but are now known to be paraphyletic grades). Until more material turns up it will be impossible to say for sure. For now we can refer to Whatcheeriids and Whatcheeriid-like forms such as *Ossinodus*, and the quite distinct but equally archaic and primitive *Crassigyrinus* as an assemblage of transitional forms intermediate bridging the temporal, morphological and phylogenetic gap between the aquatic late Devonian ichthyostegalian grade of tetrapods and the more famnilar and diverse Paleozoic leposondyl, proto-temnospondyl and reptiliomorph amphibians and proto-amniotes of the middle to late Visean onwards. MAK111112

Descriptions



Ossinodus: *O. pueri*

Range: mid Viséan of Queensland (Ducabrook Formation)

Phylogeny: Tetrapoda : *Acanthostega* + (*Ichthyostega* + (*Hynerpeton* + (*Tulerpeton* + (Whatcheeriidae + (*Crassigyrinus* ::: Tetrapoda*)) + *)))).

Comments: Although originally included under the Whatcheeriidae, new reconstruction of the skull and body shows an animal quite different in form. Phylogenetic analyses give different results depending on whether or not Ossinodus is reconstructed with or without an intertemporal bone. If the former, *Ossinodus* remains in the Whatcheeriidae, if the latter, it is more basal, indicating that the Whatcheeriidae may be a grade rather than a clade. (Warren 2007)

Image: Skull reconstruction, from Warren 2007. Note how flat the skull is, a primitive feature. Obviously, that the actual specimen is not nearly this complete

Links: Wikipedia (very stubby page when last checked) MAK111112

Whatcheeriidae: *Pederpes*, *Whatcheeria*

Range: Early Carboniferous (Tournaisian to Viséan)

Phylogeny: Tetrapoda ::: *Ossinodus* + ((*Crassigyrinus* ::: Tetrapoda*) + * : *Pederpes* + *Whatcheeria*)

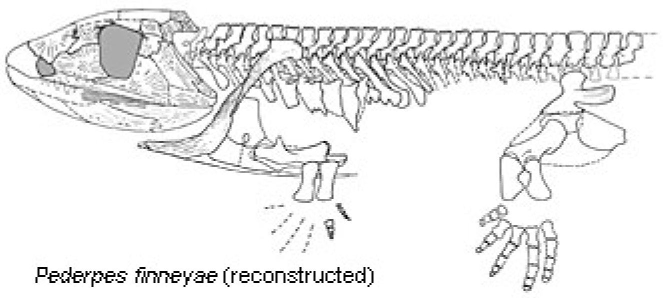
Characters: narrow, steep-sided skull with orbit deeper than its width; massive tooth on maxilla about position 5 or

6; light dermal skull ornament (Clack 2002b)

Comments: As *Ossinodus* is more primitive than the other two genera placed here, the family Whatcheeriidae is quite possibly a paraphyletic grade as originally defined (Warren 2007). For this reason *Ossinodus* is given a separate entry, and cladistic as opposed to linnaean) Whatcheeriidae is defined as including *Whatcheeria* and *Pederpes*, and any other related forms. These animals were about a metre in length, with a large, triangular head.

Links: Wikipedia (very stubby page when last checked) MAK111112

Pederpes: *P. finneyae*



Range: Late Tournaisian (Ivorian) of Scotland (Ballagan Formation, Inverclyde Group)

Phylogeny: Whatcheeriidae **:** *Whatcheeria* + * .

Characters: primitive stapes most closely resembling that of *Acanthostega* in a narrow skull with a deep wide temporal notch (Clack 2002b)

Comments: The only diagnosible specimen from Romer's gap *Pederpes* is known from a nearly complete articulated skeleton. It is the earliest known animal with five functional toes, and the earliest vertebrate to show the beginnings of fully terrestrial movement. Distinguished from the closely related *Whatcheeria* by a spike-like *latissimus dorsi* (an arm muscle) attachment on the humerus and several minor skull features. Despite the probable presence of a sixth digit on the forelimbs it was at least functionally pentadactyl. (Wikipedia)

References: Clack 2002b

Links: Wikipedia, Palaeocritti - Pederpes finneyae, Reptile Evolution - Ihthyostega MAK111112

Whatcheeria: *W. deltae* Lombard and Bolt, 1995

Range: Viséan of Iowa

Phylogeny: Whatcheeriidae **:** *Pederpes* + * .

Characters: Skull deep and snout pointed. Shares with earlier stem tetrapods a series of lateral lines across the skull, rows of teeth on the palate, and small Meckelian foramina across the surface of the lower jaw. It has a cleithrum, a bone in the pectoral girdle that extends from the scapula. The cleithrum once attached to the skull in lobe-finned fish, the ancestors of tetrapods, but detached to allow the neck to move freely. . the opening at the top of the skull behind the eyes (the parietal foramen) is relatively large. The bones on the skull surface are unusually smooth, unlike the pitted skulls of many other early tetrapods. In front of the eye socket, the prefrontal bone forms a prominent ridge. The prefrontal also projects downward to cover a possible sinus. (Lombard & Bolt1 995, via Wikipedia)

Comments: Closely related to *Pederpes*, although living some fifteen million years or so earlier. Like that genus, possesses a mixture of both primitive and derived traits. MAK111112

Page Back | **Unit Home** | **Page Top** | **Page Next**

Page by MAK111112

Tetrapoda: Carboniferous Forms

Crassigyrinus

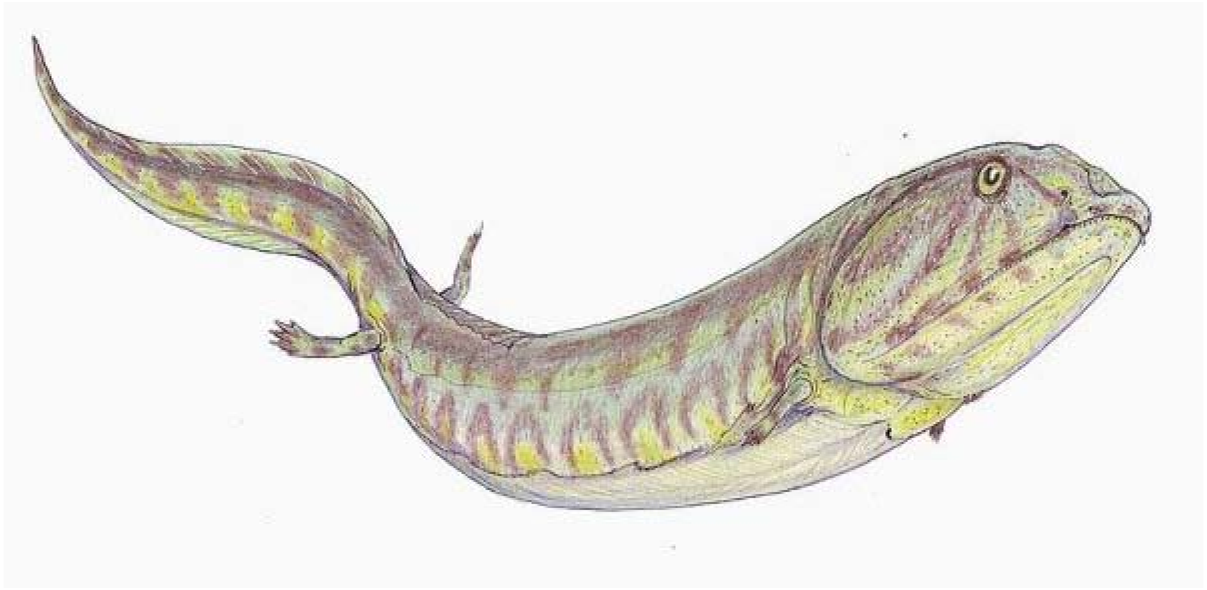
Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Hynerpeton
      `--+--Tulerpeton
         `--+--Whatcheeriidae
            `--+--Crassigyrinus
               `--+--Colosteidae
                   |   `--Greererpeton
                   `--+--Spathicephalus
                       `--+--Baphetidae
                           |--Eucritta
                           `--Tetrapoda*
                              |--TEMNOSPONDYLI
                              `--+-
-LEPOSPONDYLI
                                  `-
-REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Crassigyrinus* X



Crassigyrinus scoticus, life reconstruction, by Dmitry Bogdanov.

Crassigyrinus scoticus

Jennifer A. Clack

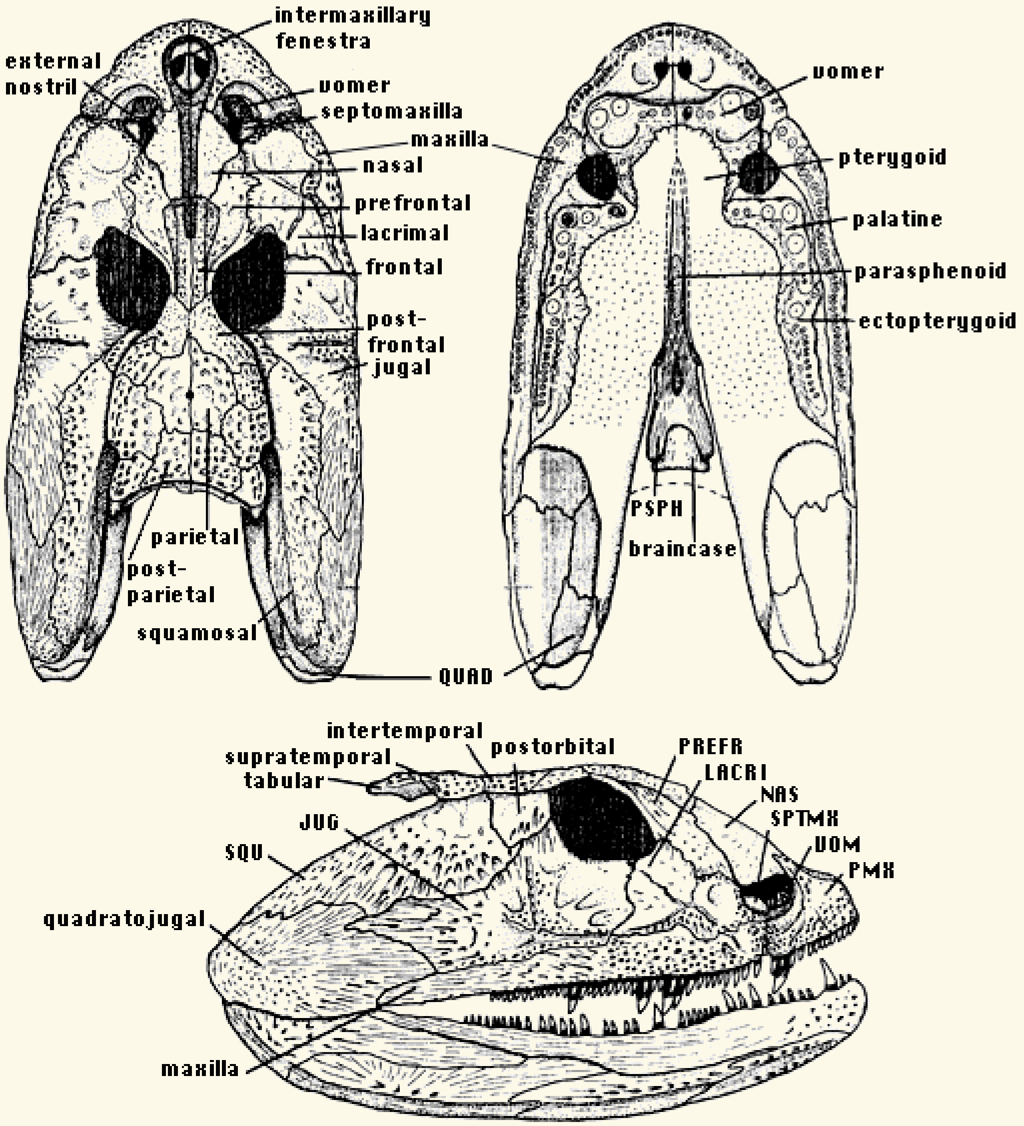
Crassigyrinus scoticus is an aquatic stem-tetrapod from the Late Mississippian and Early Pennsylvanian (Visean and basal Namurian) of Scotland, notable for combining bizarre specializations such as tiny forelimbs, with a number of primitive features such as the palatal construction. These have given rise to arguments about its taxonomic status. It is known from three skulls, one of which is in articulation with a fairly complete skeleton, and a couple of incomplete lower jaws. Not only is it taxonomically enigmatic, it must also have been a remarkable and formibable animal when alive.

Phylogenetic Position of Crassigyrinus

The taxonomic position of Crassigyrinus has been the source of some debate. Panchen (1985) regarded it as related to "anthracosaurs", that is to say embolomeres plus *Gephyrostegus* and *Eoherpeton*. The basis for this rested upon a few characters such as "dark dentine" in the teeth and the form of the dermal bone ornament. Since then, other analyses have progressively severed the link with anthracosaurs. However, the most recent descriptive work (Clack 1998b) found that it clustered with *Whatcheeria* and the embolomeres. Since then, Ruta et al. (2003) in an analysis including representatives of all Palaeozoic tetrapod groups, concluded that it was the next most basal taxon after the Devonian forms, contrasting with Clack (2002b), who placed it as the next stem taxon above the Early Carboniferous family Whatcheeriidae.

The author disagrees with the move to restrict the vernacular term "tetrapod" to a crown clade (Gauthier et al., 1989). In this page, the term "tetrapod" and "stem-tetrapod" refer only to vertebrates with limbs and digits. (Refer to the lichen page on the Definition of the taxon Tetrapoda to get more information on this topic.)

The holotype skull, from Gilmerton near Edinburgh, shows a more or less undistorted and complete side view (Panchen 1973). The short pre-orbital region, quadrangular orbit and extended suspensorial region are clear from this specimen, as is the irregular, patchy nature of the dermal ornament. The snout is somewhat compressed, obscuring its structure. Further preparation of this and a second skull specimen showed that the naris was peculiar. Though relatively large, it included a cushion-shaped septomaxilla. A skull associated with a postcranial skeleton, from the Dora Bone Bed of Cowdenbeath, Fife, (Andrews et al. 1977, Panchen 1985) shows the skull table to be similar in structure to those of embolomeres, with unsutured junctions to the cheeks. In contrast to embolomeres, however, it had a primitive bone-pattern with supra-temporal/ postparietal contact. A notch between the skull table and the cheek has been interpreted as housing a spiracle, but the stapes is unknown.

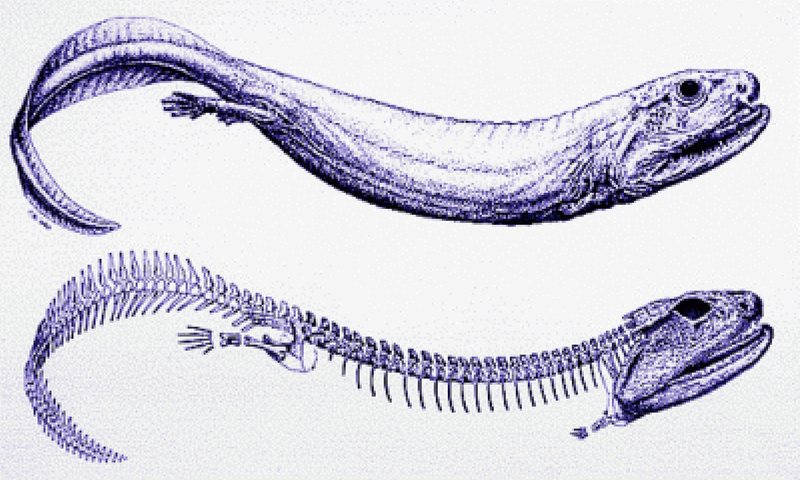


Skull reconstructions of *Crassigyrinus scoticus* in dorsal (top right), ventral (top left) and lateral (below) views. Drawing copyright © 1997 J. A. Clack.

A third skull (BMNH 30532), also from Gilmerton, shows the palate very clearly, and indicates that *Crassigyrinus* had a combination of a very osteolepiform-like configuration of the vomers, and extremely specialized, massive palatal dentition. This specimen also shows more clearly than the other two, a bizarre fenestra between the premaxillae, which communicated with an anterior palatal fenestra (Clack 1998). The function of this structure is unknown. Large holes in the dorsal surface of the dentary housed the massive palatal teeth when the jaws were closed, a feature unique to *Crassigyrinus*. In other respects the lower jaws prove to be rather primitive in construction (Ahlberg and Clack 1998)

Postcranial skeleton

If the skull was bizarre, the postcranial skeleton to which it attached (*left*) was correspondingly weird. The humerus was extremely small, no longer than the longest dimension of the orbit. It retains some of the extra foramina seen in *Ichthyostega* and *Acanthostega*. The ulna and radius were similarly reduced making the forelimbs “ridiculously small” (Panchen and Smithson 1990). They articulated with the shoulder girdle at a point very close to the jaw



joint. It is not known how many digits were present. Long curved ribs surrounded the body, attached to centra which were poorly ossified and formed ventral U-shaped supports for the persistent notochord. The hind limbs were relatively small compared with a more conventional tetrapod, but were not nearly so reduced as the forelimbs.

Paleoecology and Lifestyle

Crassigyrinus was a large, long-bodied, permanently aquatic predator, with fearsome-looking teeth in a heavily reinforced skull. The snout in particular was consolidated and buttressed, and with a kinetic inertial jaw mechanism, would have produced a bone-smashing snap-trap. Its large eyes were probably adapted for use in murky coal-swampy water. Panchen (1985) envisaged it as behaviourally somewhat analgous to a Moray eel.

Descriptions

Crassigyrinus**:** *C. scoticus*

Range: Carboniferous (Viséan) of Scotland

Phylogeny: Tetrapoda ::: Whatcheeriidae + (Colosteidae ::: Tetrapoda*) + *.)

Characters: Limited ossification of vertebral centra, no occipital condyle. No anocleithrum. Cheek (very!) moveable on skull roof, like Reptiliomorpha, intercentra & pleurocentra roughly equal, orbits close to midline, tabular does not contact parietal.

Note: The current (2002) belief is that *Crassigyrinus* is a rather weird anthracosaur. Eventually, we will get around to moving it there. Meanwhile, the current belief is also that *Crassigyrinus* is one of the major causes of cladogram instability in this area. Accordingly, until things settle down a bit, it will stay in the old neighborhood. ATW. *Update*: current cladistic analyses (Clack 1998b, Clack 2002b, Ruta et al. 2003, Ruta et al 2003b, Clack & Finney 2005, Warren 2007, Ruta & Bolt 2008) uniformly place Crassigyrinus just before or just above the Whatcheeriidae, and before Colosteidae and other basal taxa. Therefore the anthracosaurian traits are more likely to be either convergences or plesiomorphic. *Crassigyrinus* is best interpreted as a very porimitive, secondarily totally aquatic,amphibian (tetrapod). MAK111112

Comment: A bizaare, totally aquatic form. Along with the whatcheeriids, the most primitive pentadactyl (five-fingered) animal.

Links: link. 990926.

Images: *Crassigyrinus scoticus*,life reconstruction by Dmitry Bogdanov Wikipedia, GNU Free Documentation/Creative Commons Attribution Skull reconstruction copyright © 1997 J. A. Clack, from Clack, 2006 (Tree of Life Page); skeletal and life reconstructions from Panchen & Smithson 1990 Copyright 1990 Royal Society of Edinburgh

---

Page Back | Unit Home | Page Top | Page Next

checked ATW040813, new page MAK111112

Tetrapoda: Carboniferous Forms

Greerpeton

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinidae
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Spathicephalus
            `--+--Baphetidae
               `--Tetrapoda*
                  |--TEMNOSPONDYLI
                  `--+--LEPOSPONDYLI
                     `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. Colosteidae X
2. *Greererpeton* X

Colosteidae

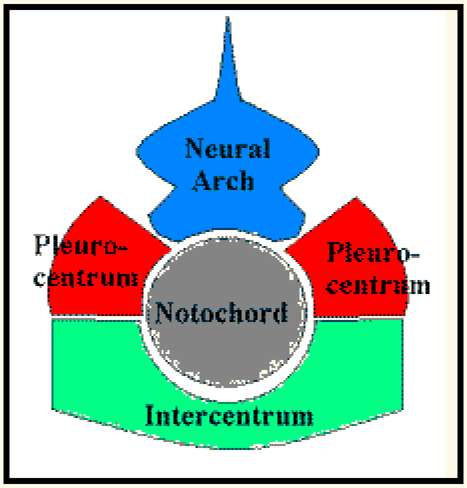
Superficially, the colosteids appear quite different from their eryopid cousins. However, the differences are largely matters of shape or degree, rather than fundamental structure. The basic form of the head is very similar, surprisingly unchanged from the common panderichthyid ancestor. Possibly because of its reduced width, the jaw apparatus is more strongly braced in the center. That is, the outer elements serve more as the arched beams of a roof, supported by continuous long bones, the frontals and prefrontals, along the mid-line. By contrast, the skull of *Eryops* is too wide to support in this manner and the dermal bones of the jaw area are more evenly sized and generally oblong.

Unlike the eryopoids, the colosteids have a shoulder girdle which may be somewhat integrated with the skull, although the extent of the integration is difficult to reconstruct. In a fish, the cleithrum would integrate the girdle closely with the opercular bones forming the cover of the gill apparatus. colosteids do not possess an operculum, but retain the cleithrum. The cleithrum in this tetrapod group is a long thin bone with no obvious static connection to any particular structure. It may well have served a function analogous to the scapula of later vertebrates, and stabilized the shoulder girdle on the trunk, generally, rather than on the skull. Of course, the colosteids also possessed a scapulocoracoid with a similar, though smaller, dorsal extension. However, the coracoid element predominates. That is, the scapulocoracoid was largely a ventrolateral plate. It is believed that the colosteids may have also possessed a cartilaginous suprascapular, but its size, properties and function are unknown.

These elements were overlaid with a layer of three dermal bones, in the form of two large, generally diamond-shaped lateral clavicles and a ventral interclavicle. Together, they formed a broad thoracic shield. In addition, the central interclavicle had a long tongue-like process which extended forward to cover the throat and perhaps articulated, at least loosely, with elements of the lower jaw. Finally, the dermal bone layer was, in turn, overlaid by skin bearing heavy scales.

There is something to be said for the proposition that tetrapod evolution is a matter of adding neurons and subtracting bones. But, aphorisms aside, why all this complexity? Defense does not seem a viable answer. Anything big enough to take on a scale-covered meter-long carnivorous salamander with fangs would not be much deterred by these relatively thin bones and, in any case, would be unlikely to try a frontal attack.

Perhaps a more likely answer lies in the way the trunk is put together, and this requires a digression into vertebral structure. Primitively, the vertebrae consisted of discrete bony elements having no fixed relation to each other. The neural arches developed around the dorsal nerve cord, above the notochord. Pleurocentra rode generally on top or sides of the notochord, on either side and/or below the neural arches. Intercentra supported the notochord from below. (Although terms like "rode" and "supported" cannot be taken literally in this context). In some lineages, one or the other of the centra came to dominate the centrum, with the virtual elimination of the other central bone, as well as the notochord. Thus, for example, the vertebral body of amniotes is composed almost entirely of the pleurocentral element.



In the early temnospondyls and their sister group, the colosteids, the various elements were more or less evenly matched. The notochord remained an important structural element. The intercentra formed a continuous crescent around the ventral half of the notochord, and the paired pleurocentra flanked a large neural arch bearing a substantial dorsal spine. All of the bony elements articulated with each other, but they did not form a solid block as in later terrestrial vertebrates. This arrangement had the advantage of flexibility, but the disadvantage of central weakness. For an eel-like organism, this would make little difference. However, the colosteids, to judge by their small but reasonably serviceable limbs, used a mixture of central, eel-like, undulation and *paraxial* (off-center) limb-powered motion. To accomplish this complex mixture of motions, the colosteids needed some method of transferring force from the limbs to the axis of the body without, as it were, getting all bent out of shape and without losing central flexibility.

Their solution to this mechanical quandary seems to have been to have several levels of substantial tendonous attachments spread out across the dorsal surface. In addition to the notochord, Colosteids had strong neural spines which presumably bore tendons linking the arches. More tellingly, the colosteids also retained strong, generally horizontal ribs which attached both to the neural arches and to the intercentrum (that is, they were bicipital and could not bend dorsoventrally). The ribs bore uncinate processes -- flanges about halfway out -- and had a twisted, spatulate (broad & flat) distal end. Again, the most likely interpretation is that longitudinal tendons linked the ribs at both of these levels. Thus, instead of relying on a single, strong vertebral column, the Colosteids used as many as six dorsal cables to achieve strength without loss of flexion.

If this interpretation is correct, the complex pectoral girdle can be explained as a method of transferring paraxial forces flexibly across a number of layers of dorsal support in a manner that did not tax the strength of any one. (99?? ??)

Descriptions

Colosteidae: *Colosteus*

Range: Early Carboniferous to Late Carboniferous.

Phylogeny: Tetrapoda :::: (*Spathicephalus* + (Baphetidae + Tetrapoda*)) + * : *Greererpeton*.

Introduction: The Colosteids were a small group of medium-sized to large secondarily aquatic fish-eaters, with elongated, eel-like bodies with up to 40 presacral (trunk and neck) vertebrae and well-developed lateral line canals in the skull. The legs were small and many species probably spent their whole lives in water. The skull and lower jaw were low and flat.

Colosteids are usually considered very primitive members of the temnospondyl order. Their ancestry is by no means certain. Computer-assisted phylogenetic analyses places them close to the Baphetidae. (see: Michel Laurin's on-line essay Phylogeny of Terrestrial Vertebrates.). But the pattern of the braincase and skull roof are very primitive and resemble that of the *Acanthostega* (Carroll (1988: 170)), so it is possible they may have even evolved separately to the baphetid-crassigyrinid line. In any case, it is clear that the Colosteids represent one of a number of short-lived early Carboniferous tetrapod radiations. Certain specialized features make it unlikely that the Colosteids were directly ancestral to the temnospondyls. (MAK 010305)

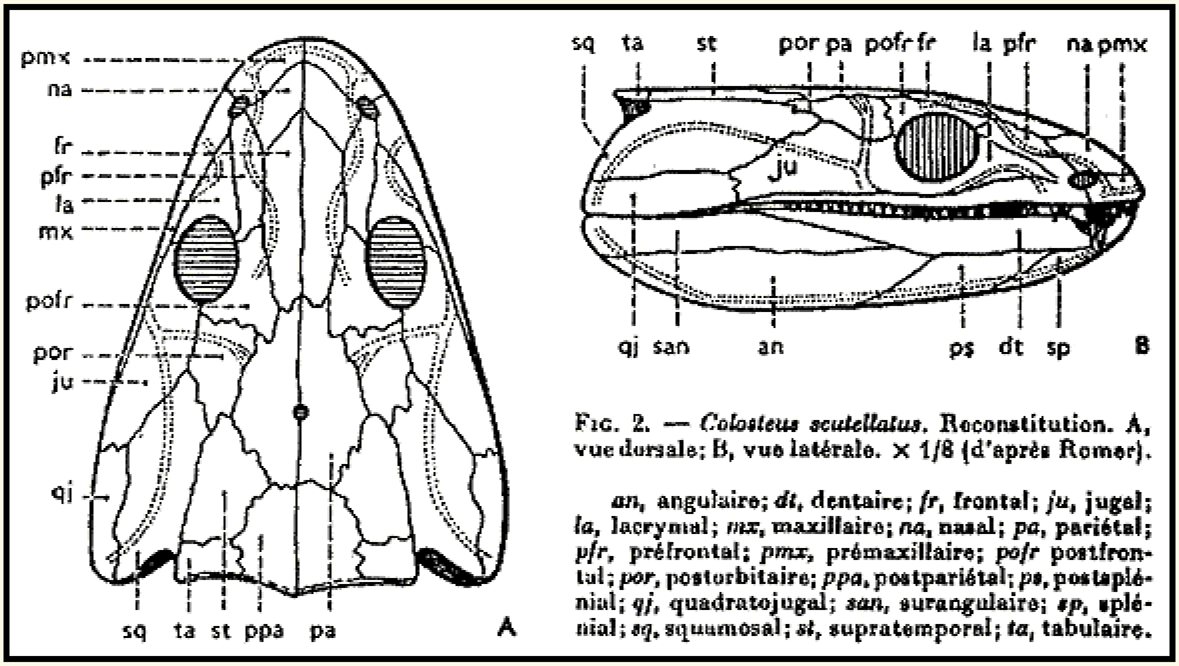


Fig. 2. — *Colosteus scutellatus*. Reconstitution. A, vue dorsale; B, vue latérale. × 1/8 (d'après Romer).

an, angulaire; *dt*, dentaire; *fr*, frontal; *ju*, jugal; *la*, lacrymal; *mx*, maxillaire; *na*, nasal; *pa*, pariétal; *pfr*, préfrontal; *pmx*, prémaxillaire; *pofr* postfrontal; *por*, postorbitaire; *ppa*, postpariétal; *ps*, postsplénial; *qj*, quadratojugal; *san*, surangulaire; *sp*, splénial; *sq*, squamosal; *st*, supratemporal; *ta*, tabulaire.

Characters: Secondarily aquatic salamander-like forms with elongate, flattened bodies and small limbs, up to 1.5m, with tail 30-50% of length. Labyrinthodont dentition; one pair of premaxillary tusks which are large and fit into notch on dentary; dentary teeth markedly larger than maxillary teeth; elongate prefrontal extending to nares which (a) contacts the maxilla and premaxilla and (b) excludes lacrimal and nasal from nares; intertemporal minute or absent; broad contact between postorbital and parietal; orbits dorsal in adults; large stapes supports braincase on pterygoids (no impedance matching ear); large interpterygoid vacuities; braincase very primitive (like *Ichthyostega*); no embayment of squamosal (*i.e.*, no otic notch); otic capsule incompletely ossified; gills(?); well-developed, about 40 presacral vertebrae; rachitomous vertebrae with ossified centra and approximately equal mass of pleurocentra and intercentra; ribs conspicuously bicipital, bearing uncinate processes, flattened and twisted distally; in *G*, probable lateral flattening and fin like surface over proximal 1/3 of tail; supraglenoid foramen absent; pectoral girdle forms broad thoracic shield; median process of interclavicle extends far anteriorly; cleithrum present, long but thin; humerus short; 4 digits on manus; one sacral rib; sacral rib unspecialized and not fused or firmly attached to ilium; no fin rays; lateral line grooves present; extensive scales dorsal & ventral; ventral scales rhomboidal in V-shaped pattern (dorsal scales vary).

Links: Batrachomorpha [Amphibia]; Dinosaurios, Tutorial interactivo (Spanish); Geol 437 amphibia, Fall, 1995; Phylogeny of stegocephalians; p7; Filogenias (Portuguese -- very strange phylogeny here, but this is an excellent and usually well-informed site);

References: Carroll (1988); Godfrey (1989). ATW030522.

Greererpeton:

Range: Early Carboniferous of North America

Phylogeny: Colosteidae **:** *.

Greererpeton buckemorani Romer
Adult Length: upto 1.5 metres long
Duration: Early Carboniferous (late Visean)
Region: equatorial Euramerica
Fossil remains: from Bickett Shale, Bluefield Formation, West Virginia
Comments: Greererpeton was one of a number of eel-like tetrapods that frequented early Carboniferous rivers and swamps. A member of the colosteid group of very primitive tetrapods, it had a low flat head, about 18 cm in length, a short neck, and an elongated body and long tail. The back contained about 40 vertebrae, about twice the usual labyrinthodont number. The legs were too small to support the weight of the creature on land. There is no otic notch for the ear-drum, but instead the skull has open grooves which in life were marked by lateral line sensory canals which could detect water-borne vibrations. (MAK 010305)

Links: Dinosaurios, Tutorial interactivo (Spanish); WVGES Mini-Museum, Photographs of Selected Fossils. ATW021030.

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW040813

Tetrapoda: Carboniferous Forms

Spathicephalus

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Spathicephalus
            `--+--Baphetidae
               |--Eucritta
               `--Tetrapoda*
                  |--TEMNOSPONDYLI
                  `--+--LEPOSPONDYLI
                     `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Spathicephalus* X

Spathicephalus: another aquatic frisbee

Like some of the much earlier Silurian galeaspids and the much later Triassic plagiosaurs *Spathicephalus* somehow made a living with an almost two-dimensional head. Exactly how it managed to do so is -- as with galeaspids and plagiosaurs -- a matter of considerable uncertainty. The enormous jaw and flat head making closing the mouth against the resistance of water a major concern. But the size of the antorbital fossa and the adductor chamber suggest that the jaw adductors were actually weaker than comparable organisms of the same, more or less baphetid, design.

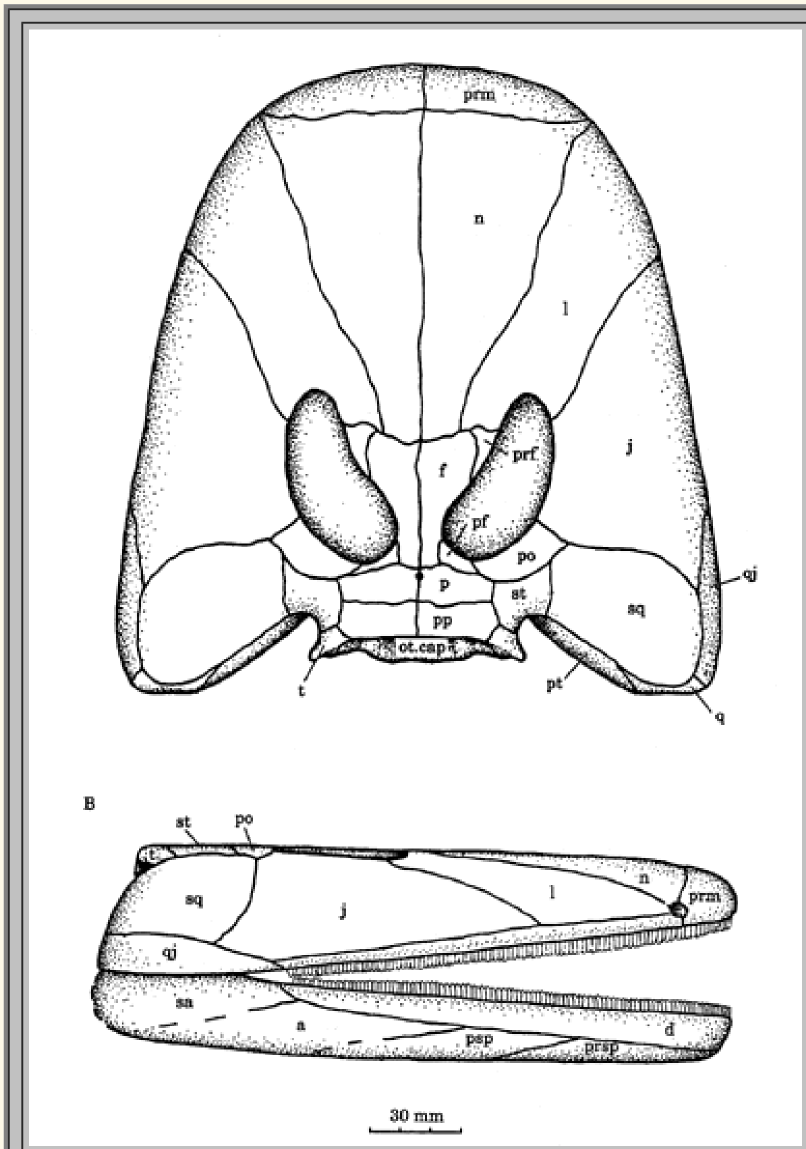
Of course the peculiar teeth of *Spathicephalus* tell us that it did not feed in the same way. Unlike the baphetids, *Spathicephalus* had numerous small, thin teeth, no fang pairs, and very few denticle-bearing areas on the palate. The teeth seem to have present all at the same time, as opposed to the usual tetrapod arrangement involving unsynchronized replacement of a smaller number of large teeth. The theory seems to be that *Spathicephalus* strained water or substrate through these teeth.

Descriptions

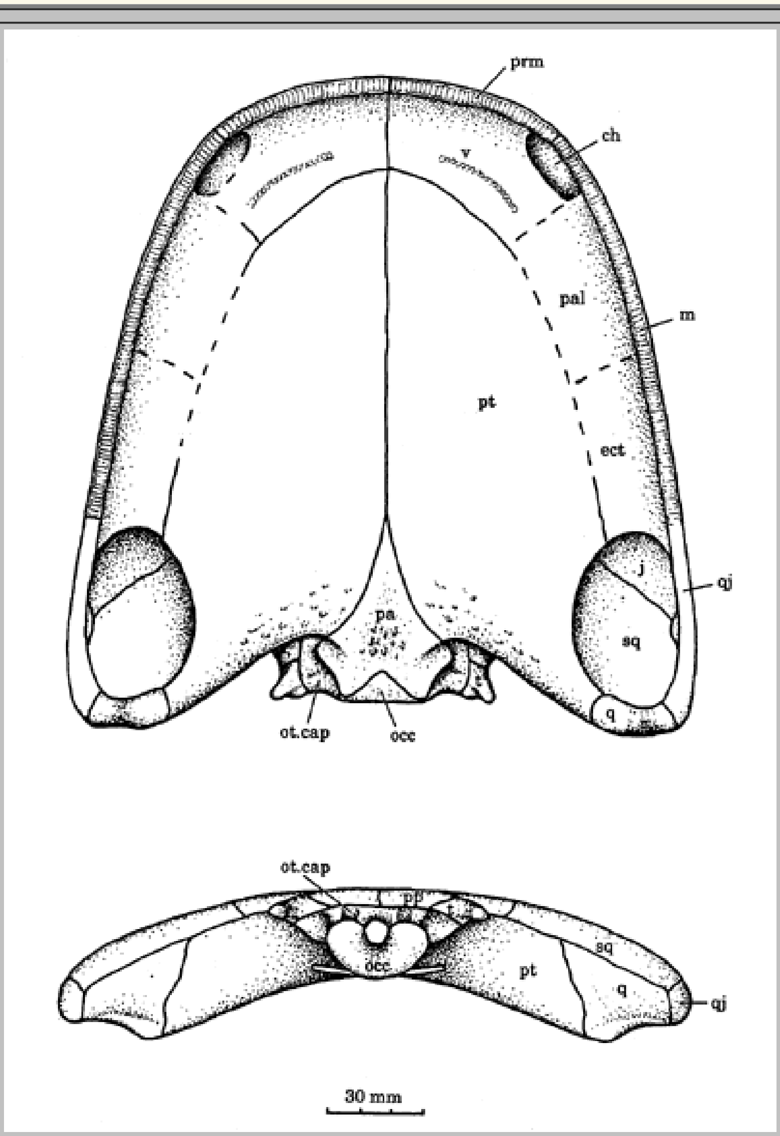
Spathicephalus: *S. mirus* Watson 1929; *S. pereger* Baird 1962.

Range: Early Carboniferous (Serpukhovian or Namurian A) of North America (Nova Scotia) and Late Carboniferous (early Bashkirian or Namurian B/C) of Europe (Britain).

Phylogeny: Tetrapoda **::::::** (Baphetidae + Tetrapoda*) + *.



Spathicephalus: skull in dorsal and lateral views. From Beaumont & Smithson (1998).



Spathicephalus: skull in palatal and occipital views. From Beaumont & Smithson (1998).

Characters: skull length to 22 cm [BS98]; skull very flat, broad & blunt [C02] [BS98]; skull width almost equal to length [BS98]; snout bones laterally expanded [BS98]; internasals absent [BS98]; antorbital large & vacuity smoothly continuous with orbit (no "key-hole") [BS98]; orbits closely spaced & strongly excavated [C02] [BS98]; orbits set 75% skull length back [BS98]; orbits face dorsally [BS98]; frontals enter orbit margin with thickened interorbital bar [BS98]; skull table very short [BS98]; intertemporal absent [BS98]; supratemporal forms anterior border of otic notch [BS98]; small pineal opening [BS98]; tabular horns and tabular posterior boss present [BS98]; quadratojugal strongly sutured to quadrate [BS98]; single occipital element [BS98]; occipital bone(s) makes no contact with skull table [BS98]; posttemporal fenestra absent **[2]** [BS98]; supraoccipital absent [BS98]; ***braincase:*** otic capsules broad & well ossified [BS98]; otic capsules strongly attached to skull roof [BS98]; stapes robust with large plate-like foot on fenestra ovalis and large distal region resting against quadrate ramus [BS98]; parasphenoid broad, forming floor of fenestra ovalis [BS98]; widely separated *basipterygoid processes* [BS98]; parasphenoid sutured to basipterygoid processes [BS98]; cultriform process short & narrow [BS98]; ***palate*****:** premaxilla without midline buttress [BS98]; pterygoids sutured along midline and probably fused with basipterygoid processes [BS98]; pterygoids, vomers & parasphenoid ornamented with pits & ridges (as pterygoid quadrate ramus of baphetids) [BS98]; pterygoid quadrate ramus forms medial wall of adductor fossa and meets squamosal dorsally [BS98]; ***lower jaw*****:** very shallow (22 mm in known specimen) [BS98]; dentaries & presplenials strongly sutured and immobile [BS98]; parasymphysial plate present (apparently with row of small teeth) [BS98]; parasymphysial teeth point medially, toward opposite ramus [BS98]; coronoids without denticles, but with fine ornamentation [BS98]; ***dentition*****:** all teeth small, chisel-shaped and numerous [C02] [BS98]; vomer with row of smaller teeth [BS98]; teeth pectinate (filter feeder?) [C02]; teeth all present at same time [C02]; dentary tooth count probably 110-120 [BS98]; palatal bones & coronoids without denticles [BS98]; ***postcranial*****:** interclavicle rhomboidal [B77].

Note: [1] *Spathicephalus* is shown as outside the Baphetidae because that's the way it came out when scored and run using a slightly modified version of the database of Clack (2001). No one has much confidence in any of the cladistic results in this area of phylospace at the moment. However, *Spathicephalus* scores so consistently primitive in many different runs, that this placement may be correct. This makes the Loxommatoidea (Baphetidae + *Spathicephalus*) paraphyletic. This is perhaps unlikely, but not really any stranger than most other possibilities. **[2]** This may be a matter of definition. The geometry of the occiput is odd, because the whole structure is so vertically compressed, laterally extended, and strongly fused. In addition, the extent of vertical compression has been exaggerated by crushing during preservation. It may be impossible to say exactly what the exact state of the occiput might have been at this point.

Links: Amphibian Skull

References: Beaumont (1977) [B77]; Beaumont & Smithson (1998) [BS98]; Clack (2001); Clack (2002) [C02]. ATW020820.

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW040813

Tetrapoda: Baphetidae

Loxomma

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Baphetidae
            |  |--Loxomma
            |  `--+--Baphetes
            |     `--Megalocephalus
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. Baphetidae X
2. *Loxomma* X

Loxomma allmanni, Visean of Scotland. Like all baphetids, this animal is known almost entirely only from fossil skulls, hence the reconstruction of the rest of the body as a typical large temnospondyl crocodile-like form is purely speculative, although not unreasonable.
Life reconstruction, by Dmitry Bogdanov, Wikipedia, GNU Free Documentation/Creative Commons Attribution

---

Descriptions

Unnamed baphetid in (more or less) dorsal view from Prof. Jennifer Clack.

Baphetidae: (= Loxommatidae). As normally used, probably a plesion of stem tetrapods, rather than a clade. Here, we stick to the undoubted clade comprised of *Baphetes*, *Loxomma*, and *Megalocephalus*, consistent with [B77].

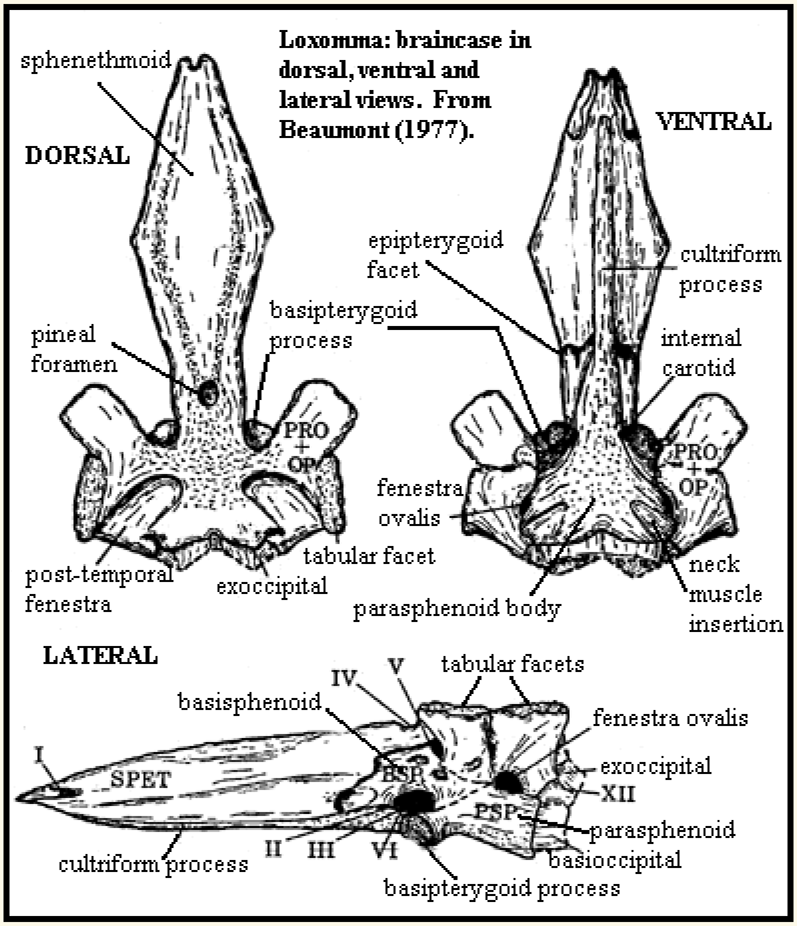
Range: Early Carboniferous (Viséan) to Late Carboniferous (Westphalian D or late Moscovian) of Europe and North America.

Phylogeny: Tetrapoda ::::: Tetrapoda* + *Eucritta* + *: *Loxomma* + (*Baphetes* + *Megalocephalus*).

Introduction: The baphetids, or loxommatids as they were formerly called [ML98], were large aquatic predators of the Carboniferous period. Not only are they included among the very early tetrapods, but they were also among the first of the Carboniferous fossil tetrapods to be found and were originally described in 1850 by William Dawson. They are known mainly from skulls, very little skeletal material. But even from this quite a lot can be deduced. The presence of lateral lines and the long rows of needle-like teeth show that they were fish-eaters. The curious keyhole-shaped orbit indicates the presence either of a gland or, it has been suggested, some sort of electrosensory organ. It may even represent an early form of skull fenestration for jaw muscles. It is not clear whether the four genera assigned to this group are really closely related.

Baphetids have been previously considered primitive temnospondyls and more recently batrachosaurs (reptile-like amphibia). It is likely however that they represent one more of a number of early Carboniferous tetrapod radiations.

Computer-assisted phylogenetic analyses of a data matrix using characteristics of most of the major groups of terrestrial vertebrates place the Baphetids close to the ancestry of subsequent tetrapod groups. For reference to this, and a number of alternative and previously considered trees, see: Michel Laurin's on-line essay Phylogeny of Terrestrial Vertebrates. It seems from the various alternative trees that the baphetids were cousins of the crassigyrinids, although whether the crassigyrinids evolved from the baphetids (as the earlier cladistic trees indicate, see also Panchen) or the baphetids from the crassigyrinids is not yet certain. (adapted from MAK 930719)


Loxomma: braincase in dorsal, ventral and lateral views. From Beaumont (1977).

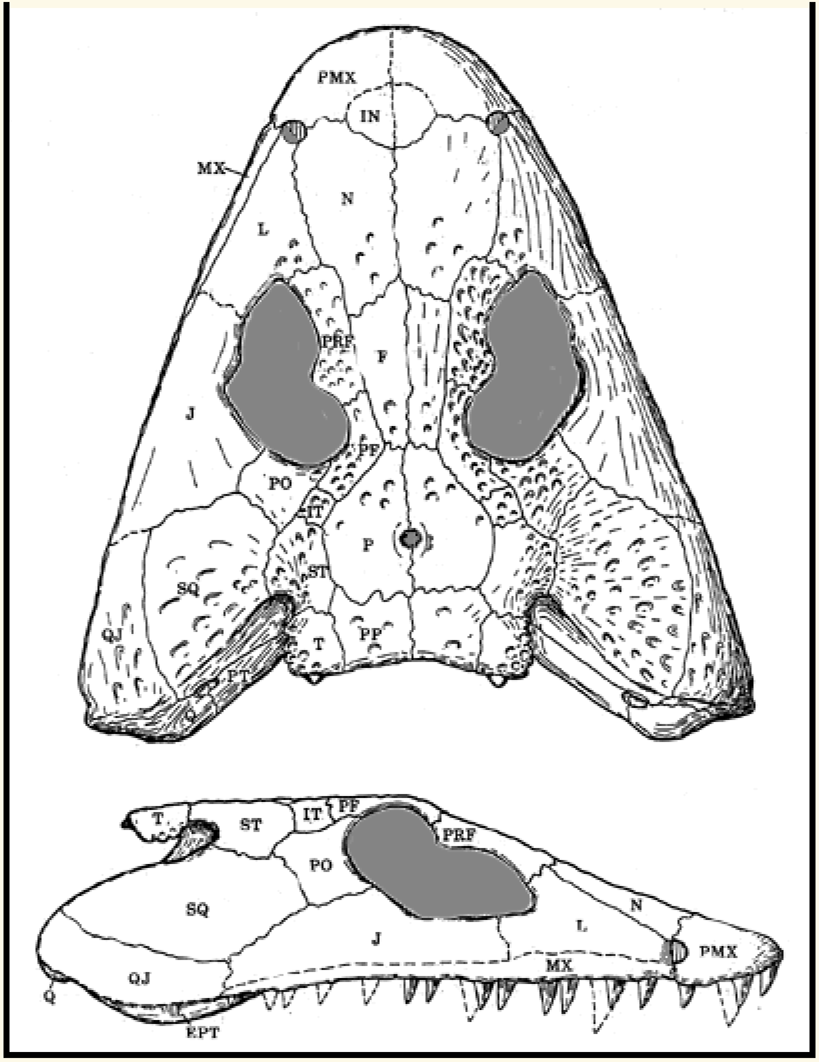
Characters: Supposedly croc-like (post-cranial skeleton essentially unknown until very recently); shallow skull; skull dermal bones similar to Edopoidea [B77]; septomaxilla appears as ornamented, relatively large surface bone [C02]; lateral line grooves present (but somewhat reduced); keyhole-shaped orbits formed by excavation of the lacrimal and prefrontal anterior to the orbit (see figure) and also bordered by jugal [ML98]; antorbital excavation at least as large as orbit [ML98]; strongly embayed spiracular notch, notch at posterolateral border of skull table, opening posteriorly [B77]; small tabulars with posterior process for attachment of mandibular depressors [B77]; orbits at mid-length of skull [B77]; orbits (*sensu stricto*) circular [B77]; cheek & skull roof sutured; quadrate well behind occiput (as most early tetrapods) [B77]; palatoquadrate probably still present as a unit, although partly formed in cartilage [B77]; exoccipitals do not reach postparietals or continue under skull table (compare *Edops*) [B77]; supraoccipital absent (not known for all genera) [B77], *contra* [B00]; stapes proximally broad; palate closed; braincase heavily ossified and extensively attached to skull roofing bones [B77]; opisthotic with two pairs of exoccipital facets (*see Megalocephalus*) [B77]; nerves IX, X, XI exit between exoccipital facets [B77]; otic capsule with two short, stout columnar processes articulating with exoccipital columns, anterior of which articulates with parietal and supratemporal [B77]; premaxilla form stout buttresses anteriorly on palate [B77]; adsymphysial plate present [ML98]; teeth "labyrinthodont" [C02]; fangs round at base, becoming laterally compressed at crown, with mesial & distal keels [ML98]; parasymphysial plate with at most 2 teeth [ML98]; coronoids have no teeth or denticles; double tooth row on dentary; shows some tendency to consolidation of jaw.

Links: Loxommatidae (Baphetidae); Air Breathers of the Coal Period; TREE2000.pdf; Eucritta; AE TREE2000.pdf; Report of Activities 1999: Calder No. 1; Class:Amphibia; Amphibian Skull.

Notes: **[1]** With the reinterpretation of *Ichthyostega* and its relatives as aquatic forms, baphetids are good candidates for the spot of first amphibious tetrapod group. If so, baphetids may be a rather important taxon. Both Clack's discovery of *Eucritta* and recent phylogenetic studies (Ahlberg & Clack (1998)) could support this conclusion. **[2]** The current candidates for the function of the preorbital excavation are (a) a salt gland, (b) an electrosensory organ; and (c) the pterygoideus muscle. Of the three, the third seems most consistent with the general observation that most serious cranial re-engineering is related to jaw mechanics. This weird adaptation may simply be an early, and very different, type of skull fenestration.

References: Ahlberg & Clack (1998); Beaumont (1977) [B77]; Berman (2000) [B00]; Clack (2002) [C02]; Milner & Lindsay (1988) [ML98]. ATW020820.

Loxomma: *L. allmani* (*almanni*?) Huxley 1862;
L. acutirhinus, *L. rankini*



Range: Early Carboniferous (Viséan?!) to Late Carboniferous (Bashkirian, Westphalian A) of Europe (Britain).

Phylogeny: Baphetidae : (*Baphetes* + *Megalocephalus*) + *.

Characters: ***dermal skull:*** skull ~25 cm and flattened [C02], *contra* [B77]; snout bluntly rounded; premaxilla long [B77]; lacrimal reaches nares [B77]; nares circular, at anterolateral margin of skull [B77]; septomaxilla not known [B77]; antorbital vacuity present and about same size as orbit [B77]; margins of vacuity solid, formed by lacrimal and nares "united" with buttresses from palatal bones, forming continuous, smooth-sided wall [B77]; orbits high on skull [C02]; orbits roughly at mid-skull length [B77]; intertemporal present [B77] [C02]; skull table large and square [B77]; pineal opening on slight raised boss [B77]; maxilla reaches quadratojugal, excluding jugal from skull margin [B77]; strong embayment between skull table & cheek area = probable spiracular notch [C02]; ***occiput:*** occipital arches weakly integrated into skull [B77]; exoccipital with limited role in braincase (primitive) [B77]; extended opisthotic forms paroccipital process [B77]; paroccipital process articulates only with tabular of skull table [B77]; opisthotics fused on the occiput? [B77]; ***braincase:*** (see image under Baphetidae) braincase strongly attached to dermal roofing bones [B77]; otic capsule with two strong lateralprocesses, each with exoccipital facet [B77]; otic capsule posterolateral wall from more posterior (opisthotic) process [B77]; same process forms dorsal border of fenestra ovalis and also floors fossa inside *posttemporal fenestra*, articulates with tabular dorsally (possible **$**) [B77]; floor of fenestra ovalis from parasphenoid [B77]; more anterior (prootic) process articulates with supratemporal & parietal [B77]; V-shaped depressions on ventral face of parasphenoid for attachment of neck muscles [B77]; basisphenoid ascends laterally anterior to otic capsule with facets for epipterygoid [B77]; sphenethmoid ossified and extends to presumed position of nasal capsules [B77]; sphenethmoid strongly ossified as interorbital septum [B77]; ***palate:*** palate not well known [B77]; interpterygoid vacuities absent [B77]; palatal anterior vacuity absent [B77]; premaxilla sutures with vomer along entire length of vomer [B77]; ***dentition:*** premaxilla with 8 teeth [B77]; premaxillary alveolar shelf broadens & teeth larger distally [B77]; jaws & palate with large, recurved teeth with slight keels [C02]; dentary parasymphysial tusks probably short [B77]; maxilla marginal teeth and alveolar shelf larger distally [B77]; maxillary marginal tooth count <30 [B77]; vomer, palatine & ectopterygoid each with *tusk pair* on a raised *boss* [B77]; palatine palatal ramus with shagreen of denticles [B77]; coronoids and prearticular with slight shagreen of denticles [AC98]; dermal pit & ridge ornament poorly developed in some specimens [B77].

Links: Class:Amphibia.

References: Ahlberg & Clack (1998) [AC98]; Beaumont (1977) [B77]; Clack (2002) [C02]. ATW020820.

Page Back | **Unit Home** | **Page Top** | **Page Next**

checked ATW040813

Tetrapoda: Baphetidae: Baphetidae (2)

Baphetes & Megalocephalus

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      |--Whatcheeriidae
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Baphetidae
            |  |--Loxomma
            |  `--+--Baphetes
            |     `--Megalocephalus
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. *Baphetes* X
2. *Megalocephalus* X

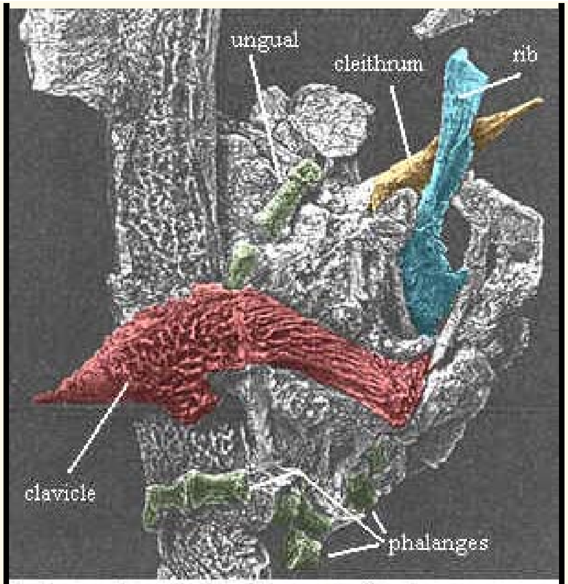
Descriptions

Baphetes: *B. planiceps* Owen 1854. *B. kirkbyi* Watson 1929; *B. bohemicus* Fritsch 1889; *B. lintonensis* Beaumont 1977.

Range: Late Carboniferous (Bashkirian - Moscovian, Westphalian B & C) of Europe (Britain & the Czech Republic); Middle Pennsylvanian (Moscovian) of North America (Ohio).

Phylogeny: Baphetidae:: *Megalocephalus* + *.

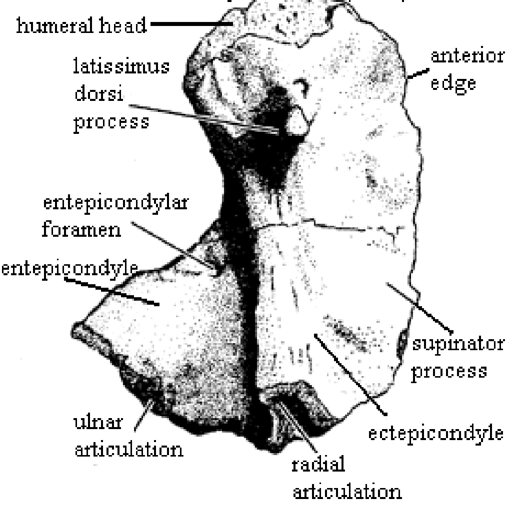
Characters: broad, flat skull [C02]; skull up to 29 cm long with rounded snout [B77] [ML98]; lateral margins of premaxilla strongly ornamented [B77]; nares more anterior than in *Loxomma*; [B77]; antorbital vacuity



Baphetes: disarticulated elements. The large ornamented bone is part of the dentary in ventral view. From Milner & Lindsay (1988)

slightly larger than orbit [B77]; postorbital with finger-like dorsomedial process [B77]; intertemporal present [B77]; skull table large & square, with long postparietals & tabulars [B77]; supratemporal extends around apex of otic notch [B77]; cheek long & deep [B77]; maxilla fairly short & does not meet quadratojugal so that jugal participates in skull margin [B77]; sclerotic plates present [ML98]; prominent suture between opisthotics on occiput in region of *synotic tectum* [B77] **[3]**; occiput and otic capsule otherwise as in other baphetids [B77]; parasphenoid with greater lateral expansion than other baphetids [B77]; ***palate:*** very similar to *Loxomma* [B77]; no anterior palatal vacuity [B77]; choanae ovoid & slightly elongate [B77]; ***dentition:*** numerous large teeth [C02]; structure as for *Megalocephalus* [B77]; highest premaxillary tooth count (10-11) [B77] [ML98]; marginal teeth lanceolate & slender with keeled crowns [ML98]; 34 marginal teeth on maxilla and usual tusk pairs [B77]; paired parasymphysial plate with fang pairs (i.e. one fang & a replacement pit on each plate) [ML98]; parasymphysial plates contact dentary & splenials, maybe coronoids [ML98]; possible ceratobranchial [ML98]; centra crescentic in anterior view, probable intercentra [ML98]; centra with ventral sagittal ridge [ML98]; dorsal ribs with flattened, triangular proximal head & thin distal expansion [ML98]; dorsal rib with little ventral curvature but some posterior curvature [ML98]; dorsal rib with longitudinal groove & posteriorly-directed uncinate process [ML98]; ***appendicular*****:** clavicle ornamented, narrow & crescentic(?), with unique rectangular process on lateral margin [ML98] **[4]**; cleithrum long & strap-like with expanded, rounded head [ML98]; humerus L-shaped, with little torsion [ML98]; humerus with large *deltopectoral crest* (on anterior edge, right of *lat. dors.* process in image) [ML98]; humerus with prominent latissimus dorsi process [ML98]; humerus with robust, broad ectepicondylar ridge [ML98]; humerus entepicondyle quarter-circle [C98] *contra* ("triangular") [ML98]; humerus with entepicondylar foramen [ML98] **[5]**; humerus with distal and anterior margins incompletely ossified and not distally weight-bearing [ML98]; radius & ulna ~50% humerus length [ML98]; radius rectangular in cross-section [ML98]; ilium with both dorsal and posterior processes (primitive?); [ML98] [C98]; U-shaped supraacetabular crest [ML98]; ischium poorly ossified [ML98]; tibia stout, with strong cnemial crest & somewhat shorter than humerus [ML98]; tibia with sharp ridge on flexor (dorsal) surface [ML98]; fibula broad & same length as tibia [ML98]; ***other:*** ventral armor of elongate gastralia [C98]; *but* ventral armor of elongate, overlapping scales, with longitudinal ridge, but no ornament [ML98].

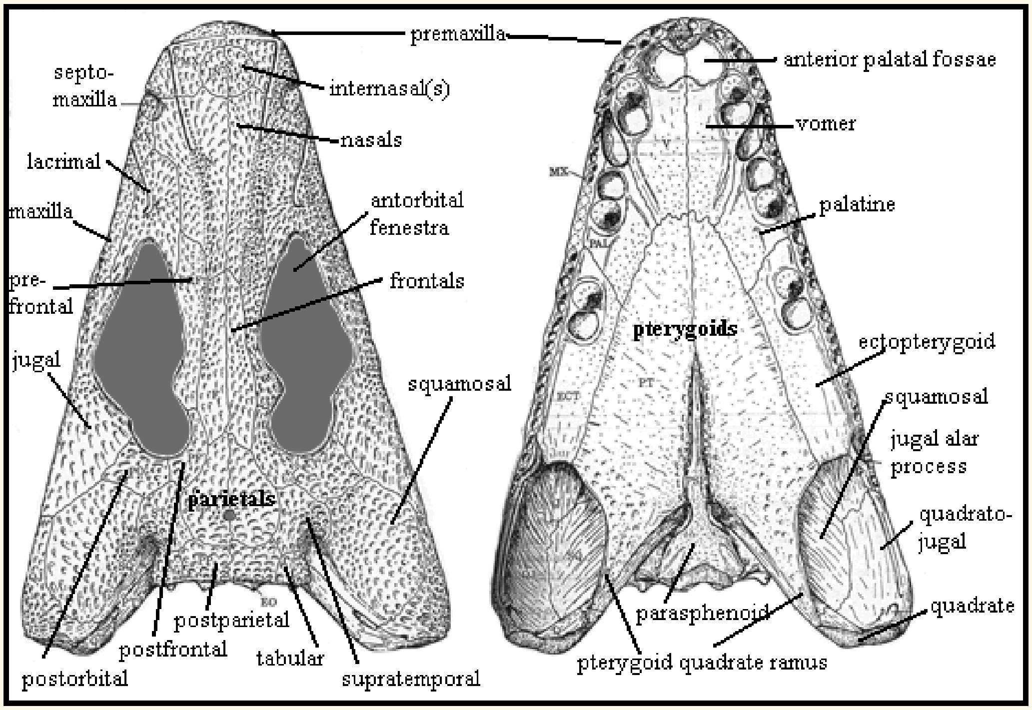
Baphetes: Left humerus (reversed) in dorsal view. From Milner & Lindsay (1988)



Notes: **[1]** in especially lateral view, the skull of *Baphetes* is almost indistinguishable from *Loxomma* save that the posterior extreme of the *Baphetes* jugal narrowly reaches the ventral margin of the skull just anterior to the quadratojugal. Dorsally, the skulls are identical in the pattern of dermal bones. However, the *Baphetes* skull is clearly broader and more *spatulate*, as well as longer, than the skull of *Loxomma*. Certain minor differences are noted above. **[2]** Apparently the only baphetid where the stapes is known. Stapes was 2 cm long and relatively stout -- plainly of little use in hearing. **[3]** Beaumont argues that this demonstrates the absence of a supraoccipital. In *Megalocephalus* there is no clear suture, and a median flange of bone forms a slight ventrally-directed flange which might be interpreted as a supraoccipital. Berman (2000) argues that a supraoccipital is present. He posits that even a median suture does not eliminate the possibility that a supraoccipital is present and fused with the opisthotic. He points out that (a) paired supraoccipitals are known in one specimen of *Limnoscelis* and (b) that the supraoccipital is normally fused to other elements of the otic capsule. This feature has considerable importance since it tends to move the baphetids into the anthracosaur area and away from the temnospondyls. **[4]** In the image, note that the clavicle appears to has been flattened during preservation. The portion to the right is the ascending ramus which would have climbed the anterior margin of the scapulocoracoid, with the ornamentation facing anterolaterally. The ornamented surface of the portion to the left would have faced, perhaps, lateroventrally, with the pointed end more or less posterior. Thus the "upper" edge in the image would have faced medially and articulated with the interclavicle. If we have this all right, the unique tab structure on the "bottom" edge is probably a form of garden-variety *pectoralis* process. Similar structures are known from the interclavicles or clavicles of, e.g. *Dimetrodon* and lizards. **[5]** as Milner & Lindsay point out, this is the *only* humeral foramen, in contrast to more basal tetrapods.

Links: Air Breathers of the Coal Period; Annual Conference Abstracts 1999.

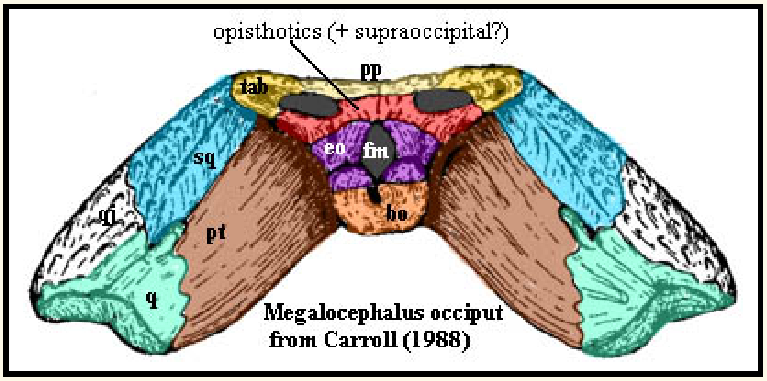
References: Beaumont (1977) [B77]; Berman (2000); Clack (1998) [C98]; Clack (2002) [C02]; Milner & Lindsay (1988) [ML98]. ATW020820.



Megalocephalus: *M. pachycephalus* Barkas 1873; *M. lineolatus* Cope 1877.

Range: Late Carboniferous (Bashkirian [Westphalian A] to Moscovian [Westphalian C]) of Europe (Britain & Ireland); also indeterminate middle Pennsylvanian (Late Carboniferous) of North America (Ohio).

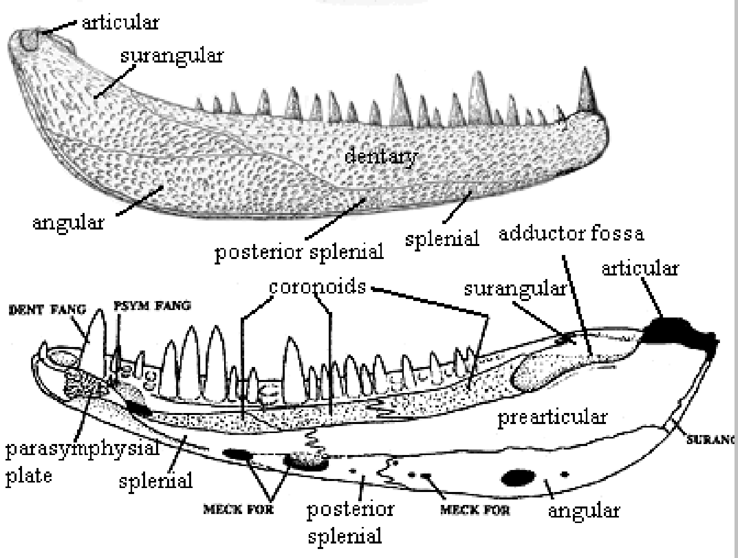
Phylogeny: Baphetidae:: *Baphetes* + *.



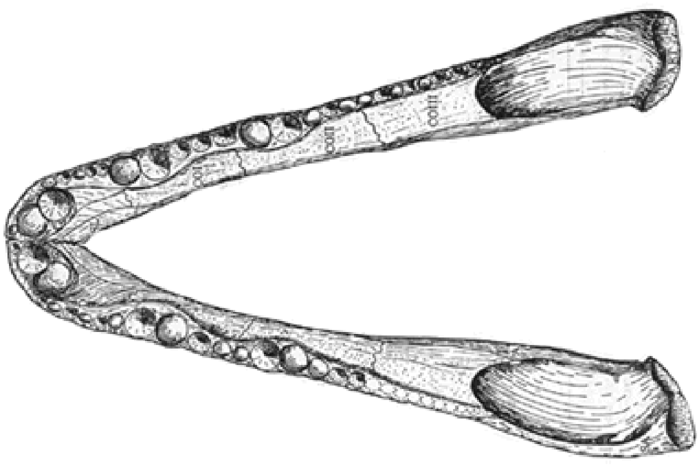
Megalocephalus occiput from Carroll (1988)

Characters: Skull 35 cm [C02]; ***dermal skull:*** skull relatively narrow and pointed [B77] [C02]; premaxilla long [B77]; lateral margins of premaxilla almost free of ornament [B77]; premaxilla with nasolabial groove from nares to jaw margin [B77]; premaxilla & maxilla suture narrowly with septomaxilla [B77]; septomaxilla ornamented & exposed on surface [B77]; nares more posteriorly placed [B77]; internasals present and may be partially pierced by anterior palatal foramina (for dentary tusks) [B77]; internasals may be paired or single [B77]; lacrimal excluded from nares by nasals & maxilla [B77]; antorbital vacuity twice length of orbit [B77]; nasals with central ridges [B77]; nasals very long, with length 4x width [B77]; frontals depressed between antorbital fenestrae, with prominent ridges on prefrontals continuing ridges of nasals [B77]; skull table small, horizontal and firmly sutured to cheek [B77]; parietals extend between orbits, meeting prefrontals [B77]; pineal foramen small, without boss [B77]; parietals broaden posteriorly [B77]; intertemporal absent [B77]; supratemporal expanded and forms anterior border of otic notch [B77]; postparietals small [B77]; orbits posteriorly placed at 2/3rds midline length [B77]; prefrontals long & narrow, forming medial border of antorbital fenestra [B77]; prefrontal does not meet jugal due to fenestration [B77]; sharp angle between skull table & cheek, which is almost vertical [B77]; postorbital vertical, meeting squamosal & jugal [B77]; jugal excluded from skull margin by maxilla-quadratojugal suture [B77]; jugal meets quadratojugal [B77]; quadratojugal with concave articular surface for convex surface on quadrate [B77]; quadrate medial surface forming palatoquadrate foramen as in temnospondyls [B77]; quadrate not firmly sutured to skull roof [B77]; squamosal large, smoothly overlapping quadrate ramus of pterygoid inside otic notch [B77]; squamosal also overlaps supratemporal in otic notch [B77]; paroccipital process articulates with tabular and supratemporal of skull table [B77]; large posttemporal fenestrae [B77]; massive concave occipital condyle with contributions from exoccipitals and basioccipital [B77]; exoccipital with massive, bifurcated dorsolateral column [B77]; nerve XII exits between branches of exoccipital column [B77]; ***braincase:*** otic capsule with two short, stout columnar processes articulating with exoccipital columns [B77]; parasphenoid sheaths anterior of basioccipital, but lateral edges ended in free rim [B77] (early homologue of *crista muscularis*?); V-shaped depressions on ventral face of parasphenoid for attachment of neck muscles [B77]; parasphenoid floors otic capsule and wraps base of basisphenoid at and posterior to *basipterygoid process* [B77]; parasphenoid with internal carotid foramina near base of cultriform process [B77]; epipterygoid with extensive quadrate ramus following pterygoid quadrate ramus, which sutures extensively with the quadrate [B77]; epipterygoid *columella* poorly ossified [B77]; epipterygoid with anterior extension fused to palatal ramus of pterygoid [B77]; ***palate:*** premaxillae with triangular buttresses meeting & interlocking on midline behind symphysis [B77]; anterior fenestrae for parasymphysial tusks [B77]; premaxillae without palatine ramus [B77] vomers thickened where they meet the anterior fenestrae and support vomerine tusks [B77]; choanae elongate, laterally placed at posterior limit of premaxilla [B77]; palatines and ectopterygoids with dorsal processes meeting lacrimals & jugals (respectively) to wall antorbital fenestrae [B77];

ectopterygoids weakly attached to maxilla, as separated by groove for dentary teeth and, posteriorly, by jugal alar process [B77]; pterygoids notched to form *conical recess* at base of quadrate ramus (articulation with braincase) [B77]; pterygoids meet for anterior 1/3 of length [B77]; jugal with very strong alar process projecting into adductor fossa [B77]; adductor fossae very large [B77]; pterygoid *quadrate ramus* almost vertically oriented, extending well below level of cheek bones [B77]; ***mandible:*** extensive roughened areas near symphysis for ligaments binding jaw rami [B77]; parasymphysial plate with small teeth ("psym fang" in image) [AC98]; dentary with little medial exposure (covered by coronoids) [B77]; 4 main medial foramina penetrating splenial, postsplenial & angular [B77]; coronoid process absent [B77]; splenial, postsplenial & angular wrap around jaw to suture with prearticular [AC98]; Meckelian fossa enters space between posterior coronoid and dentary as extension of adductor fossa [B77]; posterior coronoid with only slight, weak contact with surangular [B77]; large, deep adductor fossa (attachment of adductor muscles) walled laterally by surangular, anteriorly by posterior coronoid, & medially by prearticular [B77]; no retroarticular process [B77]; articulation terminal and above level of tooth row [B77]; articular with two articulating surfaces: main , horizontal, transverse area and, more medially, an anteromedially-directed area (could have allowed jaw to expand) [B77]; ***dentition:*** teeth larger than in *Loxomma* [C02]; premaxilla with 8-9 teeth [B77]; maxilla with 36 [B77]; dentary ~34 teeth including three tusk-like pairs [B77]; no size peak, but teeth gradually smaller posteriorly [B77]; tusk pairs and denticles on all roof bones except pterygoids [B77]; parasymphysial dentary tusks fit into anterior palatal fenestra [B77]; all teeth round at base, becoming laterally compressed with anterior and posterior cutting edges [B77]; pterygoids and parasphenoid with shagreen of small denticles [B77]; coronoids and prearticular with shagreen of small denticles [B77] *contra* [AC98]; lower teeth only on dentary [B77]; ***postcranial:*** interclavicle rhomboidal [B77]; dermal bone ornamentation marked, but with smaller individual ornaments [B77] growth zones (elongated ornament) along frontal prefrontal & nasal, as well as along lower margin of cheek and squamosal.



Megalocephalus: reconstruction of lower jaw in lateral and medial views. From Beaumont (1977) (lateral view) and Ahlberg & Clack (1998) (medial view).



Megalocephalus: reconstruction of lower jaw in dorsal view. From Beaumont (1977).

Note: [1] The history of the name "*Megalocephalus*" is a dark and gothic tale of great complexity. The story involves almost every conceivable pitfall of biological nomenclature, including, *inter alia*, published mis-spellings, misidentifications, chimeras, garbage taxa, preoccupied names, and -- finally -- the riddle of a holotype destroyed by fire after initial publication, but before complete description. **[2]** *Megalocephalus* is the most completely known baphetid skull.

Links: Loxommatidae (Baphetidae); Dinosaurclass.Com (Chinese).

References: Ahlberg & Clack (1998) [AC98]; Beaumont (1977) [B77]; Clack (2002) [C02]. ATW020820.

Page Back | **Unit Home** | **Page Top** | **Page Next**

checked ATW040813

Tetrapoda: *Eucritta*

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Baphetidae
            |  |--Loxomma
            |  `--+--Baphetes
            |     `--Megalocephalus
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

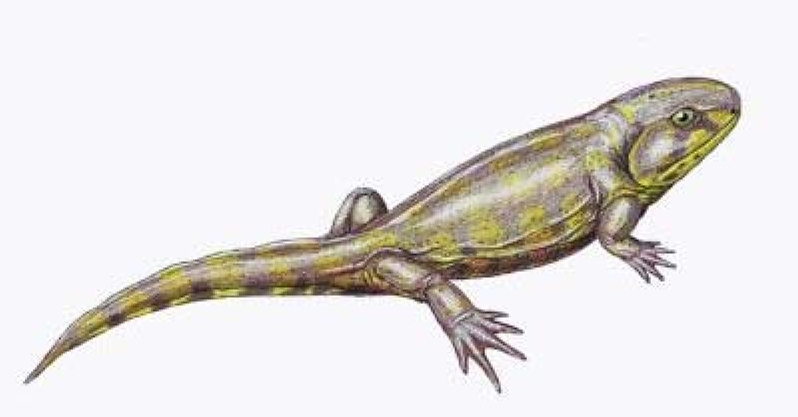
Contents

Taxa on this Page

1. *Eucritta* X

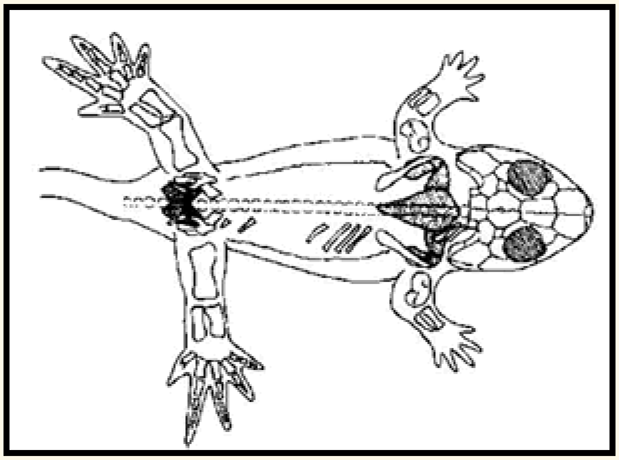
Eucritta melanolimnetes

Eucritta melanolimnetes is The Creature from the Black Lagoon. No, not *that* creature, *this* creature! It was a very primitive and modest sized (about 25 centimetres long, not nearly big enough to carry off maidens) amphibian, that is



extraordinary for its combination of amphibian and reptilian - or to put it more technically, baphetid, temnospondyli, and anthracosaurian - characteristics. The presence of so many different traits makes its exact placement uncertain. The best we can say is that it is a good representative of the sort of ancestral type from which all other tetrapods (all amphibians and reptiles apart from the primitive ancestral ones described in this unit) might have evolved. MAK111110

Descriptions

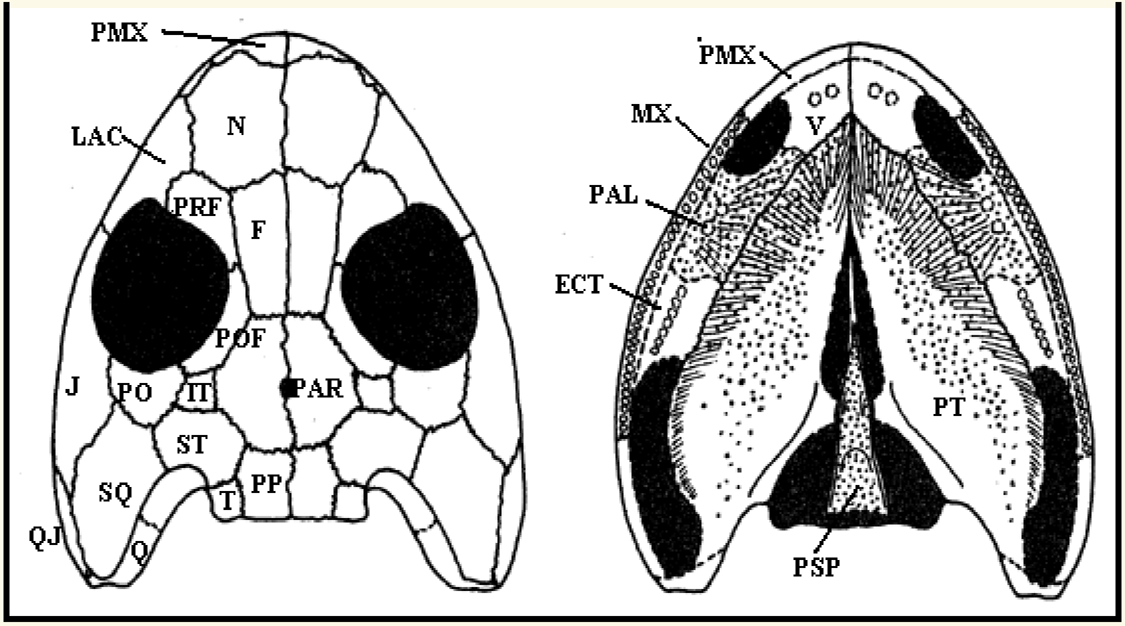


Eucritta**:** *E. melanolimnetes* Clack 1998

Range: Early Carboniferous (Brigantian, latest Viséan) of Europe (Britain).

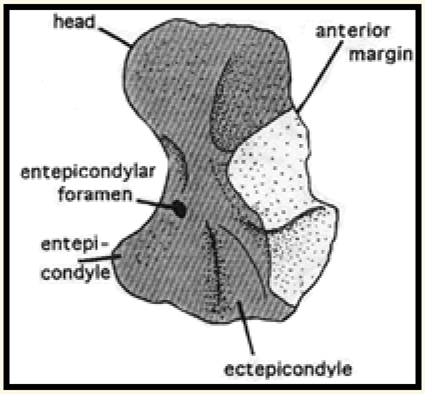
Phylogeny: Tetrapoda ::::: Tetrapoda* + Baphetidae + *.

Characters: **$** snout short with nasals square or hexagonal; full compliment of dermal roofing bones [C98]; orbit anteroventrally embayed (perhaps only in larger individuals) [C01]; frontals long & narrow, without participation in orbit [C01]; prefrontal only weakly sutured to lacrimal & nasals [C01]; **$** postorbital broadly crescentic without ventral process into orbit margin [C98]; **$** skull table approximately square [C98]; parietals short, forming hexagonal plate [C01]; pineal foramen just posterior to orbits [C01]; postparietals relatively long [C01]; intertemporal present [C01]; **$** supratemporal broadly crescentic [C98]; supratemporal contacts postparietal [C98]; supratemporal surrounds most of otic notch (not squamosal) [C98]; **$** distance from apex of otic notch to orbit less than diameter of orbit [C98]; tabulars square, without button or horn (C01 notes that horn may have been lost) [C01]; *paraquadrate foramen* present [C01]; quadrate with broad dorsal plate and ventral articular surface [C01]; parasphenoid with broad triangular body thickened at edges in anterior portion [C98] [C01]; parasphenoid body with median smooth depression [C01]; parasphenoid with narrow cultriform process [C01]; basicranial articulation not fused [C98]; palate closed [C98]; broad vomerine plate [C98]; pterygoids meeting on midline [C98];



lower jaw of "standard" tetrapod pattern [C01]; coronoid-type crest & retroarticular process both absent [C01]; **$** maxillary tooth count 38-40 with peak at positions 7-14 [C98]; fang pairs on vomers and palatines [C98]; palatines, vomers maybe all palatal bones, denticulated & striated [C01]; possible ectopterygoid tooth row [C01]; pterygoids and parasphenoid denticulated [C98]; cultriform process *not* denticulated [C01]; denticles and striations even on distal portion of quadrate ramus (!?) [C01]; pterygoids "striated" [C01]; dentary teeth unknown [C01]; axial skeleton poorly ossified circle [C98]; cervical ribs long, straight & somewhat expanded distally [C01]; trunk ribs only slightly curved & not expanded [C98] [C01]; single pair of stout sacral ribs [C01]; cleithrum present, long, straight, well-ossified, and expanded distally to wedge-shaped terminus [C98] [C01]; clavicles do not meet on mid-line [C01]; clavicle with dorsal blade having posterior face concave (cleithral articulation) [C01]; interclavicle diamond-shaped [C98]; interclavicle anterior edge crenellated (as some temnospondyls -- ATW) [C01]; scapulocoracoid single ossification, poorly ossified [C01] [C98]; humerus L-shaped [C98]; humerus entepicondyle quarter-circle [C98] **[3]**; humerus entepicondylar foramen present [C01]; ectepicondyle low [C01]; ulna more slender and slightly longer than radius [C01]; ulna with moderately developed olecranon process [C01]; manual unguals slender & tapered [C01]; ilium with both dorsal and posterior processes [C98]; femur ~ 18 mm (vs. 12-14 mm humerus) [C01]; tibia & fibula 11 mm, very similar, with interepipodial space [C01]; pes with five digits [C98]; pes phalangeal formula 2345? [C01]; ventral armor of narrow gastralia [C98]; dermal bone with pattern of radiating ridges [C01].

Notes: [1] as Clack (1998) notes, *Eucritta* is very close to basal temnospondyls in characters of the skull, except for the closed palate. **[2]** Clack (2001) makes the interesting point that the posterior stem on the interclavicle is a developmental artifact. It gradually grows out into a full diamond-shape during ontogeny. **[3]** in Clack (2001) the entepicondyle is described as "triangular." From the figure in the later paper (at right), the "quarter-circle" may refer to the *ect*epicondyle.



Comment: may be related to Temnospondyli

Links: AE TREE2000.pdf; relics: The creature from the black lagoon.

References: Clack (1998) [C98], Clack (2001) [C01]. ATW020820.

Images: Creature from the Black Lagoon (movie version) from The Uninhibited Uniform. *Eucritta melanolimnetes* life reconstruction by Dmitry Bogdanov MAK111112

Page Back | Unit Home | Page Top | Page Next

checked ATW060327, revised MAK111110

Tetrapoda: Tetrapoda*

Crown Tetrapods

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Baphetidae
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

Taxa on This Page

1. Tetrapoda*

The Tetrapods*

It is customary to celebrate the advent of the Tetrapoda* with a long paean of praise to their talents and abilities – something like the death song of a barbarian warrior reciting the deeds of his ancestors. For the moment, we are forced to make do with the following table. ATW020329.

Structure	**Changes**	**Functional Significance**
Caudal vertebrae	Development of atlas-axis complex	Allows head to be moved independent of forelimbs. Probably multiple convergent adaptations
	Numerous, divergent "experiments" including big thick ribs (*Ichthyostega*),	A difficult balancing of different needs: to support the

Ribs	virtually absent ribs (numerous examples), ribs light, but tightly bound together (colosteids)	forelimbs and gut against gravity, to reduce weight, to reinforce the vertebrae, to permit the trunk to flex, to provide a rigid cage for the lungs and heart, etc.
Dermal skull	Becomes more tightly integrated, with less kinesis, but often less massive	Since many later tetrapods (e.g. snakes) have very kinetic skulls, the significance is not entirely clear.
Dermal skull	Simplification, with loss of some bones	Probably related to loss of kinesis
Limb girdles	Loss of many elements; development of "standard" tetrapod limbs and girdles	Gradual, and perhaps rather late, acquisition of the ability to walk on land on a regular basis. But footprints are already known from the Famennian of Australia.
Hip	Ilium contacts and partially fuses with elements of vertebral column to form true sacrum	A clear necessity to allow the legs to support the body
Hindlimbs	Reverses orientation	Early tetrapods had the feet facing posteriorly, as in fish.
Hands/feet	Complete transition from fins to limbs	Walking probably predates walking *on land*
Water balance	unknown	Very important soft tissue changes must have taken place, but the timing and nature of the transition is not known.
Senses	Loss of electrical senses and lateral line, probable loss of most hearing, development of flexible lens in the eye	Senses don't work the same out of water. A "fish" out of water is nearly deaf and blind, and it can't use its pressure or electrical senses. Consider how much neural re-wiring had to be accomplished!

Descriptions

Tetrapoda*: *Rana* + Rambo. The last common ancestor of living amphibians and amniotes and all of its descendants. This is the "crown group Tetrapoda" that many paleontologists complain about. The reasons for this terminology are discussed at **What is a "Tetrapod?"**

Range: from the Early? Carboniferous.

Phylogeny: Tetrapoda ::::: Baphetidae + * : Temnospondyli + (Lepospondyli + Reptilomorpha)

Characters: see Overview.

Links: Definition of the Taxon Tetrapoda; Terrestrial Vertebrates; Herpetology- Phylogeny and Tetrapods; Phylog. Syst. of Odonata - Taxonomy; First International Phylogenetic Nomenclature Meeting Paris, July ... (see sample abstract); PII- S0169-5347(99)01780-2; PII- S0169-5347(00)01927-3 (contrasting viewpoints); Should we embrace the PhyloCode as the future of taxonomy (Best on the Web); PhyloCode Preface. ATW031013.

Page Back | **Unit Home** | **Page Top** | **Page Next**

checked ATW050703

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Tetrapod Dendrogram

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         |  `--Greererpeton
         `--+--Baphetidae
            |--Eucritta
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega •X ToL
`--+--Ichthyostega •X ToL
   `--+--Sinostega •X
      `--+--Densignathus •X
         `--+--Hynerpeton •X
            `--+--Tulerpeton •X
               `--+--Ossinodus  •X
                  `--+--o Whatcheeriidae •X
                     |    |--Pederpes  •X
                     |    `--Whatcheeria  •X
                      `--+--Crassigyrinus•X ToL
                          `--+--Colosteidae X
                             |   `--Greererpeton •X
                             `--+--Spathicephalus •X
                                 `--+--Baphetidae X ToL
                                      |   |--Loxomma •X
                                      |   `--+--Baphetes •X
                                      |      `--Megalocephalus •X
                                      |--Eucritta •X
                                      `--Tetrapoda*
                                          |--TEMNOSPONDYLI
                                          `--+--LEPOSPONDYLI
                                              `--REPTILIOMORPHA
```

Page Back | Unit Home | Page Top | Page Next

checked ATW050703, revised MAK111112

Tetrapod References

Abbreviated Dendrogram

```
SARCOPTERYGII
|
TETRAPODA
|--Acanthostega
`--+--Ichthyostega
   `--+--Crassigyrinus
      `--+--Colosteidae
         `--+--Baphetidae
            `--Tetrapoda*
               |--TEMNOSPONDYLI
               `--+--LEPOSPONDYLI
                  `--REPTILIOMORPHA
```

Contents

Ahlberg, PE (1995), ***Elginerpeton pancheni** and the earliest tetrapod clade*. **Nature**, 373: 420-425.
Tetrapoda.

Ahlberg, PE (1998), *Postcranial stem tetrapod remains from the Devonian of Scat Craig, Morayshire, Scotland*. **Zool. J. Linn. Soc.** 122: 99-141.
Acanthostega, *Ichthyostega* Tetrapoda.

Ahlberg, PE & JA Clack (1998), *Lower jaws, lower tetrapods -- a review based on the Devonian genus Acanthostega*. *Trans. Roy. Soc. (Edinburgh), Earth Sci.*, 89: 11-46.
Acanthostega, *Baphetes*; Baphetidae, *Crassigyrinus*, *Ichthyostega*, *Loxomma*, *Megalocephalus*, Tetrapoda.

Ahlberg, PE & E Luksevics (2004) *New light on the Devonian tetrapod **Ventastega curonica***. **10th Intl. Symp. Early Vert. Lower Vert.**, p.10 (abstr).
Tetrapoda.

Ahlberg, PE, JA Clack & E Lukševics (1996), *Rapid braincase evolution between **Panderichthyes** and the earliest tetrapods*. **Nature** 381: 61-64.
Tetrapoda.

Ahlberg, PE, E Lukševics & E Mark-Kurik (2000), *A near-tetrapod from the Baltic Middle Devonian*. **Palaeontology** 43: 533-548.

Andrews, S.M., Browne, M.A.E., Panchen, A.L.&. and Wood, S.P. 1977. Discovery of amphibians in the Namurian (Upper Carboniferous) from Fife. Nature 265: 529-532.
Crassigyrinus

Andrews, SM & TS Westoll (1970), *The postcranial skeleton of **Eusthenopteron foordi** Whiteaves*. **Trans. Roy. Soc. Edin.** 68: 207–329.

Acanthostega.

Beaumont, EH (1977), *Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia).* **Trans. Roy. Soc. Lond. B** 280: 29-101.
Baphetes, Baphetidae, *Loxomma*, *Megalocephalus*, *Spathicephalus*.

Beaumont, EH & TR Smithson (1998), *The cranial morphology and relationships of the aberrant Carboniferous amphibian* ***Spathicephalus mirus*** *Watson*. **Zool. J. Linn. Soc.** 122: 187-209.
Spathicephalus

Michael J. Benton (2000). "Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead?". *Biological reviews of the Cambridge Philosophical Society* 75 (4): 633–648. PMID 11117201.
Amphibians, Systematics, and Cladistics

Benton, M. J. (2005), *Vertebrate Paleontology*, 2nd Ed. 2000, 3rd ed. 2005, Blackwell Science Ltd
Amphibians, Systematics, and Cladistics

Berman, DS (2000), *Origin and early evolution of the amniote occiput*. **J. Paleontol.** 74: 938-956.
Acanthostega, *Baphetes*, Baphetidae.

Berner, RA & Z Kothavala (2001), *GEOCARB III: a revised model of atmospheric* CO_2 *over Phanerozoic time*. **Amer. J. Sci.** 301: 182-204.
Tetrapoda.

Berner, RA, DJ Beerling, R Dudley, JM Robinson & RAWildman, Jr (2003), Phanerozoic atmospheric oxygen. **Ann. Rev. Earth Planet. Sci.** 31: 105–34.
Tetrapoda.

Blom, H (2005), *Taxonomic revision of the Late Devonian tetrapod* ***Ichthyostega*** *from East Greenland*. **Palaeontology** 48: 111-134.
Ichthyostega, Tetrapoda.

Carroll, RL (1988), *Vertebrate Paleontology and Evolution*, WH Freeman & Co., 698 pp.
Amphibians, Systematics, and Cladistics, Colosteidae

Carroll, RL (2009), *The Rise of Amphibians : 365 million years of evolution*, John Hopkins University Press, Baltimore
Amphibians, Systematics, and Cladistics

Carroll, RL, J Irwin & DM Green (2005), *Thermal physiology and the origin of terrestriality in vertebrates*. **Zool. J. Linn. Soc.** 143: 345–358. *Acanthostega*, *Ichthyostega* .

Clack, JA (1989), *Discovery of the earliest-known tetrapod stapes*. **Nature** 342: 425-427.
Tetrapoda.

Clack, JA (1994), *Earliest known tetrapod braincase and the evolution of the stapes and fenestra ovalis*. **Nature** 369: 392-394.
Acanthostega, Tetrapoda.

Clack, JA (1997), *Devonian tetrapod trackways and trackmakers; a review of the fossils and footprints*. **Palaeogeog., Palaeoclimatol. Palaeoecol.**, 130: 227-250.
Tetrapoda, Tetrapoda.

Clack, JA (1998), *A new Early Carboniferous tetrapod with a mélange of crown-group characters.* **Nature** 394: 66-69.
Baphetes, *Eucritta*.

Clack, JA (1998a), *The neurocranium of* ***Acanthostega gunnari*** *Jarvik and the evolution of the otic region in tetrapods*. **Zool. J. Linn. Soc.** 122: 61-97.
Acanthostega, *Ichthyostega*, Tetrapoda.

Clack, J. A. 1998b. The Scottish Carboniferous tetrapod Crassigyrinus scoticus (Lydekker) - cranial anatomy and

relationships. Transactions of the Royal Society of Edinburgh: Earth Sciences. 88, 127-142.
Crassigyrinus

Clack, JA (2001), ***Eucritta melanolimnetes*** *from the Early Carboniferous of Scotland, a stem tetrapod showing a mosaic of characteristics*. **Trans. Roy. Soc. Edin.: Earth Sci.** 92: 72-95.
Spathicephalus, *Eucritta*.

Clack, JA (2002), **Gaining Ground: the Origin and Evolution of Tetrapods**. Indiana Univ. Press, 369 pp.
Acanthostega, *Baphetes*, Baphetidae, *Ichthyostega*, *Loxomma*, *Megalocephalus*, *Spathicephalus*, Tetrapoda, Tetrapoda.

Clack, JA (2002a), *The dermal skull roof of* ***Acanthostega gunnari****, an early tetrapod from the Late Devonian*. **Trans. R. Soc. Edin., Earth Sci.** 93: 17-33.
Acanthostega, *Ichthyostega*, Tetrapoda.

Clack, J. A. 2002b. An early tetrapod from Romer's Gap. Nature 418: 72-76. doi:10.1038/nature00824. PMID 12097908 **pdf**
Crassigyrinus, *Pederpes*, Whatcheeriidae

Clack, JA (2003), A revised reconstruction of the dermal skull roof of *Acanthostega*, an early tetrapod from the Late Devonian. **Trans. R. Soc. Edin., Earth Sci.** 93: 163-165.
Acanthostega.

Clack, Jennifer A. 2006. Crassigyrinus. Crassigyrinus scoticus. Version 09 February 2006. http://tolweb.org/Crassigyrinus_scoticus/15012/2006.02.09 in The Tree of Life Web Project, http://tolweb.org/
Crassigyrinus

Clack, Jennifer A. 2009. The Fish-Tetrapod Transition: New Fossils and Interpretations. Evo Edu Outreach (2009) 2:213–223 DOI 10.1007/s12052-009-0119-2. **pdf**

Clack, JA, PE Ahlberg, SM Finney, P Dominguez Alonso, J Robinson & RA Ketcham (2003), *A uniquely specialized ear in a very early tetrapod*. **Nature** 425: 65-69.
Acanthostega, *Ichthyostega*, Tetrapoda.

Clack, J. A., and S. M. Finney. 2005. Pederpes finneyae, an articulated tetrapod from the Tournaisian of western Scotland. *Journal of Systematic Palaeontology*, 2: 311-346.
Crassigyrinus

Clement, G, PE Ahlberg, A Blieck, H Blom, JA Clack, E Poty, J Thorez, & P Janvier (2004), *Devonian tetrapod from western Europe*. **Nature** 427: 412-413.
Ichthyostega.

Coates, MI (1996), *The Devonian tetrapod* ***Acanthostega gunnari*** *Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution*. **Trans. R. Soc. Edin, Earth Sci.** 87: 363-421.
Acanthostega, *Ichthyostega*, Tetrapoda, Tetrapoda.

Coates, MI & JA Clack (1991), *Fish-like gills and breathing in the earliest known tetrapod*. **Nature** 352: 234-236.
Acanthostega, Tetrapoda.

Coates, MI, JE Jeffery & M Ruta (2002), *Fins to limbs: what the fossils say*. **Evol. & Devel.** 4: 390-401.
Acanthostega, *Ichthyostega*, Tetrapoda, Tetrapoda.

Coates, MI, NH Shubin & EB Daeschler (2004), *Response to comment on "The early evolution of the tetrapod humerus*." **Science** 305: 1715d.
Ichthyostega.

Colbert, E.H., 1969 *Evolution of the Vertebrates*, John Wiley & Sons, 2nd ed.
Amphibians, Systematics, and Cladistics

Daeschler, EB (2000), *Early tetrapod jaws from the Late Devonian of Pennsylvania, USA*. **J. Paleont.** 74: 301-308.
Tetrapoda, Tetrapoda.

Daeschler, EB, NH Shubin, KS Thomson & WW Amaral (1994), *A Devonian tetrapod from North America*. **Science**

265: 639-642.
Tetrapoda, Tetrapoda.

Dubuisson, J-Y, P Rachebouf, & P Janvier (2003), *Du Silurien au Devonien: les sorties des eaux* **in** P. Janvier & V. Dupres [eds.] (2003-2005), **Evolution: De l'Origine de la Vie aux Origines de l'Homme**.
WWW. Tetrapoda.

Dudley, R (1998), *Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance*. **J. Exper. Biol.** 201, 1043–1050.
Tetrapoda.

Gauthier, J., Canatella, D., De Queiroz, K., Kluge, A. and Rowe, T. 1989. Tetrapod phylogeny. In: Fernholm, B., Bremer, K. and Jornwall, H., The Hierarchy of Life. London, Elsevier Science Publishers, pp. 337-353.
Crassigyrinus

Godfrey, SJ (1989) *The postcranial skeletal anatomy of the Carboniferous tetrapod* ***Greererpeton burkemorani*** *Romer, 1969*. **Phil. Trans. R. Soc (Lond.)**, B323: 75-133.
Colosteidae.

Gordon, M.S. and Long, J.A. (2004) The Greatest Step In Vertebrate History: A Paleobiological Review of the Fish-Tetrapod Transition. Physiological and Biochemical Zoology. 77(5):700-719. **pdf**
Tulerpeton

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp.
Ichthyostega.

Jarvik, E (1996), *The Devonian tetrapod* ***Ichthyostega***. **Fossils & Strata** 40: 1–213.
Tetrapoda, *Ichthyostega*.

Johanson, Z, PE Ahlberg & A Ritchie (2003), *The braincase and palate of the tetrapodomorph sarcopterygian* ***Mandageria fairfaxi****: morphological variability near the fishtetrapod transition*. **Palaeontology** 46: 271–293.
Ichthyostega.

Kellogg, EA & ND Juliano (1997), *The Structure and function of RuBisCo and their implications for systematic studies*. **Amer. J. Bot.** 84: 413–428.
Acanthostega.

Thomas S. Kuhn (1962). *The Structure of Scientific Revolutions*. University of Chicago Press. p. 102. ISBN 226458032.
Amphibians, Systematics, and Cladistics

Thomas S. Kuhn (1998). "Metaphor and theory change". In Andrew Ortony. *Metaphor and Thought*. Cambridge University Press. p. 539. ISBN 0521227275.
Amphibians, Systematics, and Cladistics

Michel Laurin (2008). "The splendid isolation of biological nomenclature". *Zoologica Scripta* 37 (2): 223–233. doi:10.1111/j.1463-6409.2007.00318.x.
Amphibians, Systematics, and Cladistics

Laurin, M, M Girondot & A de Ricqlès (2000), *Early tetrapod evolution*. **Tree** 15: 118-123.
Acanthostega.

Lebedev, OA & JA Clack (1993), *Upper Devonian tetrapods from Andreyeva, Tula Region, Russia*. **Paleontology** 36: 721-734.
Tetrapoda, Tetrapoda.

Lebedev, OA & MI Coates (1995), *The postcranial skeleton of the Devonian tetrapod* ***Tulerpeton curtum*** *Lebedev*. **Zool. J. Linn. Soc.**, 114: 307-348. doi: 10.1111/j.1096-3642.1995.tb00119.x
Acanthostega, *Ichthyostega*, Tetrapoda, Tetrapoda, *Tulerpeton*

Leebens-Mack, J & C dePamphilis (2002), *Power analysis of tests for loss of selective constraint in cave crayfish and nonphotosynthetic plant lineages*. **Mol. Biol. Evol.** 19: 1292-1302.

Acanthostega.

Lombard, R.E.; and Bolt, J.R. (1995). A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology* 38 (3): 471-495.
Whatcheeriidae

Long, JA & MS Gordon (2004) *The greatest step in vertebrate history: a paleobiological review of the fish-tetrapod transition*. **Physiol. Biochem. Zool.**, 77: 700-719.
Acanthostega, *Ichthyostega*.

Manley, GA & JA Clack (2004), *Vertebrate systematics and an outline of the evolution of vertebrate hearing organs*, **in** GA Manley, A Popper & RR Fay [eds.], **Evolution of the Vertebrate Auditory System**. Springer-Verlag, pp. 1-26.
Tetrapoda.

Milner, AC & W Lindsay (1998), *Postcranial remains of **Baphetes** and their bearing on the relationships of the Baphetidae (=Loxommatidae)*. **Zool. J. Linn. Soc.** 122: 211-235.
Baphetes, Baphetidae.

Panchen, A.L. 1973. On Crassigyrinus scoticus Watson, a primitive amphibian from the Lower Carboniferous of Scotland. Palaeontology 16: 179-193.
Crassigyrinus

Panchen, A.L. 1985. On the amphibian Crassigyrinus scoticus Watson from the Carboniferous of Scotland. Philosophical Transactions of the Royal Society of London. Series B 309: 461-568.
Crassigyrinus

Panchen, A.L. and Smithson, T.R. 1990. The pelvic girdle and hind limb of Crassigyrinus scoticus (Lydekker) from the Scottish Carboniferous and the origin of the tetrapod pelvic skeleton. Transactions of the Royal Society of Edinburgh: Earth Sciences. 81: 31-44.
Crassigyrinus

Romer, A.S. 1966. *Vertebrate Paleontology*. University of Chicago Press, Chicago. (1st ed 1933, 2nd ed. 1945; 3rd ed. 1966)
Amphibians, Systematics, and Cladistics

Ruta, M. and Bolt, J.R. 2008. The brachyopoid *Hadrokkosaurus bradyi* from the early Middle Triassic of Arizona, and a phylogenetic analysis of lower jaw characters in temnospondyl amphibians. Acta Palaeontologica Polonica 53 (4): 579-592.
Crassigyrinus

Ruta, M, MI Coates & DLJ Quicke (2003), *Early tetrapod relationships revisited*. **Biol. Rev.** 78: 251-345.
Acanthostega, *Crassigyrinus*, *Ichthyostega*, Tetrapoda,

Ruta, M., Jeffery, J. E. and Coates, M. I. 2003b. A supertree of early tetrapods. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2507-2516. . **pdf**
Crassigyrinus

Shear, WA & PA Selden (2001), *Rustling in the undergrowth: animals in early terrestrial ecosystems* **in** PG Gensel & D Edwards [eds.], **Plants Invade the Land**, Columbia Univ. Press, pp. 29-51.
Tetrapoda.

Shubin, NH, EB Daeschler, & MI Coates (2004), *The early evolution of the tetrapod humerus*. **Science** 304: 90-93.
Acanthostega, Tetrapoda, Tetrapoda.

Warren, A, 2007, New data on *Ossinodus pueri*, a stem tetrapod from the Early Carboniferous of Australia. Journal of Vertebrate Paleontology 27(4):850-862 **preview**
Ossinodus, Whatcheeriidae

Warren, A., and Turner, S. (2004). The first stem tetrapod from the Lower Carboniferous of Gondwana. *Palaeontology* 47(1):151-184.
Ossinodus, Whatcheeriidae - Overview

Zhu, M, PE Ahlberg, W Zhao & L Jia (2002), *First Devonian tetrapod from Asia*. **Nature** 420: 760-761.
Tetrapoda.

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW050703, revised MAK111112

Temnospondyli: Overview

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
`--+--Edopoidea
   `--+--Dendrerpeton
      |--Dvinosauria
      `--+--Euskelia
         |   |==Dissorophoidea
         |   |  `--LISSAMPHIBIA
         |   `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   `--+--Rhytidosteidae
               |       `--Brachyopoidea
                `--+--Capitosauria
                   `--Trematosauria
                      |--Trematosauroidea
                      `--Metoposauroidea
```

Contents

The early Permian temnospondyl *Archegosaurus* contemplates its domain. This animal was about 1.5 meters long.
Artwork by Heinrich Harder, from the card series *Tiere der Urwelt* (Animals of the Prehistoric World) circa 1916, Public domain.

Masters of rivers, lakes, swamps and watercourses, and, for a period during the Permo-Carboniferous, the terrestrial environment, the temnospondyls were the most diverse and abundant of ancient tetrapods from the late Carboniferous to the Triassic. Filling ecological roles as diverse as toads, eels, crocodiles, and long snouted marine fish-eaters, as well as guilds and ecotypes with no current representatives, such as the bizarre suction-feeding plagiosaurs, they included among their number the largest amphibians ever to live, as well as medium and smaller and more typically sized forms. And, just as dinosaurs are still with us as birds, so temnosopndyls never really died out, if the favoured hypothesis that dissorophoids are the ancestors of modern amphibians is valid. Many more pages could be written about them than the uneven coverage provided by the few included here. So, for now, here are the amazing temnospondyls.

Page Back **Unit Home** **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Temnospondyli

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
`--+--Edopoidea
   |  |--Edops
   |  `--Cochleosauridae
   `--+--Dendrerpeton
      |--Dvinosauria
      `--+--Euskelia
         |   |==Dissorophoidea
         |   |  `--LISSAMPHIBIA
         |   `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   `--+--Rhytidosteidae
               |      `--Brachyopoidea
                `--+--Capitosauria
                   `--Trematosauria
                      |--Trematosauroidea
                      `--Metoposauroidea
```

Contents

Taxa on this Page

1. Temnospondyli

Introduction

The Temnospondyls were an extremely diverse and succesful group of "labyrinthodont" tetrapods. They represent one of the three primary lines of labyrinthodont evolution, the other two being the reptilomorphs and lepospondyls. Although some temnospondyls were completely aquatic and even had external gills as adults, others probably became almost as terrestrial as reptiles, returning to water only to lay their eggs. The Temnospondyli evolved in the Early Carboniferous. Most Paleozoic forms became extinct before or during the Lopingian (Late Permian). However two aquatic Gondwanan clades, the dvinosaurs and stereospondyls, survived and even

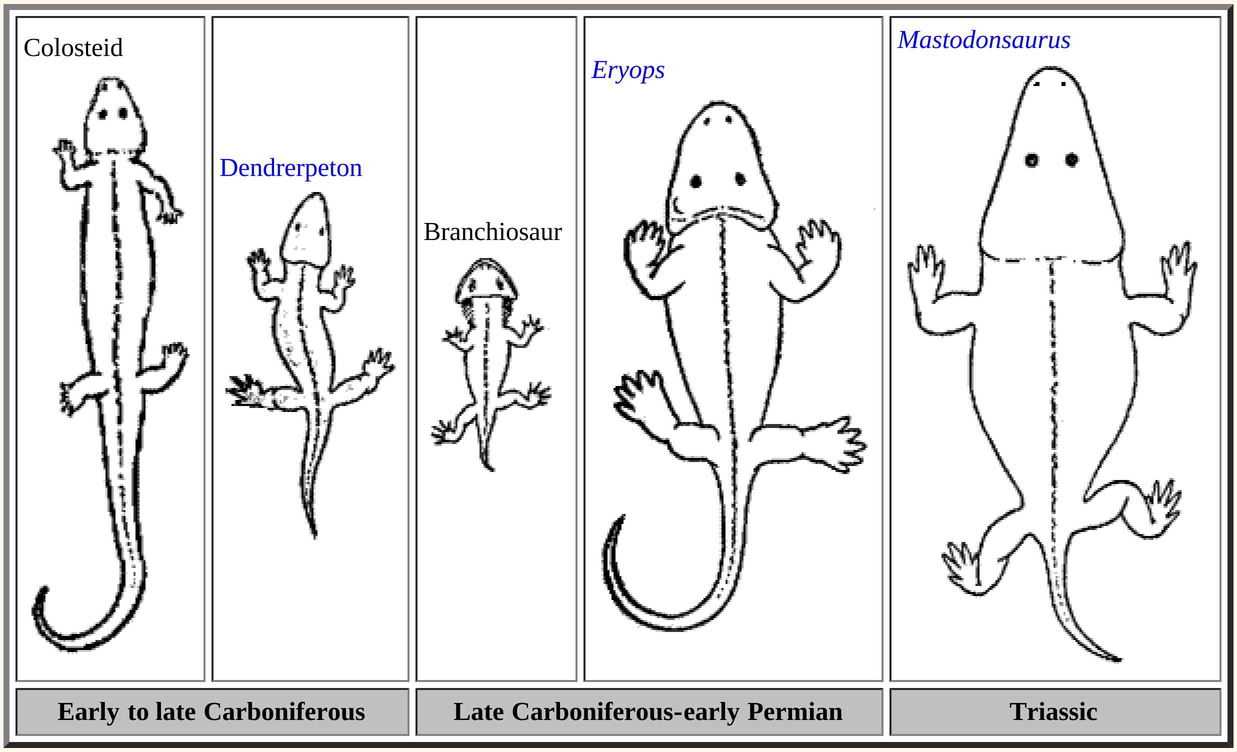
***Archegosaurus*. Early Permian period, north-central Pangea (Europe). Length 1.5 meters**

prospered in the early Mesozoic. The youngest known temnospondyl is *Koolasuchus* from the Middle Cretaceous (Barremian) of Australia.

Temnospondyls had, for the most part, relatively large heads, with rather flat, akinetic skulls. The shape of the skull was quite variable, and often distinctive. Some, like *Archegosaurus*, had the mouth drawn out into the classic "longirostrine" shape associated with reptiles which hunt small fish. Others, like *Gerrothorax*, had bizarre, wide, parabolic heads like galeaspids or other "cornuate" jawless fish. Some, *Laidleria* for example, had very flat, triangular heads with no easy parallels in any other vertebrate group, before or since.

In contrast, the temnospondyl post-cranial body plan was conservative and fairly unspecialized. The body proportions varied considerably from one group to another. As a result, we may suspect that some tended toward an eel-like style of swimming or an undulating, almost legless type of locomotion on land. Others had relatively stiff, massive bodies and presumably used their limbs for both land and water locomotion. However, no temnospondyl group developed any limb specializations as in the reptilomorph lineage. The temnospondyl fore-foot had only four toes, the hind-foot five. The vertebral structure was essentially of the primitive, intercentra and pleurocentra sort, as in the early Devonian tetrapods and osteolepiform lobe-finned fish. However there was also some variation in vertebral structure, a distinction being made between the ancestral, ratchitomous condition that characterized the majority of temnospondyls, and the more specialized sterospondylous condition of the later, aquatic, Triassic types.

Temnospondyl Evolution



Perhaps the single most successful group of non-amniote tetrapods, the temnospondyls have a long and diverse history.

Sometime in the Early Carboniferous, a lineage of early tetrapods (primitive labyrinthodont amphibians in pre-cladistic speak) gave rise to a new and important clade (or grade), the temnospondyls. Like any successful group of animals, they radiated quickly into many new forms, some of which became progressively more aquatic, while others spent more and more time on land, and others that continued a typically amphibious lifestyle.

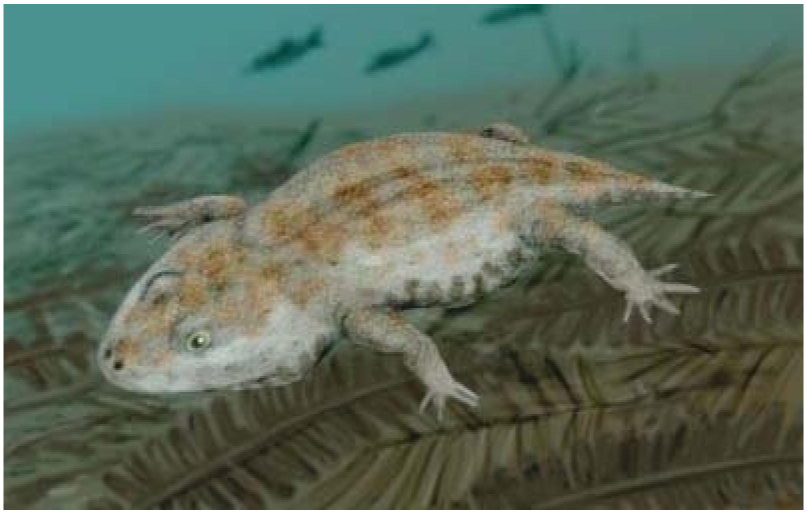
They included not only a large element of terrestrial and fresh-water aquatic faunas of the Carboniferous and Early Permian, and semi-aquatic and aquatic from the Middle Permian to the Late Triassic, and eventually (beginning in the Triassic), modern amphibians.

The first proto-temnospondyl - like species were fierce scaly aquatic animals, rather like a cross between a salamander and a moray eel. These were the Colosteids. From these arose medium to large-sized swamp dwellers known as Baphetids, and from these in turn, perhaps via forms like *Eucritta*, the first true temnospondyls.

The early temnospondyls therefore arose out of the original tetrapod radiation of the Tournaisian and Visean (early Carboniferous) epoches.

They included a number of similar, broadly crocodile-like forms, about a meter to one and a half meters in length, but quickly diversified intoa large range of forms. These animals were at their height in the tropical coal-swamp biome of the middle Carboniferous (late Visean epoch), where they shared the waterways with even bigger and fiercer eel-like animals. Already co-existing with the Colosteids during the late Visean were the massive *Eryops* and the small and rather inoffensive-looking *Dendrerpeton*. Unlike the Colosteids, these were terrestrial, or at least semi-aquatic, with larger legs stiffer bodies.

The heyday of the Paleozoic temnospondyls was during the late Carboniferous and early Permian periods. During this time there was a rich diversity of these creatures, some with huge heads and armour plates, and adapted to a terrestrial existence, such as the Dissorophid *Cacops*, others with strong robust limbs and large heads, but still semi-aquatic and rather like a cross between a crocodilian and an enormous frog (*Trematops*, *Eryops*), others aquatic with long bodies and armoured with a protective coating of scales (*Trimerorhachis*) while others again retained external gills even as adults and were unable to leave the water (*Branchiosaurus*).

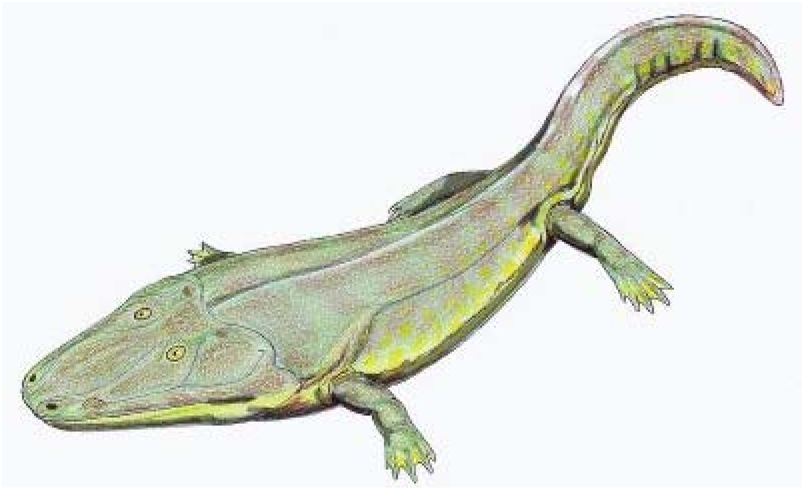


Amphibamus grandiceps, a dissorophoid - Late Carboniferous (Moscovian) of Illinois. This animals is considered to have been close to the ancestry of moidern amphibains. Length about 20 cm. Life reconstruction, by Arthur Weasley (Wikipedia)

The increasing aridity of the late Permian world, brought about the single landmass (the Pangean supercontinent) and disruption of rainfall patterns, and the sucess of the reptiles, was not the best news for these large tetrapods, and they retreated to the swamps, ponds and river courses. Originally these Late Permian temnospondyls had a crocodile-like apperance and were probably still quite capable of climbing out on land (*Actinodon*, *Archegosaurus*, *Platyoposaurus*), but these transitional types were soon replaced by their descendents, the large to very large, completely aquatic stereospondyls. One lineage of stereospondyls, the Trematosauridae, actually took up a life in the oceans, the only stem tetrapods ever to have done so. The Trematosaurs underwent quite an evolutionary radiation, and the various genera are distinguished by the proportions and shape of their skulls.

During this same period, other Stereospondyl lines continued to thrive, but also evolved in more extreme directions. Because these creatures lived their entire lives in water (although they were probably able to climb out on land for short periods) their skeletal structure became increasingly cartiliginous, and their heads increasingly large and flat. Among the Capitosaurids and Mastodonsaurids the head became so large and flat in fact that it is difficult to see how the animals could have moved their lower jaws. Presumably, they only opened their mouths by titling back the whole head.

Both large and small aquatic Temnospondyls continued as an important part of the freshwater ecosystem right up until the end of the Triassic



Cyclotosaurus, a capitosaur, Triassic (Carnian) of Europe. Capitosaurs were one of a several groups of large flat-headed forms that inhabited Triassic watercourses. Length 2 to 4 meters. Life reconstruction, by Dmitry Bogdanov (Wikipedia)

period, even co-existing with the formidable crocodile-like phytosaurid reptiles. Important at this time were the Metoposaurs of Laurasia (Europe and America), which evolved from completely different ancestors to look strikingly like the Capitosaurs. Indeed, the only easy distinction is that the Metoposaurs had eyes further forward on the skull.

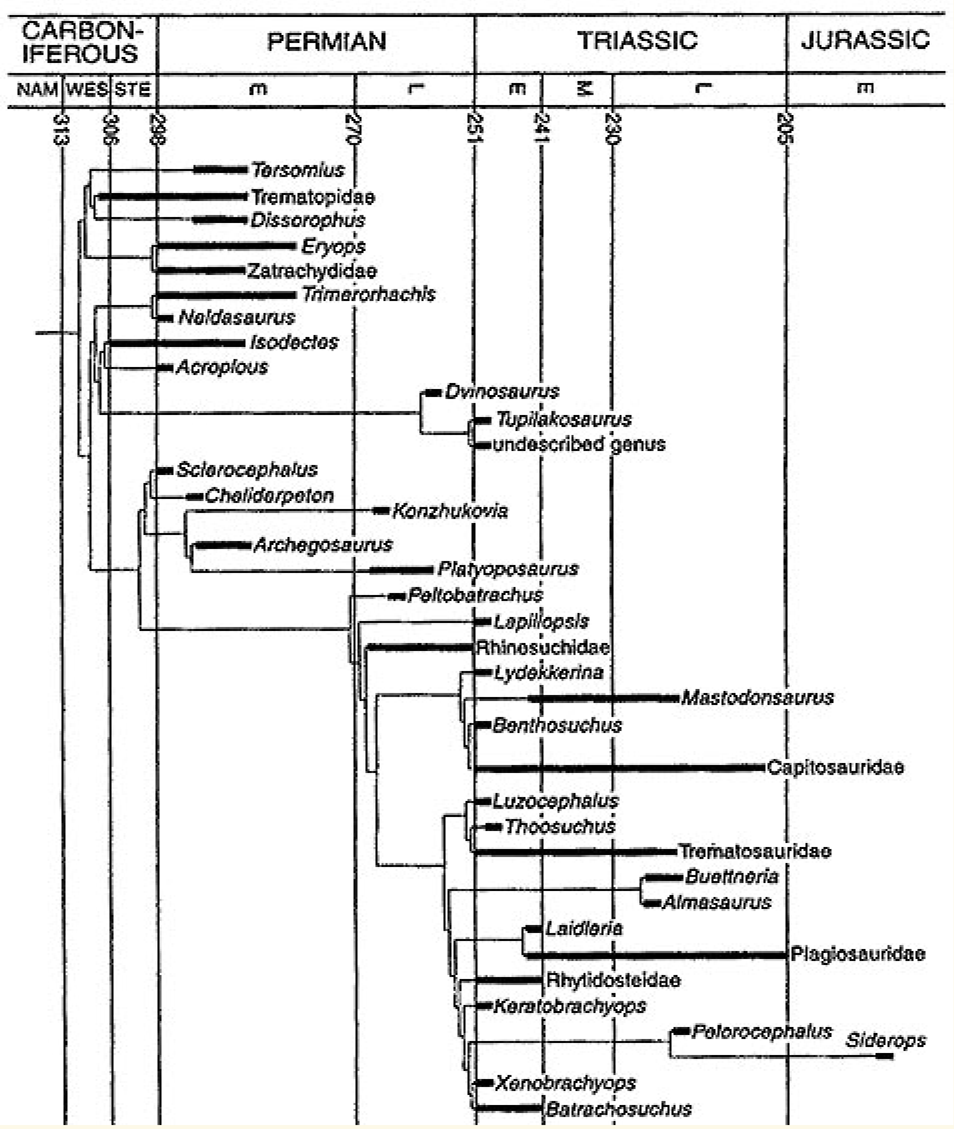
The terminal Triassic extinction killed off all the big temnospondyls, along with the phytosaurs. Only a few, short-headed stragglers making it through to the Jurassic the Brachyopoids. These survived in China and Australia (the easternmost parts of north and south Pangea respectively), perhaps protected by geographical isolation. Safe from enemies, they grew to be as big as Capitosaurs. The last temnospondyls were two and a half to three meter long giants who sought refuge in the Cretaceous polar rift valleys of south-east Gondwana, where the climate was too cold to support crocodiles, their main predators.

MAK090710

Temnospondyl Systematics

Traditionally, there were only two temnospondyl suborders, the Ratchitomi and the Stereospondyli, which were determined according to vertebral type, and these are mentioned in the older books. Romer provided a third suborder, the fish-eating marine-going trematosaurs. Other paleo-tetrapod authorities such as Nilsson and Panchen removed the short-headed Peltobatrachidae and Plagiosauridae from the Brachyopoids and placed them in a seperate order. Later writers like Carroll and Benton did away with the ratchitome - sterospondyl classification altogether, arguing that the sterospondyls were an artificial (polyphyletic) group, the stereospondylous condition having evolved seperately a number of times.

However, the relationships between the different temnospondyl families, and sometimes even the question of which family goes in which superfamily, remained very controversial. Many of these problems in temnospondyl



taxonomy were addressed by Yates & Warren (2000) in comprehensive cladistic analysis from which the following cladogram is taken.

In this diagram, the geological period is shown on the top. The known occurance of taxa (genera and families) in the fossil record is indicated by solid bars. Thin lines indicate hypothetical ancestry (cladistic techniques forbid deriving one known monophyletic genus or family from another, rather, both are derived from a hypothetical "most recent common ancestor", which gives the branching pattern as shown above).

Several things need to be said about this diagram. First, not every temnospondyl taxon is included. Many known types are not shown here. However, most of the important forms are shown. Secondly Yates and Warren revive the monophyletic Trematosauria and Stereospondyli, but replaced the Ratchitomi with the clades Euskelia and Limnarchia. And third, not everyone agrees with these particular phylogeny. A common alternative for example is to have the Dvinosauria as a very early and quite distinct clade, prior to the Euskelia and the higher "Limnarchia" (several of the dendrograms displayed here show this option)

Descriptions

Temnospondyli: *Dendrerpeton.*

Range: from the Early Carboniferous

Phylogeny: Tetrapoda*: (Lepspondyli + Reptilomorpha) + *: *Eucritta* + (Edopoidea + (*Dendrerpeton* + (Euskelia + Limnarchia))).

Characters: 20- 300 cm; large heads with akinetic skulls; skull triangular to parabolic, or longirostrine; skull heavily ornamented; sensory line grooves may be present; **$** palatal tusks common; **$** very large interpterygoid fenestrae;

tendency to develop additional cranial bones along midline (*e.g.* internasal, interfrontal, interparietal); "otic notch" frequently present, but probably did not support tympanum; "vertebrae 'rhachitomous' (with a large, dorsal, crescentic intercentrum and a small, dorsal, paired pleurocentrum) to stereospondylous (without an ossified pleurocentrum, although this element may be retained in a cartilaginous state)" [from Temnospondyli]; **$** ornamented scapula; digits 4 (manus), 5(pes); amphibious or aquatic; some forms even with probable external gills.

Links: Dendrerpeton and Joggins, Nova Scotia; Temnospondyli; Basal Temnospondyli; Historický vývoj (Czech); Phylogeny and Apomorphies of Temnospondyls. 010806.

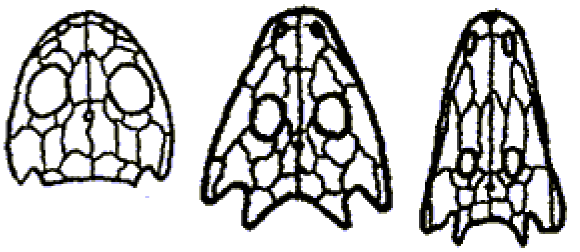


Figure 2. Larval, juvenile and adult skulls of Parotosuchus in dorsal view. Modified from Steyer (2000).

Discussion: One of the nice things about temnospondyls is that there are a great many of them. Not only did they manage to diverge into a great many species, but the more successful groups are known from numerous specimens. Thus, it is possible to examine aspects of this taxon which cannot normally be studied in paleontological material -- such as developmental biology. In several cases, there are so many specimens known that it has become possible to piece together the ontogenesis of temnospondyls. Temnospondyls are normally thought of as having three life phases: (a) a larval stage, probably aquatic and gill-breathing, (b) a juvenile transition phase; and (c) an adult form. However, in comparing species, taxonomists have largely restricted themselves to the adult morphs.

Recently, Jean-Sébastien Steyer, a graduate student at the Muséum National d'Histoire Naturelle in Paris, asked himself what would happen if one *didn't* discard all of the developmental data. Steyer (2000). Rather than (literally!) throwing out the babies with the bath water, Steyer set out to compare six different in-group taxa (plus *Dendrerpeton* as the out-group) whose developmental course was particularly well charted. The particular taxa and results were not particularly novel in this case, and were fully consistent with Yates & Warren (2000). As intended by Steyer, the point of real interest was not the results, but the method -- a method which has some very exciting possibilities.

In brief, Steyer scored the same 40 characters for each stage of each species studied, in effect treating a larval *Apateon* as separate species from the juvenile and adult forms for purposes of scoring. The scores were generally based on *Dendrerpeton* as the out-group, although there were some missing data and a few other exceptions. Separate cladograms ("ontotrees") were then generated for each morph across all species. Finally, a total evidence cladogram was generated, using all three sets of data. Interestingly, the three ontotrees were quite different. However, the combined data generated a topology which was identical with the larval cladogram and was quite robust (CI = 0.72).

Steyer was kind enough to discuss some of the fine points of the technique with me. In the process, I came to the conclusion that this method is at least as powerful as Steyer hopes it will be. In fact, one cannot easily think of a technique more likely to resolve the intractable deep nodes in the neornithine or mammalian radiations than phylogenetic taxonomy based on developmental biology. Haeckel's Law is not a "law," but it is certainly a frequent observed phenomenon. That is, we have good reason to hope that a systematic analysis of ontogeny will at least help us recapitulate (actually, recalculate) phylogeny. Conveniently, the living embryos of those species are around for all to see, so the work may be much more detailed -- and much easier -- than piecing together the shattered dermal bones of Carboniferous tetrapods.

But, first, there are some surprisingly thorny theoretical questions to be resolved. For example, just what is a synapomorphy in this context? Normally, the textbook answer is: a shared derived characteristic of a clade. Like a family recipe for lamb curry, or a tendency to practice obscurity for its own sake, some things mark a family of humans or other vertebrates and can duly be scored to produce cladograms. But what if say that our family is the one with beards? "So what?", you say, "Lots of people have beards." But no, I explain, in my family *everyone* has a beard: women, small children, parakeets, the lot. Thus the question of synapomorphy is more complex than presence or absence. It matters when those characters appear. And, if otherwise normal small children have beards in a family, would I score the beards of adult males in that family as a plesiomorphic feature of normal humans (state 0), or as the continuation of a peculiar apomorphy of my family?

Let us take a look at a very concrete example. In Figure 2, it is evident that the *Parotosuchus* has a large otic notch as a larval form, a notch which is still quite noticeable as a juvenile. This is a derived state. *Dendrerpeton*, the outgroup for almost all purposes, has little if any otic notch as a larva or juvenile. However, the adult morph of *Parotosuchus* has a small, narrow otic notch which looks very similar to the small, narrow otic notch of the adult *Dendrerpeton*.

Steyer scores the otic notch of Parotosuchus 1 (larval), 1 (juvenile), and 0 (adult). But, if the otic notch of the adult is developed from the open notch of the juvenile in *Parotosuchus*, rather than from a notchless skull as in *Dendrerpeton*, is this really the same state or a developmental homoplasy?

Perhaps the latter is a better choice. That is, "once derived, always derived" is a reasonable rule of thumb. We are essentially dealing with developmental vectors, not the usual scalar quantities of a typical cladistic study. Each stage-specific character not only has a definite description, but also a developmental direction. The adult otic notch *looks* the same, but it developed from the opposite direction. Once derived, a character does not "underive." In normal cladistics, we may discover, *ex post*, that a what appeared to be a plesiomorphy was actually a reversal. But the calculation has already been performed. Here, we know *ex ante* that the notch is developmentally different from the notch of *Dendrerpeton*, so it should be scored differently from the beginning, and before the tree is calculated.

But Steyer may yet have the better argument. Consider the example of the beards. What if the beards of the women and children (and, of course, the parakeets) are developmental neomorphs brought about by some unique hormonal aberration, while the beards of adult males are the result of the normal pattern of development reasserting itself? How can I justify scoring the adult males as derived just because the children are?

Ultimately, it may be a judgment call. Or one might separately score the direction and value, so that the 1 -> 0 transition itself is given a score different from the 0 -> 0 development of *Dendrerpeton*. The problem is that this practice clearly violates the rule of independence. That is, the scoring of transitions depends in a simple way on the underlying states, with the result that the states may effectively be double-counted. This may distort the results significantly. In Steyer's 3-stage study, for example, scoring transitions would essentially require us to count the middle, juvenile state twice as often as the larval and adult forms (i.e. la->**ju** and **ju**->ad). This is a form of weighting which has no obvious theoretical justification.

This is a powerful technique with a great deal of promise, but working out exactly how to use it is not an easy proposition.

References: Steyer (2000); Yates & Warren (2000).

Page Back | Unit Home | Page Top | Page Next

checked ATW060327

Page Back	Unit Home	Unit Dendrogram	Unit References	Taxon Index	Page Next
Unit Back	Vertebrates Home	Vertebrate Dendrograms	Vertebrate References	Glossary	Unit Next

Temnospondyli: Assorted primitive (basal) temnospondyls

Abbreviated Dendrogram

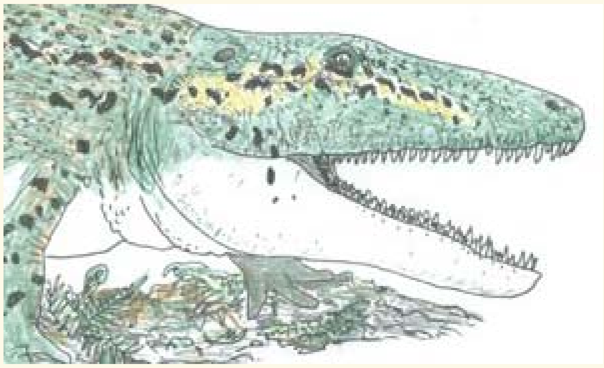
```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
 `--+--+--Edopoidea
     |  |  |--Edops
     |  |  `--+-Cochleosauridae
     |  `--Saharastega
     `--+-+--Balanerpeton
         |  `--+--Dendrerpeton
         |     `--+--Eugryinus
         |        `?--Dvinosauria (if basal -
Ruta et al 2007)
         `--+--Capetus
            |--+--Iberospondylus
            |   `--Euskelia
            |       |==Dissorophoidea
            |       |     `--LISSAMPHIBIA
            |       `--Eryopoidea
            `--+?--Dvinosauria (if Limnarchia -
Yates &Warren 2000)
                `--Stereospondyli
                    |--Rhinesuchidae
                    `--+--Lydekkerinidae
                       |--+--Plagiosauroidea
                       |   `--+--Rhytidosteidae
                       |       `--Brachyopoidea
                       `--+--Capitosauria
                           `--Trematosauria
                              |-
-Trematosauroidea
                              `-
-Metoposauroidea
```

Contents

Taxa on this Page

1. *Balanerpeton* X
2. *Capetus* X
3. *Dendrerpeton* X
4. *Iberospondylus* X
5. *Saharastega* X

Assorted basal temnospondyls



Capetus palustris, life reconstruction, copyright Darren Naish © 2007

From Darren Naish's blog *Tetrapod Zoology*: Temnospondyls the early years (part II) (July 9, 2007):

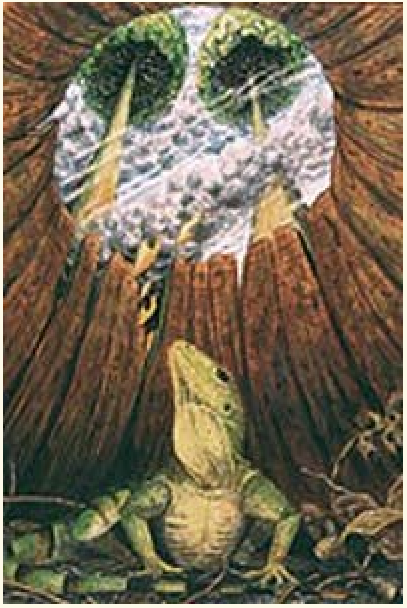
Last time we looked at the edopoids, perhaps the most basal temnospondyl clade: here we look at the rest of the basal forms. Scary predators, marine piscivores, late-surviving relics, and some unfortunate beasts burned alive in forest fires...

Studies on temnospondyl phylogeny mostly agree that 'post-edopoid' temnospondyls form a clade, the most basal members of which include *Capetus*, *Dendrerpeton* and *Balanerpeton* (Milner & Sequeira 1994, 1998, Holmes *et al*. 1998, Ruta *et al*. 2003a, b) [though some workers have found some of these taxa to be more basal than edopoids (Steyer *et al* 2006]. In contrast to the condition in edopoids, the interpterygoid vacuities of 'post-edopoids' are rounded at their anterior ends, the jugal (the bone that forms the cheek region) is shortened, and the configuration of skull bones is overall less archaic and fish-like.

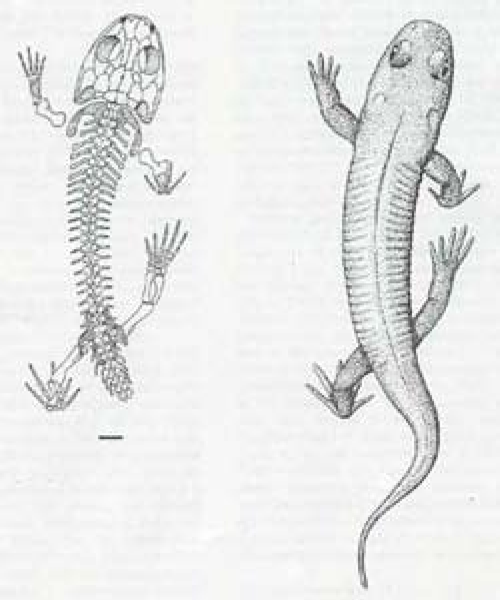
Among these basal 'post-edopoids', *Dendrerpeton* (from the Late Carboniferous of Nova Scotia and Ireland) had a rather large skull with laterally facing orbits, a short body, and well-developed, robust limbs. It lacked lateral line canals and grew to c. 1 m. These features suggest that it was predominantly terrestrial (Holmes *et al*. 1998). Several species have been named (Milner 1996). Studies of a well-preserved, three-dimensional ear indicate that *Dendrerpeton* had a frog-like tympanum (ear drum) suited for the perception of airborne sounds (Robinson *et al*. 2005). This discovery provides support for the idea that lissamphibians descend from temnospondyls (a subject we'll come back to much later), and indicates that at least some basal temnospondyls were listening to noises. But what were they listening to? Were they vocalizing, perhaps during the breeding season? It's previously been argued that the temnospondyl stapes was too massive to support a tympanum (see Laurin & Soler-Gijón 2006), so note that we have to be cautious in inferring the presence of a tympanum in *all* temnospondyls.

The Canadian *Dendrerpeton* specimens come from the famous Joggins Tree Stump Locality where the fossils of several tetrapod taxa (and the earliest land snails) have been discovered inside the hollowed trunks of lycopsid trees. It used to be thought that the animals had fallen into these natural traps and eventually died there of starvation, but the presence of abundant charcoal within the deposits now raises the possibility that the animals were taking refuge from forest fires, and that at least some of these unfortunate creatures were roasted alive (Falcon-Lang 1999, Scott 2001) [the adjacent picture depicts the early reptile *Hylonomus*, trapped in a hollow tree stump and about to be killed as a forest fire advances overhead].

Another basal temnospondyl is *Balanerpeton woodi* from the Viséan of East Kirkton in Scotland, a famous locality that has yielded a phenomenal diversity of Carboniferous invertebrates, fishes and early tetrapods. With a length of about 50 cm, *Balanerpeton* was superficially like a big salamander but it was odd in that, while the 40-42 teeth lining each half of the upper jaw were small, the 25-30 in

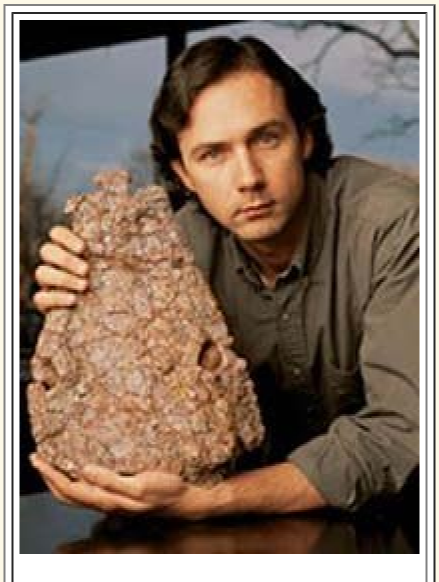


each half of the lower jaw were much longer. The absence of lateral line canals, ossified wrist and ankle bones, and the apparent presence of eyelids indicate that it also was a terrestrial animal, although its larvae were aquatic (Milner & Sequeira 1994) [*Balanerpeton* skeletal reconstruction and life restoration immediately below is from Milner & Sequeira (1994), and borrowed from here].



Also somewhere around the base of Temnospondyli was *Capetus palustris* from the famous Upper Carboniferous Nýrany desposits of the Czech Republic: this is one of the richest Late Carboniferous fossil sites in the world, yielding at least 700 tetrapod fossils, discovered from the 1870s onwards. Previously, *Capetus* was regarded by some authors as an edopoid, close either to *Edops* or to the cochleosaurids, but recent studies have shown that it is not an edopoid, being closer to *Balanerpeton* (Steyer *et al*. 2006).

Capetus was a fairly scary looking, broad-headed predator with a deep posterior lower jaw: its skull was about 40 cm long, suggesting a total length of c. 1.5 m. As Sequeira & Milner (1993) noted, this makes *Capetus* one of the largest tetrapods in the Nýrany assemblage. Its teeth were mostly subconical, but those in the anterior part of the lower jaw seem to have been slightly laterally compressed, and possibly with weakly developed keels. As is the case in edopoids and some other basal temnospondyls, its skull bones lack lateral line canals. Sequeira & Milner (1993) suggested that *Capetus* was an alligator-like amphibious predator specializing on slow-moving tetrapod prey, and that it exploited a different lifestyle from that pursued by its contemporaries, the cochleosaurid *Cochleosaurus*, and the baphetids *Baphetes* and *Megalocephalus*. It was apparently rare in the fauna, with only eight fossils out of 700 from the Nýrany assemblage belonging to this taxon.



Among the most surprising of the basal temnospondyls is the recently described *Saharastega moradiensis* from Niger. The big deal is that - while *Saharastega* is apparently way down near the base of Temnospondyli (and hence close to the Carboniferous taxa *Balanerpeton* and *Capetus*) - is it from the Upper Permian Moradi Formation, and hence was very much a 'late-survivor', hanging on for long, long after other basal forms had bit the dust. As we saw in the edopoid article, the Moradi Formation seems to contain a strongly provincial, relictual fauna. *Saharastega* had a fairly nondescript, flattish and subtriangular skull with widely separated and laterally-facing orbits located close to the skull margins. The tabular horn - a pointed projection, growing from the tabular bone at the rear corner of the skull - was particularly odd in this taxon in being directed laterally, rather than posteriorly, and the jaw joint was positioned unusually anteriorly. These peculiarities suggest that *Saharastega* was doing something interesting, but we don't know what that was. Although originally argued to belong to Edopoidea (Sidor *et al*. 2005), restudy has shown it to be outside of this clade (Steyer *et al* 2006).

Christian Sidor with *Saharastega* skull.

Another basal temnospondyl, the Upper Carboniferous Spanish taxon *Iberospondylus schultzei*, is interesting in that it was discovered in sediments deposited in coastal marine waters (Laurin & Soler-Gijón 2001, 2006). In contrast to the taxa we've looked at so far, it possesses lateral line canals, and therefore was very likely to have been aquatic (though we'll return later to how reliable lateral line canals are in demonstrating aquatic habits). Furthermore, the articulated condition of one of the specimens indicates that little post-mortem transport had occurred, so *Iberospondylus* was local to the environment in which it was preserved. It's been known for some time that at least some temnospondyls were marine animals (and we'll look at these other marine temnospondyls in a later post), but the basal position of *Iberospondylus* within temnospondyl phylogeny suggests that members of the group were able to inhabit the marine environment very early on in the group's history. As Laurin & Soler-Gijón (2001) argued, there are indications that this might have been true of even more basal tetrapods: if so, this would explain how Devonian tetrapods became near-globally distributed so early on in their evolution [*Iberospondylus* skull shown in adjacent image].

This ends our look at the most basal members of Temnospondyli - or, at least, it does according to the phylogenetic schemes I've decided to follow. You will note that at least some of these animals, including the edopoids, *Dendrerpeton* and *Balanerpeton*, were apparently terrestrial or mostly terrestrial. It is inferred that a total length of perhaps 40 cm or so was primitive for the group, but a size of 1.5 m or more was evolved within Edopoidea, and also exhibited by broad-skulled *Capetus*. Some basal temnospondyls were aquatic, and even marine, and some hung on until as late as the Late Permian: about 40 million years longer than we'd thought prior to 2005.

Problems in basal temnospondyl relationships

Although there is agreement on what constitute basal (primitive) and what the more advanced memebers of the temnospondyl family tree - for example both the edopoids and the various genera recviewed here are all recognized as basal - the precise evolutionary relationships among these various basal forms remain controversial. It may be that, instead of a number of well demarcated groups, there is an evolutionary "bush" of many similar forms during the Carboniferous, all of which share a number of primitive features, and perhaps also evolved specialized features in parallel. No doubt future discoveries will clear things up somewhat, but for the present we are faced with a number of conflicting cladograms and evolutionary trees. A few of these are shown below:

```
-+-Edops
 | `-+- Cochleosaurus
 |   `- Chenoprosopus
 `-+- Capetus
   |-+- Trimerorhachis
   `-+- Sclerocephalus
     `-Onchiodon
(Eryopidae)
```

Sequeira & Milner 1993

```
-+-+- Balanerpeton
 | `-+- Dendrerpeton
 |   `-+- Capetus
 |     `-+-+- Edopidae
 |       | `- Cochleosauridae
 |       `-+- Iberospondylus
 |         `-+- Eryopoidea
 |           `- Dissorophoidea
 `- Limnarchia
```

Laurin and Steyer 2000

```
-+- Baphetids (outgroup)
 `-+- Balanerpeton
   |- Capetus
   `-+- Saharastega
     `-+- Edopoidea
```

```
-+- Greerpeton
 `-+- Proterogyrinus
   `-+-+-Saharastega
     | `-+- Edops
     |   `- Chenoprosopus
     `-+- Capetus
       `-+-+- Dendrerpeton
         | `- Balanerpeton
         `-+- Trimerorhachis
```

```
-+- Edopoidea
 `-+-+- Dendrerpeton
   | `- Balanerpeton
   `-+- Trimerorhachis and
Dvinosauria
     `-+- Capetus
       `-+- Saharastega
         `-+- Iberospondylus
```

```
     `- Eryops
```

Steyer *et al*. 2006

```
                 `-+- Zatrachys
                   `-+-
Sclerocephalus
                     `- Eryops
```

Damiani *et al* 2006

```
                   `-+- Palatinerpeton
                     `-+- Eryops, Euskelia
                       `- Stereospondyls etc
```

Ruta *et al* 2007

For now, we have adopted the sequence of edopoids first (shown on the previous page) and then various assorted forms like *Dendrerpeton* (this page), and then higher temnospondyls but this arrangement could just as easily been reversed (e.g. Steyer *et al*. 2006, above). Or as a third option, there may be some very basal forms, then the edopoid clade, then some even more derived but still basal lineages, and finally the "higher" temnospondyls (e.g. Laurin and Steyer 2000 excluding the Limnarchia). And until there's some serious resolution of these problems, we just have to resort to inserting question marks!

MAK090710

Descriptions

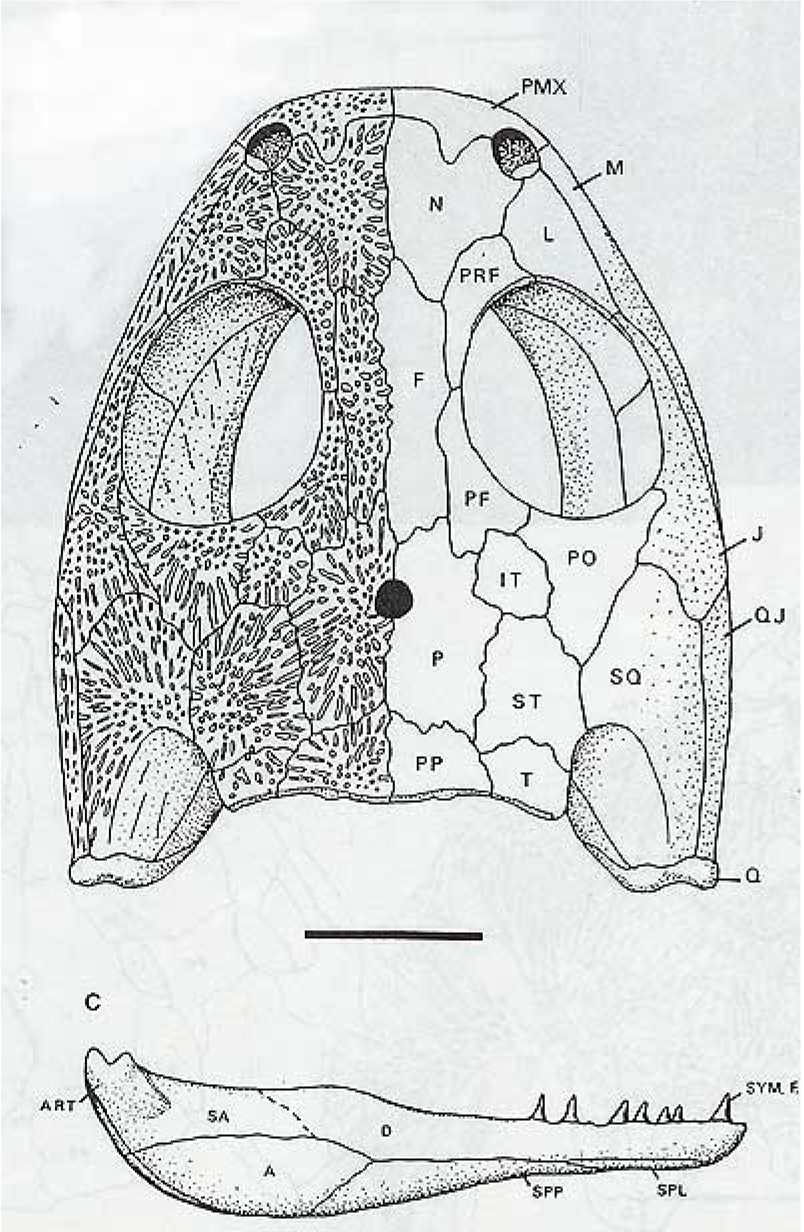
***Balanerpeton woodi*:**

Range: Early Carboniferous (Visean) of East Kirkton , Scotland (Central Euramerica)

Phylogeny: Temnospondyli::: ((:::(Euskelia + Limnarchia)) + *) - See comments on early temnospondyl phylogeny

Characters: Large external nares, large interpterygoid vacuities, ear with large tympanic membrane with rod-like stapes, absence of lateral line sulci, ossified carpals and tarsals (Milner & Sequeira 1994, although Laurin & Soler-Gijón 2006 reject the idea that many temnospondyls possessed a tympanum).

Comments: Named after its discoverer Stanley Wood, *Balanerpeton woodi* is the most common tetrapod iwhose remains hare found at the East Kirkton locality. It appears similar to *Dendrerpeton*. The structure of the ear suggests the ability to hear high-frequency sound. This was clearly a terrestrial animal; not only is the locality a terrestrial one (terrestrial arthropods but no fish are known from East Kirkton), but *Balanerpeton* lacked lateral line sense organs or ossified branchial system, the bony (rather than

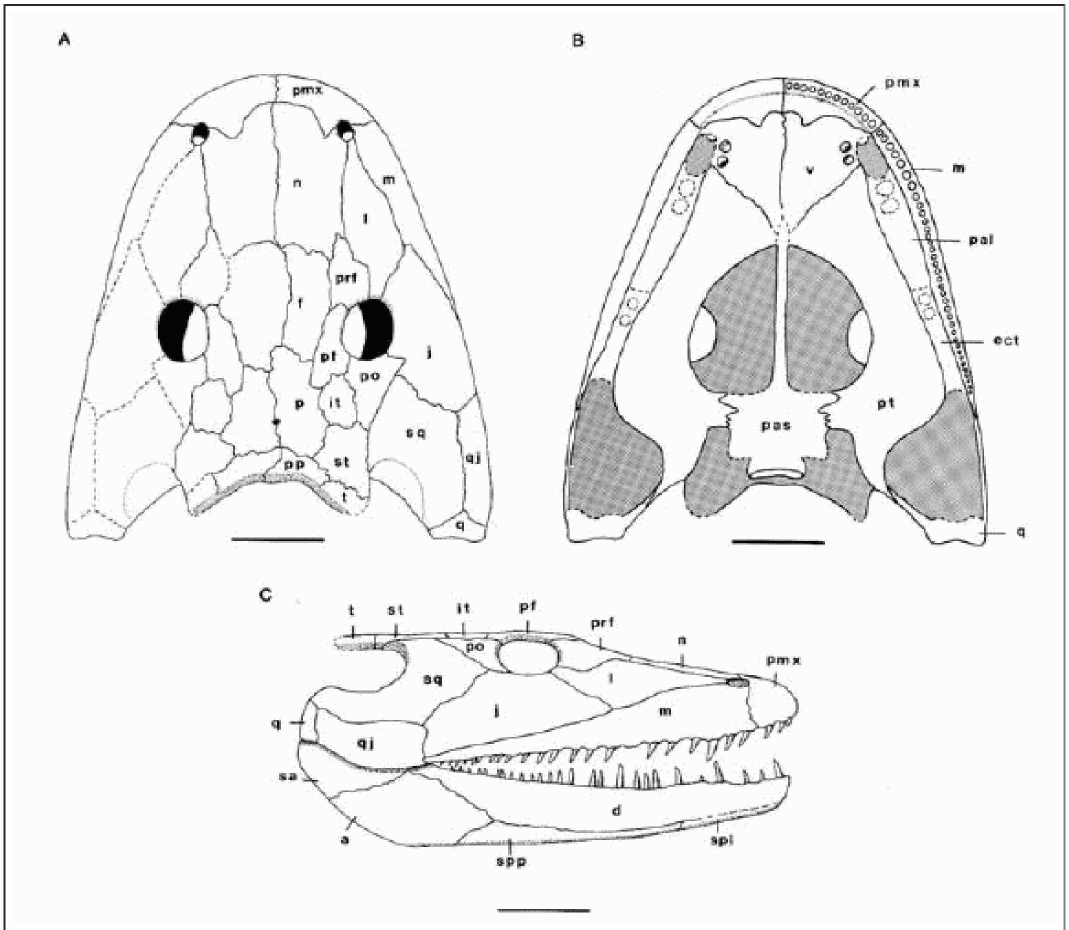


Balanerpeton woodi, reconstruction of skull; from Milner & Sequeira 1994 (via Tetrapoda - Balanerpeton) cartiligenous) wrists and ankles, and seems to have possessed eyelids.

References: Milner & Sequeira 1994

Links: Tetrapoda - Balanerpeton, Wikipedia

MAK090723



Capetus palustris, reconstruction of skull of large specimen in dorsal (A), palatal (B), and lateral (C) views. Scale bar is 5 cm. Sequeira & Milner1993 p.672

***Capetus palustris*:**

Range: Late Carboniferous (Westphalian D - Late Moscovian) of Nýrany, Czech Republic

Phylogeny: Temnospondyli::: ((:::(Euskelia + Limnarchia)) + *) - See comments on early temnospondyl phylogeny

Size. Skull length of upto 40 cm. Sequeira & Milner 1993 estimate from there a total length of 1.5 meters, although if we assume *Balanerpeton* or *Dendrerpeton*-like proportions, the length was probably a little larger.

Comments: A generalized basal temnospondyl, it has no features that would place it either with the Edopoidea or with the Eryopoidea. Instead it would seem to be a transitional form more advanced than the former but not as specialized as the latter. Shared its environment with another large temnospondyl, *Cochleosaurus*. It was among the largest animals of its environment, and probably filled an *Eryops*-like role of amphibious apex preditor.

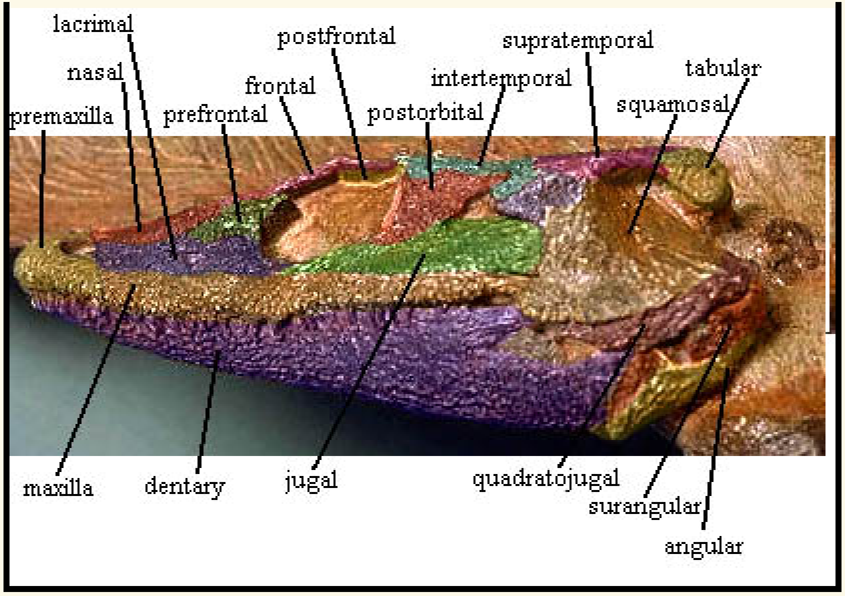
Reference: Sequeira & Milner 1993

MAK090724

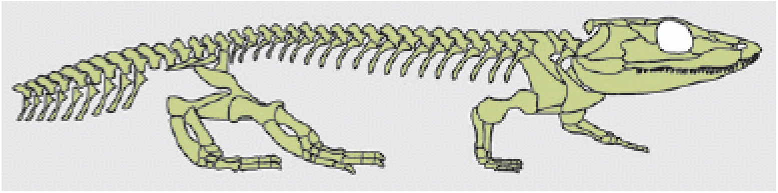
***Dendrerpeton*:**

Range: Early? to Late Carboniferous of North America & Ireland(?)

Phylogeny: Temnospondyli::: ((:::(Euskelia + Limnarchia)) + *) - See comments on early temnospondyl phylogeny



Characters: Up to 100 cm; large laterally facing orbits; **$** jugal narrowing to a point, making a point contact with the lacrimal; large, rounded "otic notch" in squamosal; stapes massive [suggesting support structure, not related to hearing -- but the "massive stapes" may be controversial, see Biology 356]; possible lanceolate expansion on anterior tip of cultriform process; lateral line sulci absent; short presacral column of 24 vertebrae, less than twice skull length; large stout limbs.



Skeleton of *Iberospondylus Dendrerpeton*, from diagram in Schoch 2008 p.221

Note: according to one source, these characteristics "suggest a terrestrial lifestyle distinct from the aquatic and semiaquatic adaptations of most contemporary Carboniferous amphibians"

Image: photograph colorized and labelled per the diagram at Dendrerpeton and Joggins, Nova Scotia.

Links: Dendrerpeton and Joggins, Nova Scotia; Joggins Cliffs; Biology 356; Phylogeny and Apomorphies of Temnospondyls; Fundy Geological Museum, Paleontology, Fossils, Vacation ...; Localities of the Carboniferous-; Ontogeny and phylogeny in temnospondyls- a new method of analysis (pdf of Steyer, 2000). ATW031216.

Skull of *Iberospondylus schultzei*, from La radiation évolutive des stégocéphales permo-carbonifères (Michel Laurin)

Iberospondylus schultzei:

Range: Late Carboniferous (Stephanian C - Early Gzhelian) of Spain (Puertollano Basin.)

Phylogeny: Temnospondyli::: Euskelia + * - synapomorphies indicate that *Iberospondylus* is more closely related to eryopoids and dissorophoids than to edopoids, although the phylogeny, like others on temnospondyls, is not robust (Laurin & Soler-Gijón 2006). See also comments on early temnospondyl phylogeny

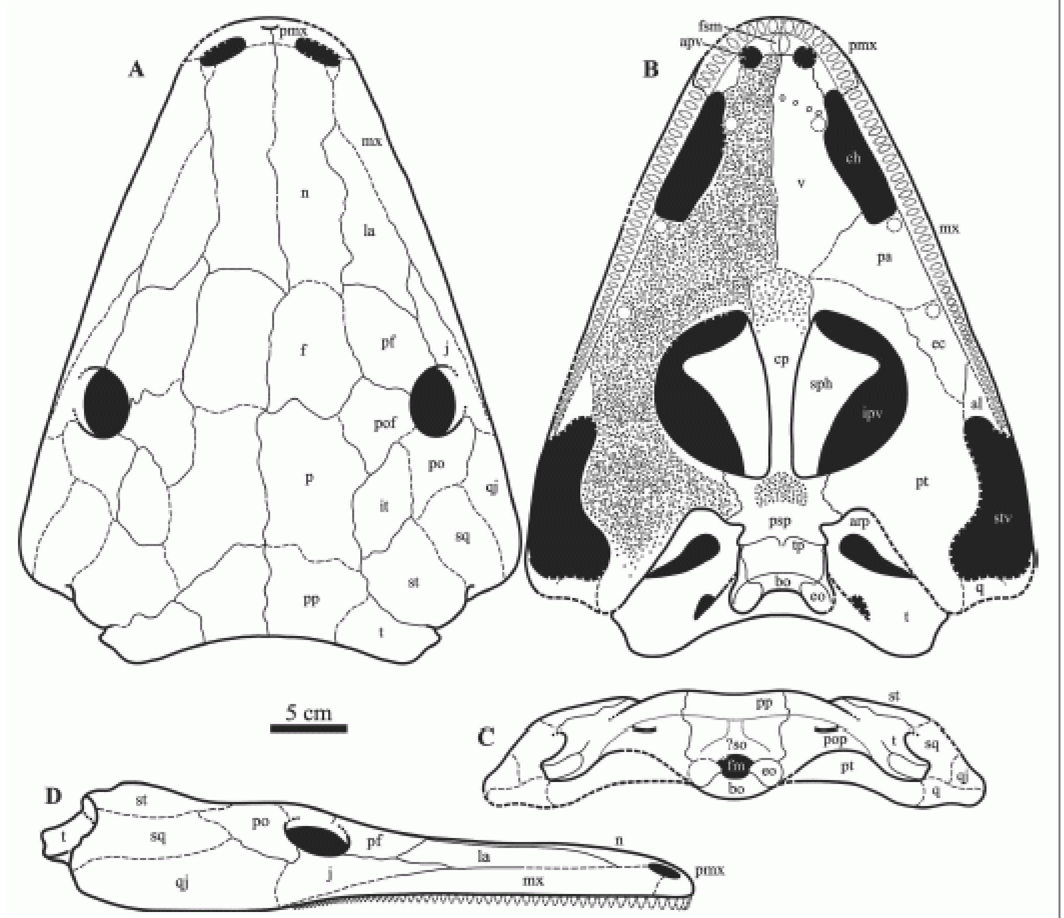
Comments: Previously all Permo-Carboniferous amphibians were thought to have been fresh-water only, but *Iberospondylus* apparently lived in a coastal marine environment. Spanish The first and to date only known occurrence of a Paleozoic amphibian in Spain.

References: Laurin & Soler-Gijón 2001, Laurin & Soler-Gijón 2006 - abstract.

MAK090723

Saharastega :

Range: Late Permian (Wuchiapingian?) of Niger (Moradi Formation|.



Reconstruction of the holotype skull of *Saharastega moradiensis* in dorsal (A), palatal (B), occipital (C), and lateral (D) views. There is little or no evidence for the presence of palatal fangs, although they are tentatively included in the reconstruction. Scale bar is 5 cm. Damiani *et al* 2006 p.564

Phylogeny: Here there are two options to choose from:

Damiani *et al* 2006: Temnospondyli:: (*Capetus* + (Euskelia + Limnarchia)) + (Edopoidea + *)
i.e. *Saharastega* and Edopoids form a clade which is the sister group to all other Temnospondyls; in other words the most primitive or basal outshoot of the temnospondyl ancestry

or Steyer *et al*. 2006 : Steyer *et al*. 2006: Temnospondyli:: (Edopoidea + *Eryops*) + * *Saharastega* represents a primitive but not the most primitive form; Edopoids + Saharastega are a grade not a clade, and *Saharastega* is the sister group to the Edopoids and Eryopoids.

Characters: Nostrils narrow and elongated; premaxillae-maxillae articulation via extensive tongue-and-groove contact; exceptionally large tabular "horns" directed both laterally and ventrally; dorsal region of occiput comprises a complex "occipital plate" . (Damiani *et al* 2006, p.561)

Comments: A large but very primitive temnosopondyl; a Carboniferous-grade "living fossil" that survived till the end of the Permian, thanks to geographical isolation. More terrestrially adapted than its equally primitive crocodile-like cousin *Nigerpeton* (Steyer *et al*. 2006 p.226). Curiosuly, there seems to have only been the small teeth around the margins of the mouth, with no trace of vomerine and palatine tusks that are always present in temnospondyls (Damiani *et al* 2006 p.567). This may be a result of unfavourable preservation. Or it may be that *Saharastega* was simply specialized as a harmless fish-eater (although in that case why the terrestrially adaptations?)

Reference: Damiani *et al* 2006, Steyer *et al*. 2006, Sidor *et al*. 2005

MAK090710

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW060327

Edopoidea

Abbreviated Dendrogram

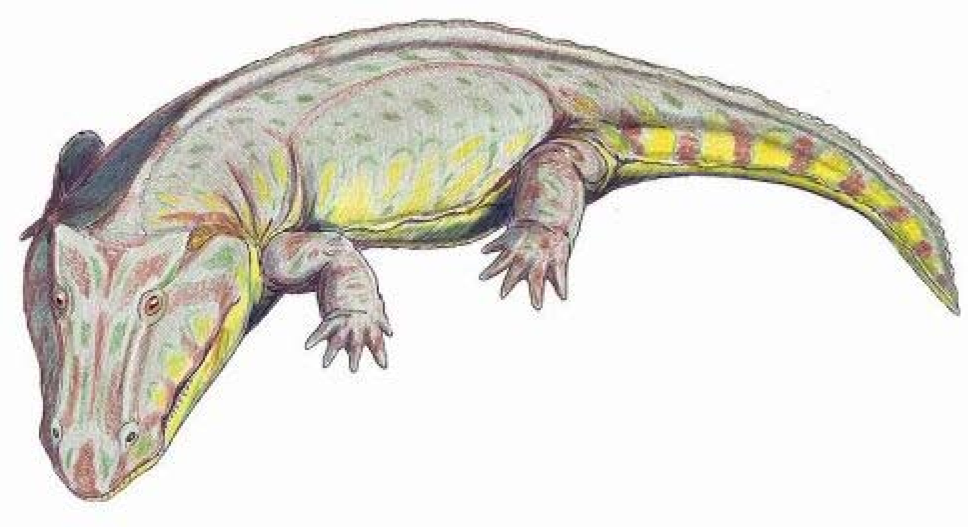
```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
`--oTEMNOSPONDYLI
   `--+---+--Edopoidea
      |   |   |--Edops
      |   |   `--+-Cochleosauridae
      |   |      `--+-Procochleosaurus
      |   |         `--+-Adamanterpeton
      |   |            `--+-Cochleosaurinae
      |   |               `--+-Cochleosaurus
      |   |                  `--+-Chenoprosopus
      |   |                     `--Nigerpeton
      |   `--Saharastega
      `--+--Dendrerpeton
         |--Dvinosauria
         `--+--Euskelia
            |   |==Dissorophoidea
            |   |  `--LISSAMPHIBIA
            |   `--Eryopoidea
            `--Stereospondyli
               |--Rhinesuchidae
               `--+--Lydekkerinidae
                  |--+--Plagiosauroidea
                  |   `--+--Rhytidosteidae
                  |       `--Brachyopoidea
                  `--+--Capitosauria
                     `--Trematosauria
                         |--Trematosauroidea
                         `--Metoposauroidea
```

Contents

Taxa on this Page

1. *Adamanterpeton* X
2. *Chenoprosopus* X
3. Cochleosauridae X
4. Cochleosaurinae X
5. *Cochleosaurus* X
6. Edopoidea X
7. *Edops* X
8. *Nigerpeton* X
9. *Procochleosaurus* X

The Edopoids

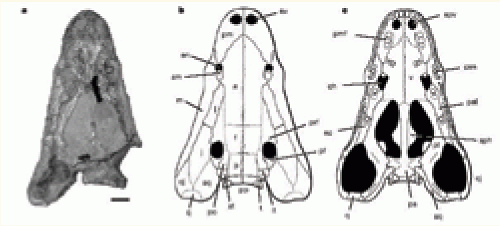


Edops craigi, life reconstruction, by Dmitry Bogdanov, 2007 (Wikipedia)

From **Darren Naish's blog *Tetrapod Zoology*: Temnospondyls the early years (part I) (June 29, 2007)**:

Often regarded as the most primitive temnospondyl group is the Edopoidea (previously known as Edopsoidea). Unlike more advanced kinds they exhibited an archaic pattern of palatal bones, and still possessed various additional bones at the back of the skull. Edopoids also had particularly big premaxillae (the bones that form the tip of the snout) and proportionally small external nostrils. Within the clade, the most basal member seems to be *Edops* from the Early Permian of the USA, a broad-skulled animal with large palatal teeth. It was fairly big, at 2 m in length. Fragmentary remains from the Viséan of Scotland appear to come from *Edops* or a close relative and hence predate the type *Edops* material of the Permian.

Cochleosaurids were long-snouted edopoids, ranging in length from c. 30 cm to perhaps 3 meyers, known from swamp and lacustrine habitats of Nova Scotia, Ohio, the Czech Republic, Ireland and Africa. Lateral line canals are absent (with one exception: read on), so they are thought to have been mostly terrestrial (although it is known that they produced aquatic gilled larvae). While their skulls are decorated by a sculpturing of pits and furrows, a distinctive feature of the group is that a zone along the skull midline is only lightly sculptured (Sequeira 1996, 2004, Milner & Sequeira 1998). Cochleosaurids might have been amphibious predators and they have typically been imagined as rather crocodile-like in basic lifestyle. The broader-skulled forms were perhaps similar to *Edops* in being amphibious ambush predators of fish and smaller tetrapods, while some of the more narrow-snouted cochleosaurids, like the cochleosaurine *Chenoprosopus milleri* [above], may have foraged on land for arthropods and small tetrapods. However, even *Edops* is interpreted as terrestrial by some workers (Schoch 2001, p. 341).



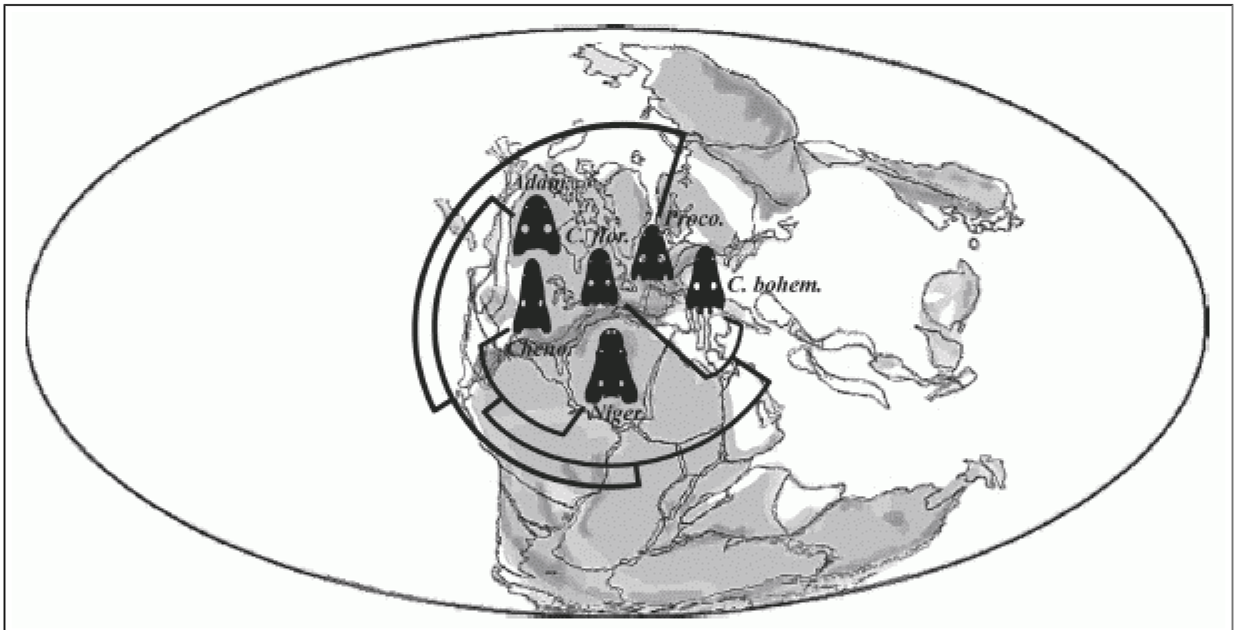
Nigerpeton, the only African cochleosaurid, is closely related to *Chenoprosopus* but is in many ways a highly unusual member of the group. It was gigantic compared to some of its relatives, with a long, flattened skull 45-56 cm long, and its lateral line system contrasts with their absence in other edopoids. Like many temnospondyls, *Nigerpeton* possessed particularly large fang-like palatal teeth as well as enlarged teeth in the lower jaw, but the degree of heterodonty it possessed is extraordinary: the teeth at its premaxillary tips were large, and tooth size then declined posteriorly before increasing again in the maxilla, before decreasing again further posteriorly. Particularly big fangs - bigger than those lining the jaws - were present in patches on parts of the palate, while huge fangs near the lower jaw tip fitted through special openings in the skull roof when the mouth was closed [in the adjacent image, the big holes near the snout-tip are not the nostrils (those are much further back), but are instead the openings for the fangs of the lower jaw]. Protruding lower jaw teeth are also seen in a much later group of temnospondyls, the mastodonsauroids (and are also present in some living crocodilians). These specialized teeth suggest that *Nigerpeton* was an effective carnivore, presumably capable of grabbing large tetrapods (Steyer *et al*. 2006). While other cochleosaurids are Carboniferous and from the

Northern Hemisphere, *Nigerpeton* is unusual in being from the Late Permian of Niger. Discovered alongside captorhinids, pareiasaurs, and the late-surviving basal temnospondyl *Saharastega*, *Nigerpeton* provides further support for the idea that Late Permian west African was home to a strongly endemic fauna (Sidor *et al*. 2005, Steyer *et al*. 2006).

Edopoids - perhaps the most basal temnospondyl clade we know of - therefore included mid-sized terrestrial and amphibious taxa as well as late-surviving big-toothed macropredators.

Geographical distribution

The edopoids and their relatives were typical elements of the tropical and mostly equatorial Euramerican Coal Swamp biome (the "Edaphosaur-Nectridean faunal province" of Milner 1993). The distribution and relationships of some representative taxa are shown on the map at the right.



Biogeography of the Cochleosauridae, from Steyer *et al* 2006 p.25. Plains in clear grey, uplands and mountains in dark grey. From left to right: *Adamanterpeton* (top left); *Chenoprosopus* (bottom left); *Cochleosaurus florensis* (center); *Nigerpeton* (bottom); *Procochleosaurus* (right); and *Cochleosaurus bohemicus* (far right).

During the post-Asselian early Permian, the edopoids dissapeared from the known regions, although other Permocarboniferous tetrapods continued to flourish. The discovery of an edopoid (*Nigerpeton*) and edopoid-cousin (*Saharastega*) from the late Permian of North-West Africa (equatorial Gondwana) shows that these animals continued to exist and flourish right up till the end of the Permian.

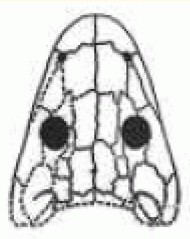
They were part of a unique province made up of highly endemic fauna, that included Carboniferous-grade basal temnospondyls, Permian grade Captorhinids, and late Permian Parierasaurs. Therapsids seem to be rare or absent. It may be that there were geographical factors which kept these animals isolated from the rest of the world.

These animals inhabited the valleys of an equatorial mountain chain; the Central Pangean Mountains (Scotese, 2001) that was the result of the collision of Laurussia with Gondwana. This had an estimated altitude of more than 2000 m at the end of the Permian. It seems that the edopoids (and relatives) crossed the Central Pangean Mountains at least twice during their evolutionary history (Steyer *et al* 2006 p.26).

The edopoidian grade temnospondyls do not appear to have expanded their geographic range into southern Gondwana, despite the milder conditions of the high latitudes following the retreat of the glaciers. Perhaps this was due to competition from other temnospondyls, or it may simply have been geographical isolation

MAK090710

Descriptions



Adamanterpeton ohioensis:

Range: Late Carboniferous (Middle Pennsylvanian - Moscovian) of Linton, Ohio

Phylogeny: Cochleosauridae : *Procochleosaurus* + (Cochleosaurinae + *)

Reference: Milner & Sequeira 1998

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710

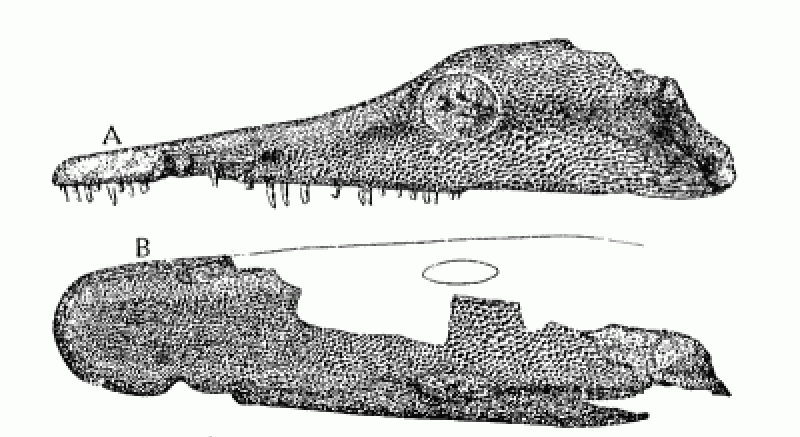


Fig. 231.

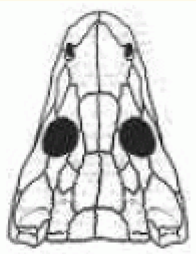
Chenoprosopus :

Range: Permo-Carboniferous (Gzhelian to Asselian) of North America

Phylogeny: Cochleosaurinae: *Cochleosaurus* + (*Nigerpeton* + *).

Illustration: Wikipedia (Mehl, 1913)

MAK090710



Chenoprosopus lewisi :

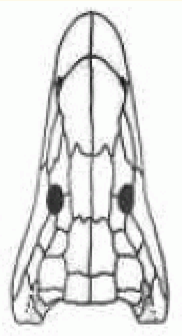
Range: Permo-Carboniferous (Gzhelian to Asselian) of North America (Texas)

Phylogeny: *Chenoprosopus*: *C. milleri* + *.

Characters: short snout

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710



Chenoprosopus milleri:

Range: Permo-Carboniferous (Gzhelian to Asselian) of North America (Abo Formation of New Mexico; Land-Coyotean vertebrate faunachron, includes Permo-Carboniferous boundary (Lucas, 2006)

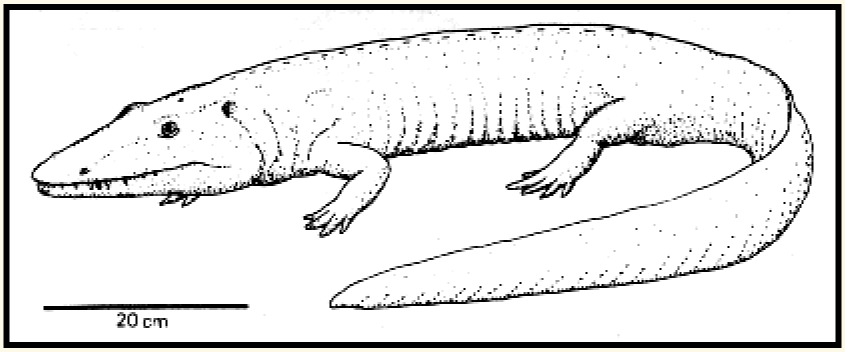
Phylogeny: Chenoprosopus: *C. lewisi* + *.

Characters: Long snout

Reference: Mehl, 1913

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710



Cochleosauridae: *Cochleosaurus*, *Chenoprosopus*, *Nigerpeton*.

Range: Late Carboniferous of Europe and North America to Late Permian of North Africa.

Phylogeny: Edopoidea: *Edops* + * : *Procochleosaurus* + (*Adamanterpeton* + Cochleosaurinae)

Introduction: This group is best known from *Cochleosaurus bohemicus* (Fritsch 1885), from the Late Carboniferous of Central Europe (equatorial Pangea). A reconstruction is shown at right from Milner (1980). *Cochleosaurus* was a medium-sized (120-160 cm) temnospondyl with a flattened skull of up to 16 cm. It lived as a fresh water aquatic predator of the "East Edaphosaurid-Nectridean Empire." Numerous specimens of various growth stages are known, and it is believed that *Cochleosaurus* was a common predator in its size range.

Characters: **$** depressed areas with subdued sculpture between parallel sculpture ridges on the skull table; **$** relatively elongate prechoanal region of the vomer; **$** ectopterygoid separating from the subtemporal fossa.

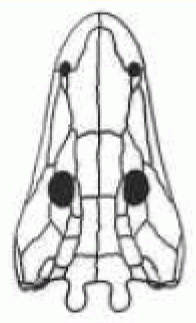
Links: CARBONÍFERO PENSILVANIANO; Phylogeny and Apomorphies of Temnospondyls

References: Milner (1980). 020412

Cochleosaurus :

Range: Bashkirian to Moscovian of Europe and North America.

Phylogeny: Cochleosaurinae: (*Chenoprosopus* + *Nigerpeton*) + * : *C. bohemicus* + *C. florensis*.



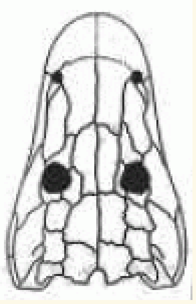
Cochleosaurus bohemicus:

Range: Late Carboniferous (Westphalian D - Late Moscovian) of Nýrany, Czech Republic

Phylogeny: *Cochleosaurus*: *C. florensis* + *.

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710



Cochleosaurus florensis:

Range: Carboniferous (Middle Pennsylvanian - Late Bashkirian) of Joggins, Novia Scotia

Phylogeny: *Cochleosaurus*: *C. bohemicus* + *.

Reference: Rieppel, 1980

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710

Cochleosaurinae: *Cochleosaurus* + *Chenoprosopus* (node-based taxon).

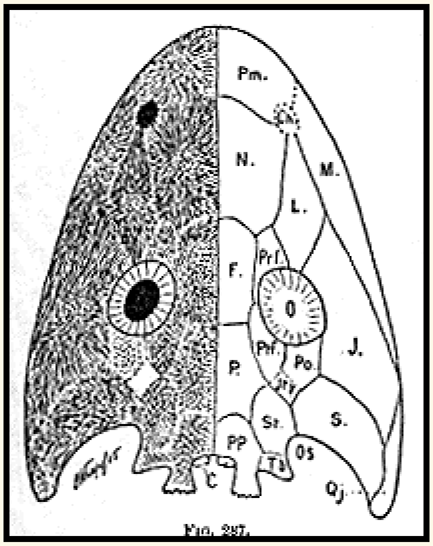
Range: Late Carboniferous of Europe and North America to Late Permian of North Africa.

Phylogeny: Cochleosauridae: *Procochleosaurus* + (*Adamanterpeton* + *): *Cochleosaurus* + (*Chenoprosopus* + *Nigerpeton*).

Characters: **$** depression in vomer anterior to choana; **$** elongate and narrow sphenethmoid; pineal foramen closed in skulls greater than 120 mm in midline length (convergent with *Saharastega*).

Reference: Steyer *et al* 2006 p.18

MAK090710



Edopoidea: *Cochleosaurus*, *Edops*.

Range: Late Carboniferous to Early Permian of North America & Europe to Late Permian of North Africa.

Phylogeny: Temnospondyli:: (*Dendrerpeton* + (Euskelia + Limnarchia)) + *: *Edops* + Cochleosauridae.

Characters: **$** marginally elongate premaxilla; retain intertemporal and moveable articulation between base of braincase and pterygoid; squamosal embayment supported ventrally by the quadratojugal and a quadrate process.

Image: *Cochleosaurus* skull.

Links: Dendrerpeton and Joggins, Nova Scotia (**Best on the Web**); Air Breathers of the Coal Period; The Joggins Fossil Cliffs; Phylogeny and Apomorphies of Temnospondyls; Historický vývoj (Czech). ATW030219

Edops:

Range: Permo-Carboniferous (Gzhelian to Asselian) of North America

Phylogeny: Edopoidea: Cochleosauridae + *.

Characters: marginal dentition with pseudocanine peaking with maxillary swellings above the peaks.

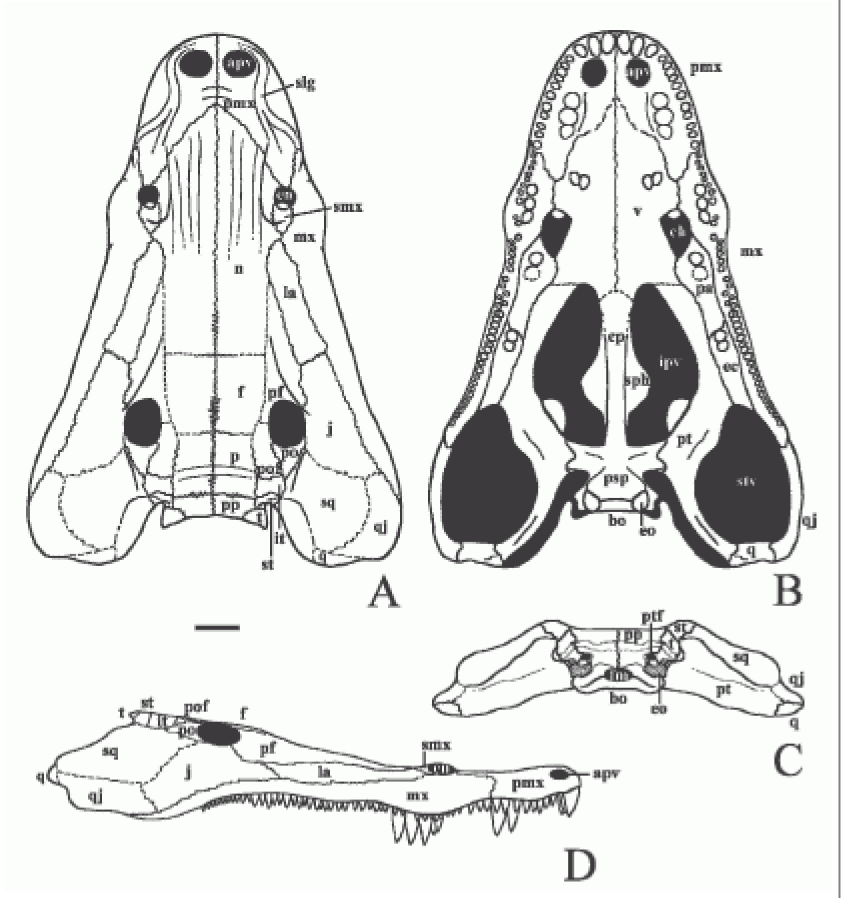
Links: Les quatre autres extinctions de masse; Basal Temnospondyli; Phylogeny and Apomorphies of Temnospondyls. 020412

Nigerpeton :

Range: Late Permian (Wuchiapingian?) of Niger (Moradi Formation|.

Phylogeny: Cochleosaurinae: *Cochleosaurus* + (*Chenoprosopus* + *).

Characters: orbits positioned far back resulting in very elongated preorbital region (~70% of



Reconstruction of the skull of Nigerpeton in dorsal (A), palatal (B), occipital (C), and lateral (D) views.. Scale bar is 5 cm. Steyer *et al* 2006 p.23

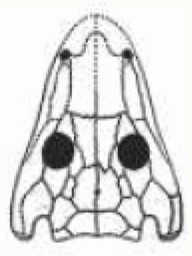
total skull length); tip of snout pierced by mandibular fangs; supratemporal bone highly reduced; maxilla bearing two or three medially positioned fangs at level of maxillary swelling; high occipital and posterior regions of skull; lateral-line system in adult. (Steyer *et al* 2006 p.19)

Comments: An aquatic or semi-aquatic form, with a long alligator-like snout, and sensory line canals for detecting movement in murky water. It probably lived in river and lake systems in the equatorial Gondwanan mountains.

Reference: Steyer *et al* 2006

Illustration: Reconstruction of skull of *Nigerpeton ricqlesi* Sidor et al., 2005 in dorsal (A), palatal (B), occipital (C), and lateral (D) views. Scale bar equals 5 cm. From Steyer *et al* 2006 p.23

MAK090710



***Procochleosaurus jarrowensis*:**

Range: Middle Carboniferous (Bashkirian) of Jarrow, Ireland

Phylogeny: Cochleosauridae : (*Adamanterpeton* + Cochleosaurinae) + *.

Reference: Sequeira 1996

Comments: The oldest known and also the most primitive cochleosaurid

Illustration: From cladogram in Steyer *et al* 2006 p.25

MAK090710

Page Back | Unit Home | Page Top | Page Next

checked ATW060327

Temnospondyli: Dvinosauria

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
`--+--Edopoidea
   |  |--Edops
   |  `--Cochleosauridae
   `--+--+--Dendrerpeton
      |  `--+--Eugryinus
      |     `?--Dvinosauria  (Ruta et al
2007, etc)
      |                 |--+--Trimerorhachidae
      |                 |  `?--Dvinosaurus (
Holmes 2000)
      |                 `--+--Perryella
      |                    `--+--Isodectes
      |                       `--+?--Dvinosaurus
     |                           `--+--Kourerpeton
      |                               `-
-Tupilakosauridae
      |                                         `-
-Slaugenhopia
      |                                              `-
-Tupilakosaurus
      `--+--Euskelia
         |   |==Dissorophoidea
         |   |  `--LISSAMPHIBIA
         |   `--Eryopoidea
         `--+?--Dvinosauria (Yates &Warren
2000)
            `--Stereospondyli
               |--Rhinesuchidae
               `--+--Lydekkerinidae
                  |--+--Plagiosauroidea
                  |  `--+--Rhytidosteidae
                  |     `--Brachyopoidea
                  `--+--Capitosauria
                     `--Trematosauria
                        |--Trematosauroidea
                        `--Metoposauroidea
```

Contents

Taxa on this Page

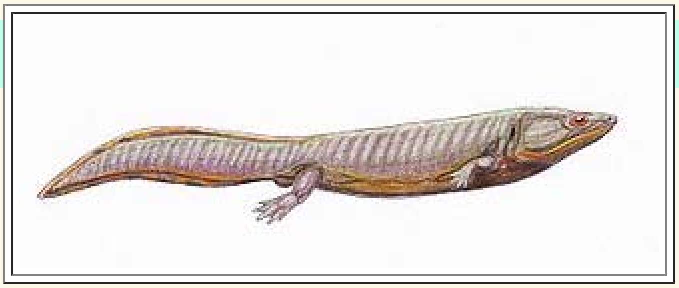
1. Dvinosauria X
2. *Dvinosaurus* X
3. *Eugryinus* X
4. *Isodectes* X
5. *Kourerpeton* X

6. *Perryella* X
7. *Slaugenhopia* X
8. Trimerorhachidae X
9. Tupilakosauridae X
10. *Tupilakosaurus* X

The Dvinosauria

Dvinosaurus egregius, life reconstruction by Dmitry Bogdanov.
Wikipedia, GNU Free Documentation/Creative Commons Attribution.

Phylogenetic relationships



The Dvinosaurs are an assemblage of primitive, aquatic, mostly eel-like temnospondyls. They appear in the late Carboniferous but are most common in the Permian and earliest Triassic. Their exact relationship on the temnospondly family tree is uncertain, and their unfortunate fate has been to be a ping pong ballon successive cladograms. It all began when Milner 1990, in an early study of the group, gaves them a basal placement, just above Dendrerpetontidae and the Edopoids (two of of the most primitive Temnosopndyl groups) and basal to all other temnosondyls. Holmes 2000 assigned them a similar position. Yates and Warren 2000, in their groundbreaking cladistic review of the temnospondyls, place them crownward as one of the two main clades of Limnarchia, the other being the Stereospondylomorpha. Ruta and Bolt 2006 move them back to the stem, this time as the sister clade of the Dissorophoidea) Ruta et al 2003b and Ruta et al 2007 in their supertree analyses likewise place them near the bottom of the tree, near *Dendrerpeton*, while the Dissorophoids are rescued from their primitive assignment and made the sister clade of the Eryopoidea, in agreement with Yates and Warren. Pawley 2006 chapter 5 pp.155f. has a similar placement, the dvinosaurs as basal but above the Cochleosaurs, and with Dendrerpetontidae included in a paraphyletic Edopoidea. But the dvinosaurs didn't languish as troglodytes for long because Englehorn et al. 2008 returned them to the base of the Limnarchia.

Clearly, the problem here is a combination of primitive and advanced characteristics that make the placement of these animals difficult, despite the fact that forms such as *Trimerorhachis* have been well known for over a century. If the Dvinosaurs are primitive, then the Middle Carboniferous *Eugryinus* (Carroll 2009, p.169, 172) could represent a transitional form between Dendrerpetontids and higher dvinosaurs MAK111114

Trimerorhachis

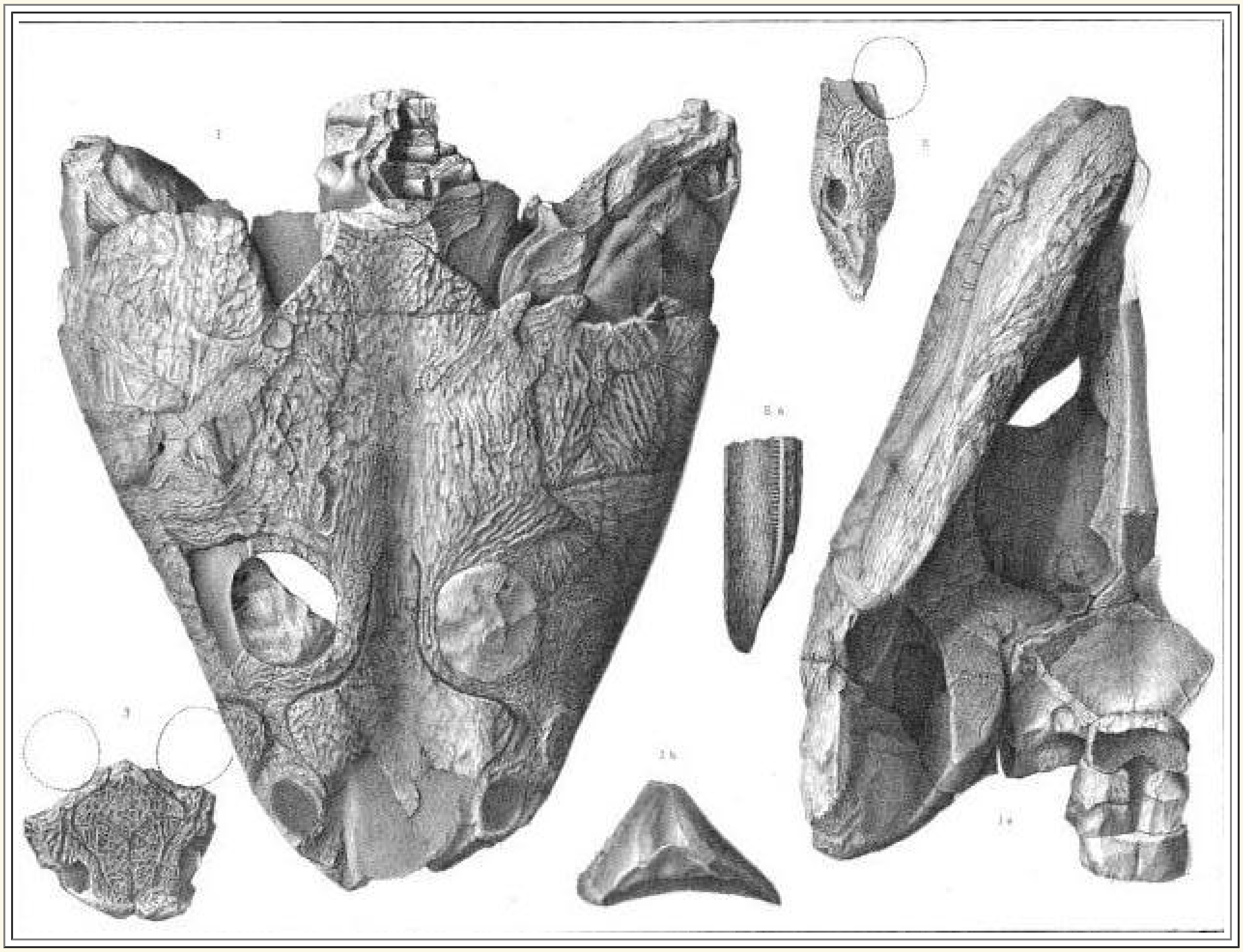
Trimerorhachis is the best known of dvinosaurs. The following material by Smokeybjb (from Wikipedia) illustrates some details of what we know of this creature. Of lot of this would also apply to other dvinosaurs as well. MAK111114

Trimerorhachis is an extinct genus of dvinosaurian temnospondyl within the family Trimerorhachidae. It is known from the Early Permian of Texas. Its fossils are very common in the north-central part of the state. The type species of *Trimerorhachis*, *T. insignis*, was named by American paleontologist Edward Drinker Cope in 1878. A second species, *T. sandovalensis*, was named from New Mexico in 1980.

The length of the largest specimens of *Trimerorhachis* is estimated to have been almost a metre in length. *Trimerorhachis* has a large triangular head with upward-facing eyes positioned near the front of the skull. The trunk is long and the limbs are relatively short. The presence of a branchial apparatus indicates that *Trimerorhachis* had external gills in life, much like the modern axolotl (Case 1935). The body of *Trimerorhachis* is also completely covered by small and very thin osteoderms, which overlap and can be up to 20 layers thick. These osteoderms act as an armor-like covering, especially around the tail. Their weight may have helped *Trimerorhachis* sink to the bottom of lakes and rivers where it would feed (Olson 1979).

History of discovery

Edward Drinker Cope's illustration of fossils of *Trimerorhachis insignis*.
Wikipedia - Public Domain



Trimerorhachis was first described by Edward Drinker Cope in 1878. Specimens are often preserved as masses of bones that are mixed together and densely packed in slabs of rock (Williston 1915). Fossils are rarely found in articulation, although a slab of rock has been found with sixteen skulls and their associated vertebrae in an intact position (Case 1935). Most of these fossils preserve skulls and dorsal vertebrae, but rarely any other bones. Paleontologist S.W. Williston of the University of Chicago commented in 1915 that "it will only be by the fortunate discovery of a connected skeleton that the tail, ribs, and feet will be made known." (Williston 1915). A nearly complete specimen was discovered the following year near Seymour, Texas, and Williston was able to describe the entire postcranial skeleton of *Trimerorhachis* (Williston 1916)

In 1955, paleontologist Edwin Harris Colbert described the scales of *Trimerorhachis*. He noted that they were oval-shaped and overlapping and that each had a base layer of longitudinal striations covered by another layer ring-like ridges, the growth rings of the scales. The scales were more similar to fish scales than they were to reptile scales (Colbert 1955). In 1979, paleontologist Everett C. Olson claimed that there were no such scales in *Trimerorhachis*, and that Colbert was incorrect in his interpretation of the body covering of *Trimerorhachis* (Olson 1979).

A second species called *T. sandovalensis* was named from New Mexico in 1980. A nearly complete skeleton from the Abo Formation near Jemez Springs has been designated the holotype, but other fossils of the species are found throughout the state, giving it a wide distribution (Berman & Reisz 1980).

Paleobiology

Environment

Trimerorhachis was a fully aquatic temnospondyl. Like most dvinosaurs, it had external gills. The interclavicle and clavicle of the pectoral girdle are both very large, a feature that is shared with other aquatic temnospondyls. Many bones are poorly ossified, indicating that *Trimerorhachis* was poorly suited for movement on land (Pawley 2007). *Trimerorhachis* was probably an aquatic predator that fed on fish and small vertebrates (Olson 1979).

During the Early Permian, the area of New Mexico and Texas was a broad coastal plain that stretched from an ocean in the south to highlands in the north. Other common animals that lived alongside *Trimerorhachis* included lungfish and crossopterygians, the lepospondyl *Diplocaulus*, and the large sail-backed synapsid *Dimetrodon* (Berman & Reisz 1980).

Brooding

Small bones that likely belong to immature *Trimerorhachis* individuals have been found in the pharyngeal pouches of larger *Trimerorhachis* specimens. At first these bones were thought to be part of the branchial arches which surround the pouch, or remains of prey that had just been eaten before the animal died. If *Trimerorhachis* was a mouth brooder, the closest living analogue would be Darwin's Frog, which broods its young in its vocal sac. The bones in *Trimerorhachis* belong to juveniles that were much larger than those of Darwin's Frog, however. The young of the Gastric-brooding frog of Australia are comparable in size to those of *Trimerorhachis* but are brooded in the stomach rather than the throat. The number of brooded young in Darwin's Frog and the Gastric-brooding frog is also much higher than that of *Trimerorhachis*, as only a few individuals can be distinguished in the collection of bones. The only living amphibian that raises similarly sized young is the Golden coquí, although it does so through ovovivipary rather than brooding (Olson 1979).

Another possible explanation for the small bones is that they were originally located in the throat and were pushed into the pharyngeal pouch during fossilization. If this was the case, *Trimerorhachis* may have eaten its young instead of brooding them. This type of cannibalism is widespread in living amphibians, and most likely occurred among some prehistoric amphibians as well (Olson 1979). Smokeybjb110806

Descriptions

***Eugryinus*:**

Range: early Late Carboniferous - Bashkirian Westphalian A of Lancashire, England

Phylogeny: Temnospondyli **:** Edopoidea + (*Dendrerpeton* + (Dvinosauria + *))

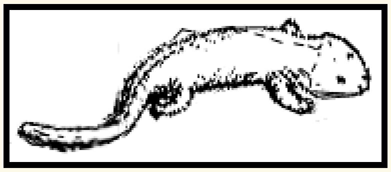
Comments: Knonw from a single juvenile, neotonous skull less than 2 cm in length. Resemble bothprimitive temnospondyls and Trimerorhachids in retention of intertemporal bone, distinct otic notch and large palatal openings. Lateral lines show aquatic lifestyle. If dvinosaurs are primnitive this is a good transitional form, if they are limnarchans (hence more advanced) then these are simply shared primitive features (plesiomorphies) MAK111114

Reference: Carroll 2009, pp.169-70

Dvinosauria: These are a group of primitive semi-aquatic to completely aquatic forms, mostly Permian period. Includes dvinosaurids, tupilakosaurids, and trimerorhachids.

Range: Permian & Triassic

Phylogeny: Limnarchia: Stereospondylomorpha + *. (Yates and Warren 2000); *or* Temnospondyli **:** Edopoidea + (*Dendrerpeton* + (*Eugryinus* + * (Ruta et al 2003b, Ruta et al 2007, Carroll 2009) **:** Trimerorhachidae + *Dvinosaurus* + (*Isodectes* + Tupilakosauridae) or whatever; phylogenies differ MAK111114



Characters: **$** otic notch reduced to shallow embayment; **$** pterygoid, palatine ramus, postero-lateral flange absent; **$** 28+ presacral vertebrae.

Links: Dvinosauria Yates & Warren, 2000; Phylogeny and Apomorphies of Temnospondyls.

Notes: This is a diverse and interesting group, the smaller of the two temnospondyl clades which survived the Permian and radiated into the Triassic. ATW020414.

Comment: most reconstructions show animals of salamander-like appearance. Given their mostly small size and totally aquatic existence, I wonder if some of them were like leposondyls, more elongate and eel-like? MAK111115

Trimerorhachidae: *Neldasaurus, Trimerorhachis*

Range: *Late Carboniferous (Gzhelian) to late Early Permian (Kungurian)*

Phylogeny: *Dvinosauria* **:** *(Dvinosaurus (Isodectes + + Tupilakosauridae)) + **

Characters: *Anterior palatine fenestrae (openings in the front of the roof of the mouth for the lower tusks, also in cochleosaurids, a logical result of a very falttened snout), upward facing orbits (eyes face upwards - bott9om dweller), reduced ossification of limbs (aquatic lifestyle, limb bones have more cartilage and less solid bone)*

Comments: *Advanced relative of Isodectes, may or may not be ancestral to Dvinosaurus (or to use cladistic formalism, may or may not be a sister taxon to Dvinosaurus) MAK111114*

Reference: *Carroll 2009,*

Isodectes:

Range: *Late Carboniferous to Early Permian*

Phylogeny: *Dvinosauria* **:** *Trimerorhachidae + (Dvinosaurus + (Isodectes + Tupilakosauridae)) + *)*

Comments: *It's a shame that the wonderful original name Saurerpeton is not valid, Isodectes sounds like a lycopod. But perhaps appropraite even so. These were long-lived animnals; a single species continued unchanged from the Moscovian* (Westphalian D) *to the Early permian, a period of some 35 million years. (Sequeira. 1998, cited in Carroll 2009 p.172). Probably ancestral to Tupilakosaurus MAK111115*

Perryella: *P. olsoni*

Range: *Early Permian (Artinskian) Wellington Formation of Oklahoma.*

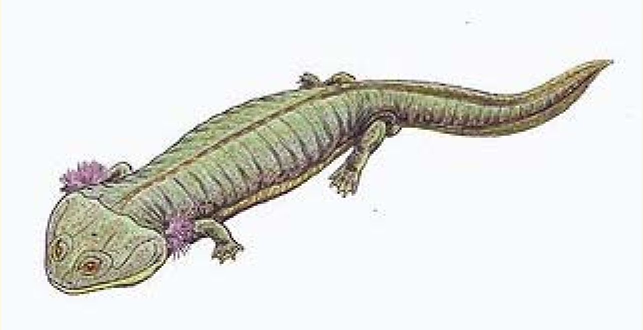
Phylogeny: *Dvinosauria* **:** *Trimerorhachidae + ((Isodectes + (Dvinosaurus + Tupilakosauridae)) + *)*

Characters: *large orbits (eye sockets) and otic notches (rounded indentations at the back of the skull). A bone called the palatine, which is usually found on the underside of the skull, is partially exposed on the top of the skull. Present on the margin of the orbit, the palatine takes the place of the lacrimal bone, which usually touches the orbit in temnospondyls. Another distinguishing feature of Perryella is the presence of two small projections on the quadratojugal bone at the back of the skull. The lowermost projection forms a cup-like shape that attaches to the lower jaw. (Carlson 1987)*

Comments: *Shares features with two unrelated groups, the Trimerorhachidae and Dissorophoidea. A phylogenetic analysis by Ruta and Bolt (2006) placed it in the Dvinosauria. If so it represents a good ancestor (both morphologically and stratigraphically) for Kourerpeton, which it predates by several millions of years*

References *Carlson 1987, Ruta & Bolt 2006, via Wikipedia*

Dvinosaurus: *D. primus Amalitzkii, 1921 (type), D. secundus Amalitzkii, 1921, D. egregius Shishkin, 1968, D. purlensis Shishkin 1968*



Range: *Wuchiapingian (D. primus and D. secundus) to Changhsingian (D. egregius to D. purlensis) of Russia.*

Phylogeny: *Dvinosauria* **:** *Trimerorhachidae + (Perryella + (Isodectes + (Kourerpeton + Tupilakosauridae) + *))*

Comments: *: A reasonably sized form, with a skull length 20 to 22 cm long. First described by Russian paleontologist Vladimir Prokhorovich Amalitskii in 1921, who rather pragmatically named the three species D. primus, D. secundus, and D. tertius. Named after the Northern Dvina River, which was close to the locality where it was discovered. D. tertius is now considered synonymous with D. secundus. Two additional species, D. egregius, and D. purlensis, were named by Mikhail Shishkin in 1968, from a different localities and later strata (latest Permian). Conisdered the sister group to the Trimerorhachidae by Holmes 2000 and intermediate between a paraphyletic Trimerorhachidae and crown dvinosauria by Ruta et al 2007, but given a more crownward position of sister taxon to Tupilakosauridae by Englehorn et al. 2008. In short there seem to be two basic hypotheses, either a late large Trimerorhachid or an abarrent proto-Tupilakosaurid. Like the modern day axotl, this was a neotonic, totally aquatic form*

Link: *Wikipedia*

Image: *Dvinosaurus primus, life reconstruction by Dmitry Bogdanov, Wikipedia*

References *Shishkin et al 2000 pp. 52-3, Carroll 2009, p.176-7*

Kourerpeton: *bradyi Olson & Lammer, 1976*

Range: *Probably late Early Permian (Kungurian) of Texas.*

Phylogeny: *Dvinosauria* **:** *Trimerorhachidae + (Perryella + (Isodectes + (Dvinosaurus + (Tupilakosauridae + *)))*

Characters:

Characters: *Milner and Sequeira 2004 suggested that Kourerpeton may be a tupilakosaurid based on similarities with the genus Slaugenhopia. Like Slaugenhopia, Kourerpeton possesses enlarged postorbitals and reduced postfrontals, bones that form the portion of the skull roof above the eye sockets. Both Kourerpeton and Slaugenhopiapossess incomplete-ring intercentra, which form the cenra of vertebrae. The pleurocentra, which also comprise the centra, are slender and crescentic in both genera. Unlike Slaugenhopia, Kourerpeton lacks an incisure, or notch, on the pterygoid bone of the palate. In Slaugenhopia, this incisure appears as a deep notch in the posterior margin of the central palate. In Kourerpeton, the posterior edge of the skull table is strongly undulated, and has a medial concavity. This is unlike Slaugenhopia, which has a relatively straight skull roof margin. Based on these differences, Milner and Sequeira (2004) considered Kourerpeton to be a primitive stem-tupilakosaurid. - Wikipedia*

Comments: *Discovered in a window of a barber's shop. Because it was not found in situ, the provenance and age of Kourerpeton is unknown, although Early to Middle Permian is most likely. Milner and Sequeira (2004) have proposed that Kourerpeton may have been from the Early Permian San Angelo Formation in Texas, which has also been the source of the tupilakosaurid Slaugenhopia. The San Angelo Formation is in close proximity to the Glen Rose Formation, occurring in a north-south belt across north-central Texas about 80 miles (130 km) west of Glen Rose. Wikipedia*

References *Milner and Sequeira 2004, Warren 1999, via Wikipedia*

Tupilakosauridae: *Slaugenhopia, Thabanchuia, Tupilakosaurus*

Range: *Early Permian (Kungurian) to Early Triassic (Induan) of Texas, Greenland, Russia, and France.*

Phylogeny: *Dvinosauria* **:** *Trimerorhachidae + (Perryella + (Isodectes + (Dvinosaurus + (Kourerpeton + ** **:** *Slaugenhopia + Tupilakosaurus))))*

Characters: *embolomerous centra in their vertebrae, which are diplospondylous, deep notch in the pterygoid bone of the palate.*

Comments: *Aquatic, undulatory eel-like swimming mode.*

References *Milner and Sequeira 2004, Werneburg et al 2007, via Wikipedia*

Slaugenhopia:

Range: *Latest Early Permian (Late Kungurian) San Angelo Formation in Texas*

Phylogeny: *Tupilakosauridae* **:** *Tupilakosaurus + **

Characters: *Characteristics include a notch in the pterygoid bone of the palate called the pterygoid incisure; the wideness of a projection of bone in the palate called the cultriform process, a wide contact between the parasphenoid and basisphenoid bones on the underside of the skull, and uniquely "L"-shaped postparietal bones at the back of the skull. The related Kourerpeton shares the enlarged postorbital bone and a small postfrontal bone near the eye sockets and similar vertebrae with ring-like intercentra and small, crescent-shaped pleurocentra. While the posterior margin of the skull is relatively straight in Slaugenhopia, the same margin is curved and irregular in Kourerpeton. (Milner and Sequeira 2004 via Wikipedia)*

Comments: *Considered by Everett C. Olson intermediate between Trimerorhachis and Dvinosaurus based on the shape of the skull. On the basis of similarities with the recently discovered (1999) South African form Thabanchuia now considered a Tupilakosaurid (Warren 1999). A fragmentary, porly known form, it seems to be transitional between Isodectes and Tupilakosaurus (Carroll 2009 p.177)*

References *Milner and Sequeira 2004, Warren 1999, via Wikipedia*

Tupilakosaurus: *wetlugensis Shishkin 1961*

Range: *Early Triassic (Induan) of Greenland, Russia, and Spitzberg.*

Phylogeny: *Tupilakosauridae* **:::** ***

Comment: *small, eel-like form, skull length 8-10 cm. Abundant in the earliest Triassic, it seems to have been a pioneer species taking advantage of the situation following the P-T mass extinction. Depsite being close in time to the latest Permian Dvinosaurus, the shorter snout suggests origins with earlier forms such as Slaugenhopia and Isodectes (Carroll 2009 p.177)*

References *Shishkin et al 2000 pp. 53-4*

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW060327

Temnospondyli: Dissorophoidea

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
|
TEMNOSPONDYLI
`--+--Edopoidea
   `--+--Dendrerpeton
      |--Dvinosauria
      `--+--Euskelia
         |   |==Dissorophoidea
         |   |  `--LISSAMPHIBIA
         |   `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   `--+--Rhytidosteidae
               |       `--Brachyopoidea
                `--+--Capitosauria
                   `--Trematosauria
                      |--Trematosauroidea
                      `--Metoposauroidea
```

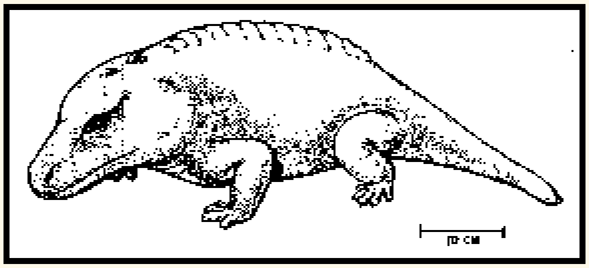
Contents

Taxa on this Page

1. Dissorophoidea

This is an important and ecologically diverse group of Carboniferous and early Permian amphibians. They represent one of the major radiations of early temnosopondyl evolution, including everything from small aquatic and neotenous branchiosaurs and micromelopertontids to sturdy terrestrial *Cacops* to Eryops-like *Trematops* to ancestral lissamphibians like *Doleserpeton* and *Gerobatrachus*. They really deserve a page or even several pages dedicated to them and their evolutionary history, and hopefully these will be added soon. Until then (and even afterwards) we couldn't do better than recommend Darren Naish 's Tetrapod Zoology blog post on the subject. Apart from that, all we can offer at the moment on this fascinating group is a short technical description and an under construction sign. MAK111122

Descriptions



Dissorophoidea: *Amphibamus, Cacops, Doleserpeton, Platyhystrix.*

Range: from the Carboniferous.

Phylogeny: Euskelia: Eryopoidea + *: Lissamphibia.

Characters: prefrontal not contacting postfrontal; otic notch extremely large & semi-circular; otic notch occupies entire back of squamosal; **$** palatine dorsolateral margin exposed in orbital margin; **$** narial, prefrontal and supratympanic flanges (?); **$** orbits and pineal foramen large; interclavicle short & square; clavicles with narrow blades; long, slender limb elements; humerus slightly elongate & lacks supinator process.

Links: Dissorophoidea; Phylogeny and Apomorphies of Temnospondyls; Dissorophoidea (an older phylogeny); Zajic Milner Klembara 1990.pdf; Herpetology: Phylogeny and Tetrapods; Biology 356; ANFÍBIOS.

Notes: Those who favor a temnospondyl origin for extant amphibians generally identify the dissorophids as the ancestral stock. ATW021002.

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW060327

Temnospondyli: Eryopoidea

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLIi
|--Edopoidea
`--+--Dvinosauria
    `--+--Euskelia
         |  |==Dissorophoidea
         |  |  `--LISSAMPHIBIA
         |  `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
                |--+--Plagiosauroidea
                |   `--+--Rhytidosteidae
                |       `--Brachyopoidea
                 `--+--Capitosauria
                    `--Trematosauria
                       |--Trematosauroidea
                       `--Metoposauroidea
```

Contents

Eryops at the Münchehagen Dino-Park, photo by GermanOle (Wikipedia, GNU Free Documentation License)

Taxa on this Page

1. Eryopoidea X
2. *Eryops* X
3. Euskelia

Euskelia


Eryops skeleton. Photo by Joshua Sherurcij © 2007

The classical temnospondyl is *Eryops* (*right*): a big, flat slow-looking tetrapod with an enormous mouth. The classical *definition* of a temnospondyl involved vertebral characters. That is, the principal vertebral component was the intercentrum which (to varying degrees) tended to grow up and around the notochord and provided the basic structural support for the axial skeleton. By contrast, in reptilomorphs (*i.e.* amniotes and their immediate ancestors), the pleurocentrum grows down over the notochord, fuses with the neural arches, and eventually drives the intercentrum into anatomical oblivion. Actually, the intercentrum of *Eryops* is not all that well developed, even compared to *Ichthyostega*. Nevertheless, *Eryops* is the archetype around which the idea of a temnospondyl revolves.

Like most Carboniferous and Permian tetrapods, *Eryops* is a cipher. Even on a page devoted to speculation, it is difficult to find a way to fit these parts together. For example, it is all well and good to say that it used an inertial snap of the jaws to capture prey; but it is difficult to snap anything that big underwater, and equally difficult to imagine *Eryops* as a terrestrial hunter. Nevertheless, the dentition is rather unambiguous. It ate relatively large things that were not happy about the idea. The mouth appears to be well-designed for swallowing animals more or less whole and for keeping them there, in spite of strenuous objections, with such devices as internal fangs.

Perhaps the back forms a sort of an arch, peaking in front of the tall pelvis. This would bring the intercentra into relatively close contact, supporting the arch from below. The neural arches are not smooth curves, as in *Ichthyostega*. Instead, they are strongly sculpted, working tools for complex attachments of tendon and muscle. One could imagine a style of movement or predation in which substantial energy is stored in arching the back by movement of the hind legs, and then releasing it - perhaps quite suddenly - by stepping forward with the arms and contracting muscles anchored on the dorsal spine. This may be consistent with the odd pattern of early "tetrapod" tracks found in Nova Scotia as well as the structure of the ribs, which appear capable of sliding past each other. ATW000213.

Descriptions

Euskelia:

Range: from the Late Carboniferous.

Phylogeny: Temnospondyli::: Limnarchia + *. Eryopoidea + Dissorophoidea.

Characters: Some large, wide forms up to 2 m. Description is largely of *Eryops*. Large, wide skull; skull shape generally U-shaped; lower jaw triangular in lateral view; long, sharp labyrinthodont teeth; some accessory fangs on ectopterygoids, palatine, vomers, etc. (probably used inertial snap of jaws); nares almost terminal; depth of skull increases posteriorly, with fairly pronounced upward curvature ant to orbits; orbits face antero-laterally (variable); dermal skull ornamented with pits; **$** intertemporal absent; **$** parasphenoid firmly attached (sutured) to pterygoid, with no moving articulation between braincase and pterygoid; no separate cervical vertebral series (no neck!); dorsal vertebrae with moderately tall, thick neural arch; both pleurocentrum and intercentrum rather small; ribs broad (pronounced in *Eryops*); ribs shorten post, and may be absent at level of sacrum; 1 sacral, not (or not completely?) fused to ilia; caudal ribs variable in number and morphology, but tail is not longer than dorsal series; pectoral girdle not attached to skull; massive scapula; coracoid expanding to plate ventro-medial to glenoid; ilia oddly tall; humerus and femur short and massive; humerus & tibia oriented horizontally; radius & ulna short and well-separated, as are tibia & fibula; 3 carpals; 5 (4?) digits on manus, 5 on pes; Branchiosaurs may be embryonic and/or neotenous euskelians with external gills.

Links: The Field Museum of Natural History Eryops; subcl98 (labyrinthodont teeth, link to sketch); eryops (dorsal skull); permian image page (life, beautiful!); Euskelia (Mikko's phylogeny). ATW030129

Eryopoidea: *Eryops*

Range: Early to Late Permian of North America & Europe.

Phylogeny: Euskelia: Dissorophoidea + *.

Characters: choana relatively rounded; iliac blade vertical.

Note: The Eryopoidea were for a long time a sort of waste-basket taxon for mostly late Carboniferous and Early Permian temnospondyls that could not be slotted anywhere else. Yates & Warren (2000) reduce this to two families, the Eryopidae and Zatracheidae, although other families may also belong here.

Image: *Eryops* image courtesy of Crash Jones. ATW020213.

Links: Temnospondyli; Eryopoidea; JOINT ADVENTURE Ulla Lohmann; (**Best on the Web**, also in German. The figures are included in the German text); Phylogeny and Apomorphies of Temnospondyls (ToL). ATW030616.

Eryops - a study of a Permian amphibian

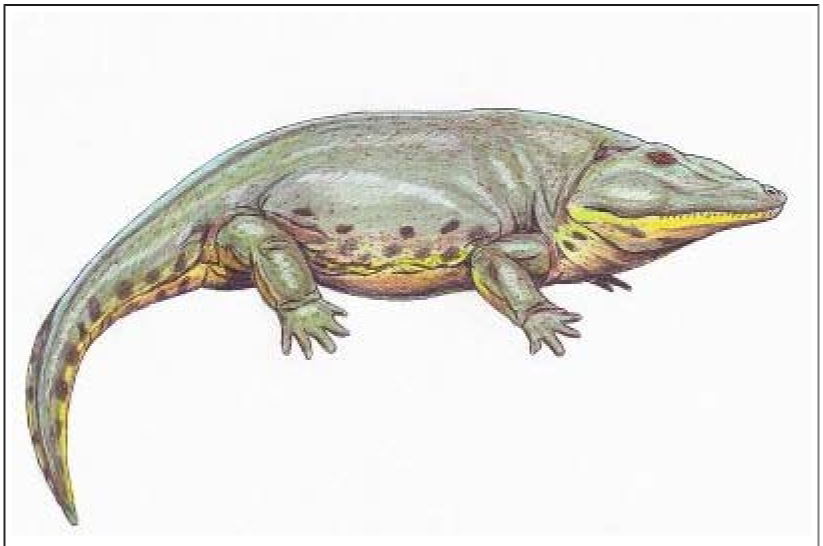
Timothy Pilgrim - from the Wikipedia history log of *Eryops*

Note by editor - a useful essay (although using pre-cladistic terminology) that appeared on the Wikipedia Eryops page before being successively whittled away. I thought it worth including in its entirety (The images were added to later revisions of the page). - MAK090723

Introduction

Two hundred eighty million years ago marked the beginning of the Permian period in the history of the Earth. The continents of Laurasia and Gondwana were coming together, forming the supercontinent Pangea. The waters were populated with fish and invertebrates, and the land-bound margins were swampy areas, covered by dense vegetation.

These swamps are of significant importance to natural history, for they were the residence of the first tetrapods, who had evolved beyond lobe-finned fish into air-breathing, quadrapedal animals, designated the amphibians.



Eryops megacephalus - artwork by Dmitry Bogdanov, wikipedia

Aside from the fact that they gave rise to the reptiles, the amphibians are an intriguing group in their own. One such animal was *Eryops*, a six-foot long, semi-aquatic belly-dragger found in the Wichita and Clear Fork deposits of Texas and New Mexico. Additional fossils have also been found in the eastern United States. Although it gave no evolutionary progeny of its own, *Eryops* is the most well known Permian amphibian, and a remarkable example of natural engineering.

The transition from an aquatic lobe-finned fish to a quadrapedal air-breathing amphibian was a momentous occasion in the natural history of the vertebrates. For an animal to live in a gravity negligible, aqueous environment, then invade one which is entirely different required major changes to the overall body, in form and in function. *Eryops* is an example, one of many, of such an adaptation. It retained, and refined, most of the traits found in its fish ancestors. Sturdy limbs supported and transported its body while out of water. A thicker, stronger backbone prevented its body from sagging under it own weight. And by utilizing available fish jaw bones, a rudimentary ear was developed allowing *Eryops* to hear new airborne sounds.

Ancestry

Amphibians arose from a piscian ancestor since fish were the only existing vertebrates before the invasion of the tetrapods. Such a fish must have possessed similar traits to that of the early amphibians and then passed them on, including internal nostrils (to separate the breathing and feeding passages) and a large fleshy fin which could give rise to the tetrapod limb. It was the rhipidistian crossopterygians which fulfilled every requirement for ancestry. Their palatal and jaw structures were identical to amphibians and the dentition was identical, with labyrinthine teeth fitting in a pit-and-tooth arrangement on the palate. The crossopterygian paired fins were smaller than tetrapod limbs, but the skeletal structure was very similar in that the crossopterygian had a single proximal bone (analogous to the humerus or femur), two bones in the next segment (forearm or lower leg), and an irregular subdivision of the fin, roughly comparable to the structure of the carpus / tarsus and phalanges.

The major difference between crossopterygians and amphibians was in relative development of front and back skull portions; the snout is much less developed than in most amphibians and the post orbital skull is exceptionally longer than an amphibian's.

A great many of the early amphibians lived during the Carboniferous, therefore, an their ancestor would have lived earlier, during the Devonian. Ichthyostegids were the earliest of amphibians with a skeleton directly comparable to that of rhipidistian ancestors. Early Labyrinthodonts (Late Devonian to Early Mississippian) still had some ichthyostegid features such as similar skull bone patterns, labyrinthine tooth structure, the fish skull-hinge, pieces of gill structure between the cheek & shoulder, and the vertebral column. They had, however, lost several other fish features such as the fin rays in the tail.

Tetrapod Origin

Early amphibians undoubtedly lived in near-land areas of water. If the water had dried up, any fish would have become stranded and soon die, but amphibians could move (albeit cumbersome) to the next water hole and continue to exist. Some may have lingered around the newly formed mudhole and fed on stranded fish; others may have remained on land and eaten smaller amphibians, eventually establishing a true terrestrial fauna.

In order to propagate in the terrestrial environment, certain challenges were to be overcome. The animal's body needed additional support because buoancy was no longer a factor. A new method of respiration was required in order to extract atmospheric oxygen instead of oxygen dissolved in water. A means of locomotion would need to be developed to traverse great distances between waterholes with little difficulty. Water retention was now important since it was no longer the living matrix, and it could be lost easily to the environment. Finally, new sensory input systems were required if the animal was to have any ability to function reasonably while on land.

Classification

Diagnostic features unique to the Labyrinthodontia are hard to find at first glance; the complex dentine infolding tooth structure was shared with crossopterygian fish. The labyrinthodonts are divided into the Temnospondyli and the Anthracosauria, the main difference between the two groups being their respective vertebral structures. The Anthracosauria had small pleurocentra which grew and fused, becoming the true centrum in vertebrates higher than themselves. In contrast, the Temnospondyli had a conservative vertebral column in which the pleurocentra remained small in primitive forms, vanishing entirely in the more advanced ones. The intercentra are large and form a complete ring.

A diagnostic feature of the Temnospondyli was that the tabular bone in the skull roof is relatively small and had no contact with the parietal, whereas contact between the two bones was present in all anthracosaurs.

Although the temnospondyls flourished in many forms in the Late Palaeozoic and Triassic, they were an entirely self-contained group and did not give rise to any later tetrapod groups. It was the sister group Anthracosauria which gave rise to the reptiles.

Front view of *Eryops megacephalus*

Within the Temnospondyli are the two suborders Rachitomi and Stereospondyli, also distinguished by their types of vertebrae. There were three distinct successive stages within the Rachitomi, the first occuring in the Carboniferous. The second happened mostly in the Pennsylvanian, continuing into Permian, of which *Edops* is characteristic. The third and final stage was in the Late Carboniferous and Early Permian, from which *Eryops* of the Texas Permian red beds is best known. Just as there were numerous side branches throughout the evolution of the temnospondyls, so too were there many of the rachitomes; *Eryops* represents but only one.

Of special interest in regards to the Rachitomi, is *Branchiosaurus*. This tiny amphibian, relatively speaking, lived from the Late Pennsylvanian to the Early Permian and was very similar to the Rachitomi, differing only in its small size. However, it had a much less ossified skeleton, a short skull and other distinguishing features. Clear traces of gills are present in many fossilized samples, hence the name. Thought to have differed from rachitomous vertebrae, it was placed in a separate order named Phyllospondyli. Only later was it realized, by studying growth stages and seeing increasing ossification in larger specimens, that it was in fact the larval stage of a much larger rachitome like *Eryops*.

Pelosaurus laticeps, a possible tadpole of *Eryops* (reference)

Backbone

There are two major forms of vertebrae found within the Amphibia. The first is the lepospondylous (husk) vertebra which is found in numerous small Palaeozoic forms as well as in modern amphibians. The second type is the labyrinthodont (arch) vertebra which occured in labyrinthodonts and, in a modified form, in all higher vertebrates. The latter type is a direct inheritance from the Crossopterygia, with the intercentrum and the pleurocentrum present.

Of the labyrinthodont vertebra, there are two subdivisions. Members of the Stereospondyli had intercentra which grew upwards, forming a ring about the notochord, and lacked any pleurocentra. The second, of which*Eryops* is an example, is the rachitomous-type vertebra which is the most primitive arch of all tetrapods. The intercentrum was a median ventral element encircling the persistant notochord, becoming the major element in construction of the centrum. The pleurocentra, which were small paired blocks flanking inbetween the intercentrum and neural arch, combine with the intercentum to make up the true centrum in higher vertebrates. The rachitomous vertebra is present in the oldest of amphibians, Ichthyostega, which were nearly identical to those of Crossopterygia, and the majority of Temnospondyli. The smaller pleurocentra were well ossified and occupied the space between the successive intercentra, making a vertebral column which was well built to support the weight of a terrestrial body. The development of anterior and posterior zygopophyses was an envolutionary necessity for tetrapods in order to strengthen the spine and control its flexibility. *Eryops*, like the majority of amphibians, had a single sacral rib with a broad head. This wielded a large capitulum and tuberculum, a short broad neck, and an expanded spatulate shaft. In addition, amphibians were the first vertebrates to have developed a neck which contained a more flexible cranio-vertebral joint than that of their ancestors.

Skull

The most notable characteristic that is different between a fish and amphibian skull are the relative frontal and rear portion lengths. The fish had a long rear portion while the front was short; the orbital vacuities were thus located towards the anterior end. In the amphibian, the front of the skull lengthened, positioning the orbits farther back on the skull. The lacrimal bone was not in contact with the frontal anymore, having been separated from it by the prefrontal bone. Also of importance is that the skull was now free to rotate from side to side, independent of the spine, on the newly forming neck. The average length of an *Eryops* skull was between 320 mm and 335 mm.

Side view of *Eryops megacephalus*

As with the flattening body, the skull of *Eryops* was dorsal-ventrally compressed, with a pitted surface of about 25 pits per square inch. The eyes which were originally on the sides, facing outward, were necessarily on the dorsal side of the skull looking up and forward. Although ossified in crossopterygians and ichthyostegids, the braincase of *Eryops* was not, in the orbital and otic regions. At the rear of the skull the once single occipital condoyle began to divide into two, but never fully separated.

A diagnostic character of temnospondyls is that the tabular bones (which formed the posterior corners of the skull-table) were separated from the respective left and right parietals by a sutural junction between the postparietals and supratemporals. Also at the rear of the skull, all bones dorsal to the cleithrum were lost.

The lower jaw of *Eryops* resembled its crossopterygian ancestors in that on the outer surface lay a long dentary which bore teeth. There were also bones below the dentary on the jaw: two splenials, the angulary and the surangular. On the inside were usually three coronoids which bore teeth and lay close to the dentary. On the upper jaw was a row of marginal labyrinthine teeth, located on the maxilla and premaxilla. In *Eryops*, like all early amphibians, the teeth were replaced in waves which traveled from the front of the jaw to the back in such a way that every other tooth was mature, and the ones in between were young.

Dentition

The Labyrinthodontia had a peculiar tooth structure from which their name was derived and, although not exculsive to the group, the labyrinthine dentition is a useful indicator as to proper classification. The important feature of the tooth is that the enamel and dentine were folded in such a way as to form a complicated corrugated pattern when viewed in cross section. This infolding resulted in strengthening of the tooth and increased wear resistance. Such teeth survived for 100 Ma, first among crossopterygian fish, then stem reptiles. Modern amphibians no longer have this type of dentition but rather pleurodont teeth, in fewer numbers.

Sensory Organs

There is a density difference between air and water that causes smells (certain chemical compounds detectable by chemoreceptors) to behave differently. An animal first venturing out onto land would have difficulty in locating such chemical signals if its sensory apparatus was designed for aquatic detection.

Fish have a lateral line system which detects pressure fluctuations in the water. Such pressure is non-detectable in air, but grooves for the lateral line sense organs were found on the skull of labyrinthodonts, suggesting a partially aquatic habitat. Modern amphibians, which are semi-aquatic, exhibit this feature whereas it has been retired by the higher vertebrates. The olfactory epithelium would also have to be modified in order to detect airborne odours.

In addition to the lateral line organ system, the eye had to change as well. This change came about because the refractive index of light differs between air and water, so the focal length of the lens was altered in order to properly function. The eye was now exposed to a relatively dry environment rather than being bathed by water, so eyelids developed and tear ducts evolved to produce a liquid, moistening the eyeball.

Hearing

The balancing function of the middle ear was retained from the fish ancestory, but delicate air vibrations could not set up pulsations through the skull in order for it to function a proper auditory organ. Typical of most labyrinthodonts, the spiracular gill pouch was retained as the otic notch, closed in by the tympanum, a thin, tight membrane.

The hyomandibula of fish migrated upwards from its jaw supporting position, and was reduced in size to form the stapes. Situated between the tympanum and braincase in an air-filled cavity, the stapes was now capable of transmitting vibrations from the exterior of the head to the interior . Thus the stapes became an important element in an impedance matching system, coupling airborne sound waves to the receptor system of the inner ear. This system had evolved independantly within several different amphibian lineages.

In order for the impedance matching ear to work, certain conditions had to be met. The stapes must have been perpendicular to the tympanum, small and light enough to reduce its inertia and suspended in an air-filled cavity. In modern species which are sensitive to over 1 kHz frequencies, the footplate of the stapes is 1/20th the area of the tympanum. However, in early amphibians the stapes was too large, making the footplate area oversized, preventing the hearing of high frequencies. So it appears that only high intensity, low frequency sounds could be detected, with the stapes more probably being used to support the braincase against the cheek.

Girdles

The pectoral girdle of *Eryops* was highly developed with a larger size for an increased muscle attachment to it and to the limb. Most notably, the shoulder girdle was disconnected from the skull resulting in improved terrestrial locomotion. The crossopterygian cleithrum was retained as the clavicle, and the interclavicle was well developed, lying on the underside of the chest. In primitive forms, the two clavicles and the interclavical could have grown ventrally in such a way as to form a broad chest plate, although such was not the case in *Eryops*. The upper portion of the girdle had a flat, scapular blade with the glenoid cavity situated below performing as the articulation surface for the humerus, while ventrally there was a large, flat coracoid plate turning in toward the midline.

The pelvic girdle also was much larger than the simple plate found in fishes, accomodating more muscles. It extended far dorsally and was joined to the backbone by one or more specialized sacral ribs. The hind legs were somewhat specialized in that they not only supported the weight, but also provided propulsion. The dorsal extension of the pelvis was the ilium, while the broad ventral plate was comprised of the pubis in front and the ischium in behind. The three bones met at a single point in the center of the pelvic triangle called the acetabulum, providing a surface of articulation for the femur.

The main strength of the ilio-sacral attachment of *Eryops* was by ligaments, a condition structurally, but not phylogenetically, intermediate between that of the most primitive embolomerous amphibians and early reptiles. The condition which is more usually found in higher vertebrates is that cartilage and fusion of the sacral ribs to the blade of the ilium are utilized in addition to ligamentous attachments.

Limbs

The humerus was the largest bone of the arm, its head articulating with the glenoid cavity of the pectoral girdle, distally with the radius and ulna. The radius resided on the inner side of the forearm and rested directly under the humerus, supporting much of the weight, while the ulna was located to the outside of the humerus. The ulna had a head, which muscles pulled on to extend the limb, called the olecranon that extended above the edge of the humerus.

The radius and the ulna articulated with the carpus which was a proximal row of three elements: the radiale underlying the radius, the ulnare underneath the ulna and an intermedium between the two. A large central element was beneath the last and may have articulated with the radius. There were also three smaller centralia lying to the radial side. Opposite the head of each toe lay a series of five distal carpals. Each digit had a first segment, the metacarpal, lying in the palm region.

The pelvic limb bones were essentially the same as in the pectoral limb, but with different names. The analogue to the humerus was the femur which was longer and slimmer. The two lower arm bones corresponded to the tibia and fibula of the hind leg, the former being the innermost and the latter the outermost bones. The tarsus is the hind version of the carpus and its bones correspond as well.

Feeding

Early amphibians like *Eryops* had a wide, gaping jaw with weak muscles with which to open and close it. Within the jaw were fang-like palatal teeth which, when coupled with the gape, suggests an intertial feeding habit. This is when the amphibian would grasp the prey and, lacking any chewing mechanism, toss the head up and backwards, throwing the prey farther back into the mouth. Such feeding is seen today in the crocodile and alligator.

The tongue of modern adult amphibians is quite fleshy and attached to the front of the lower jaw, so it is reasonable to speculate that it was fastened in a similar fashion in primitive forms, although it was probably not specialized like it is in a frog.

It is taken that *Eryops* was not very active, thus a predatory lifestyle was probably not the norm. It is more likely that it fed on fish either in the water or on those which became stranded at the margins of lakes and swamps. Also abundant at the time was a large supply of terrestrial invertebrates which may have provided a fairly adequate food supply.

Respiration

Modern amphibians breathe by inhaling air into their lungs, where oxygen is absorbed, as well as through the moist lining of the mouth and skin. So too did *Eryops*, but its ribs were too closely spaced to suggest that it simply expanded the rib cage. More likely, it depressed the hyoid apparatus to expand the oral cavity, and elevated the floor of the mouth while it and the nostrils were closed, forcing air back into the lungs. Air could then be forced back out by contraction of the elastic tissue in the lung walls. The other special respiratory methods were probably also made use of.

Locomotion

Eryops had typical amphibian posture exhibited by the upper arm and upper leg extending nearly straight out from its body while the forearm and the lower leg extended downward from the upper segment at a near right angle. The body weight was not centered over the tops of the limbs, but rather was transfered 90 degrees outwards and down through the lower limbs, which contacted the ground. Most of the animal's strength was used to just elevate the body off the ground in order to walk which was slow and difficult. With this sort of posture, only short, broad strides could be achieved, and have been so confirmed by fossilized footprints found in Carboniferous rocks.

Ligamentous attachments within the limbs were present in *Eryops*, being important because they were the precursor to bony and cartilagenous variations seen in modern terrestrial animals which use their limbs as a means of transport.

Of all body parts, the spine was the most affected with the move from water to land. It now had to resist the bending caused by body weight, and had to provide mobility where needed; previously, it was able to bend along its entire length. Likewise, the paired appendages had not been formerly related to the spine, but the slowly strengthening limbs now transmitted their support to the axis of the body.

Page Back | Unit Home | Page Top | Page Next

checked ATW060327

Temnospondyli: Archegosauroidea

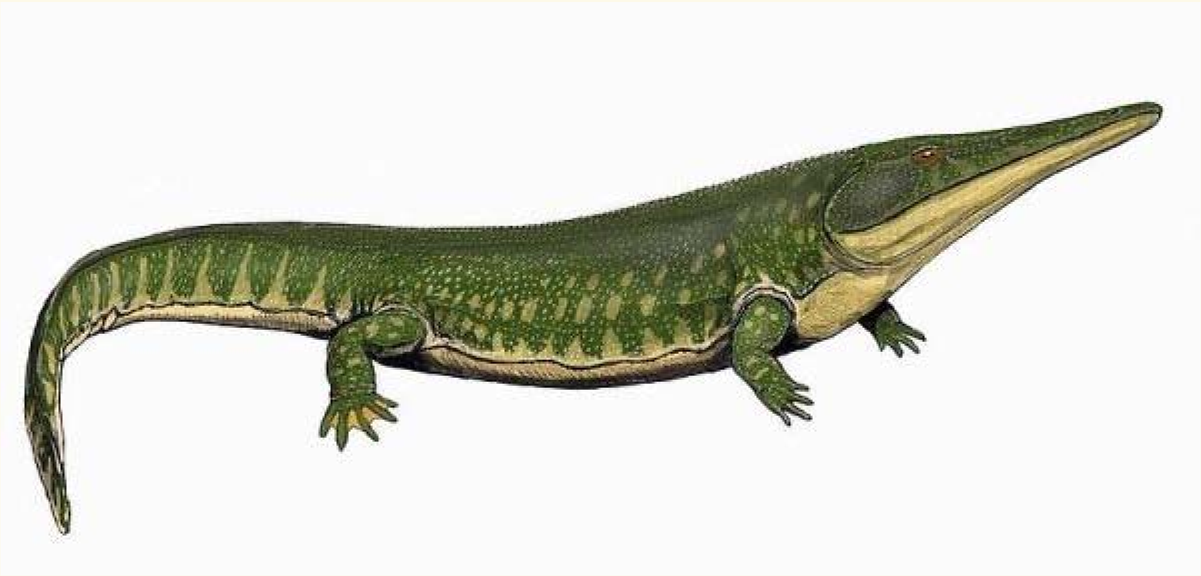
Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+?--Dvinosauria  (Ruta et al 2007)
    `--+--Euskelia
        |   `==Dissorophoidea
        |     `--LISSAMPHIBIA
        `--Limnarchia
             |?--Dvinosauria (Yates &Warren
2000)
             `--Stereospondylomorpha
                 |--Archegosauroidea
                 `--Stereospondyli
                     |--Lapillopsidae
                     |--Rhinesuchidae
                     `--+--Lydekkerinidae
                         |--+--Plagiosauroidea
                         |   `--+-
-Rhytidosteidae
                         |       `-
-Brachyopoidea
                         `--+--Capitosauria
                             `--Trematosauria
                                |-
-Trematosauroidea
                                `-
-Metoposauroidea
```

Contents

Taxa on this Page

1. Archegosauroidea X
2. Limnarchia X
3. Stereospondylomorpha X



Archegosaurus decheni, Early Permian of Germany. Life reconstruction by Dmitry Bogdanov.

The Archegosaurs were group of medium to very large crocodile- or gavial-like amphibians, common in the Permian of what is now Western and Eastern Europe (and doubtless elsewhere as well). *Archegosaurus decheni*, shown above, is a typical form. These animals represent a transitional type between the large terrestrial and semi-aquatic Permo-Carboniferous forms (e.g. Eryopoidea and similar) and the more specialised and totally aquatic Stereospondyls (although in the great tree of life, all species are transitional, apart from those that die out without leaving descendents. Hopefully more material will be added on them in due coaurse. MAK111122

Descriptions

Limnarchia:

Range: Permian to middle Cretaceous.

Phylogeny: Temnospondyli::: Euskelia + *: Dvinosauria + Stereospondylomorpha.

Characters: **$** paraquadrate foramen on occipital face of quadratojugual; **$** perforated anterior palatal fossa; **$** ectopterygoid toothrow; **$** pterygoid with conical recess dorsal to pterygoid - parasphenoid articulation; **$** maxilla sutured to vomer; vomer denticles absent; **$** discrete postglenoid area on mandible; relatively elongate interclavicle.

Links: Limnarchia after Yates & Warren, 2000; Phylogeny and Apomorphies of Temnospondyls;

References: Yates & Warren (2000). 020414.

Comment: If Dvinosauria has a more basal position (Ruta et al 2007) then either Limnarchia is diphyletic and invalid, or Limnarchia minus Divinosauria, and Stereospondylomorpha, become synonymous MAK111113

Stereospondylomorpha: The stereospondylomorphs are the more significant of the two temnospondyl groups which survived the Permian. The name refers to the structure of the vertebrae, in which the intercentrum was the dominant or only component of the centrum (*i.e.* the pleurocentrum was absent).

Range: Early Permian to middle Cretaceous.

Phylogeny: Limnarchia: Dvinosauria + *: Archegosauroidea + Stereospondyli.

Characters: **$** Jugal extends anterior to orbit; **$** prefrontal sutured to jugual; **$** maxilla-nasal suture; **$** "arcadian groove" on the postglenoid area of the mandible. 020414.

Archegosauroidea: *Archegosaurus, Bashkirosaurus, Cheliderpeton, Collidosuchus, Intasuchus, Konzhukovia, Melosaurus, Platyoposaurus, Prionosuchus, Sclerocephalus, Tryphosuchus*

Range: Assellian - Wuchiapingian

Phylogeny:
Stereospondylomorpha:
Stereospondyli + *.

Introduction: These are a diverse assemblage of mostly large to very large crocodile-like semi-aquatic Permian forms. The constitute a transitional grade between the basal, rhachitomous temnospondyls and the more specialised aquatic families (Stereopondyls) which dominated the Triassic waterways.

Characters: premaxilla without triangular process projecting posteriorly, medial to the naris; premaxilla with rugose, medial tubercle between anterior palatal fossae.

Image: (skull) *Platyposaurus* from **Gondwana Studios**

Links: Phylogeny and Apomorphies of Temnospondyls; PaleoNET | Библиотека (new *Melosaurus* species and revision of related taxa); ATW030927.

More to be added...

Page Back | Unit Home | Page Top | Page Next

checked ATW060327

Rhinesuchids & other primitive Stereospondyls

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
   `--+--Euskelia
      `--Stereospondyli
         |--Lapillopsidae
         |==Rhinesuchidae
         |  |--Rhinesuchus
         |  |--Laccocephalus
         |  |--Uranocentradon
         |  `--Broomistega
         `--+--Lydekkerinidae
            |--+--Plagiosauroidea
            |   `--+--Rhytidosteidae
            |       `--Brachyopoidea
             `--+--Capitosauria
                |   `--+--Mastodonsaurus
                |      `--Capitosauridae
                `--Trematosauria
                   |--Trematosauroidea
                   `--+--Metoposauroidea
```

Contents

Taxa on this Page

1. *Broomistega* X
2. *Laccocephalus* X
3. Lapillopsidae X
4. Lydekkerinidae X
5. Rhinesuchidae X
6. *Rhinesuchus* X
7. Stereospondyli X
8. *Uranocentradon* X

Evolving from archegosaur ancestors, the Stereospondyls were the last of the groups of great classic Palaeozoic amphibians, yet also among the most diverse and successful. Following the trend among dvinosaurs and advanced Euskelia, they abandoned the terrestrial and semi-aquatic lifestyle of the eryopoids in favour of a totally aquatic existence. The backbones became simplified and weakened, the legs small and vestigal, the heads huge and flattened. Some reached gigantic size, four meters or more in length, with heads alone a meter or more in length. Such animals were clearly efficient aquatic ambush preditors on fish and smaller amphibians and reptiles. One highly specialised group, the meter-long Plagiosaurs, were neotenic, retaining their larval gills in adulthood.

As with temnospondyls as a whole, the phylogeny of the Stereospondyls is highly controversial, with different cladistic analysies coming up with quite different results. There seem to be a few points of agreement though. The large Rhinesuchids and small Lapillopsids are the most primitive (basal) and constitute the general ancestral condition. At some point, these ancestral forms diverged into three or four subsequent evolutionary branches: the short-headed brachyopoids and plagiosaurs (which may or may not be related); the large, flat headed capitosaurs; and the longer headed, marine trematosaurs and their cousins the short-lived but abundant late Triassic metaposaurs which mimicked the capitosaurs and could only be distinguished by details of the skull (such as the eyes being forwad rather than placed in the middle of the head). Another grup, the rather unspecilaised Rhytidosteids may be early stereospondyls or more advanced forms on the brachyopid stem

The heyday of the Stereospondyls was during the Triassic, although a few stragglers continued through to the later Mesozoic, relicts in a world inhabited by lissamphibians and dinosaurs. MAK111115

Descriptions

Stereospondyli:

Range: Late Permian to middle Cretaceous.

Phylogeny: Stereospondylomorpha: Archegosauroidea + *: Lapillopsidae + (Rhinesuchidae + (Capitosauria + Trematosauria))).

Characters: **$** Lacrimals excluded from both orbit & nares [Y99]; **$** pterygoid, palatine ramus posteriorly retracted; **$** pterygoid with flat, broad internal process articulating with most of lateral edge of parasphenoid plate; **$** pterygoid sutured to parasphenoid early in ontogeny; [Y99] **$** pterygoid ornamentated on ventral surface; **$** mandible with distinct post-glenoid region [Y99].

Links: Stereospondyli; Phylogeny and Apomorphies of Temnospondyls; The Lapillopsidae; Axial Skeleton; Untitled Document.

References: Yates (1999) [Y99].

Lapillopsidae: *Lapillopsis, Rotaurisaurus*

Range: Early Triassic of Australia.

Phylogeny: Stereospondyli: (Rhinesuchidae + (Capitosauria + Trematosauria))) + *.

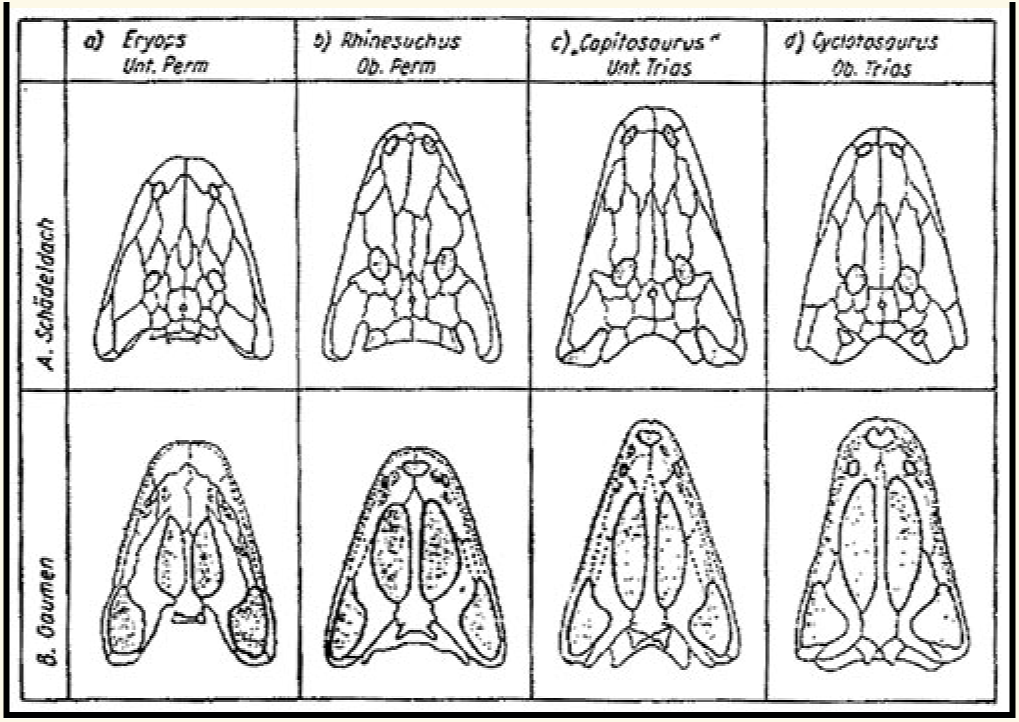
Characters: small, semi-terrestrial; **$** narrow pterygoid-parasphenoid articulation.

References: Yates (1999) [Y99] ATW030112.

Comment: combination of primitive and advanced features make taxonomic and phylogenetic placement diofficult (Carroll 2009, p.214) MAK111115

Rhinesuchidae:

Range: Late Permian to Early Triassic of South Africa.



Phylogeny: Stereospondyli:: (Capitosauria + Trematosauria) + *: *Rhinesuchus* + *Laccocephalus* + *Uranocentradon* + *Broomistega*.

Introduction: The Rhinesuchids are relatively massive temnospondyls known, as yet, only from the later Permian and earliest Triassic of South Africa. They were large to very large (200-400 cm) flat-headed, semi- or perhaps completely aquatic tetrapods, transitional between the eryopids and the Capitosaurs, and fulfilling the same ecological role of large semi- to fully-aquatic predator. The eyes are small and face upwards, located towards the rear of the skull. The pubis is ossified, but the wrist and ankles only seem to be partially so. We may imagine that the animal would lie motionless on a pond bottom, then lunch at fish or smaller tetrapods that would swim past or above it. Carroll (1988) lists six genera, which may include junior synonyms. MAK

As the illustration from Müller (1968) shows, the Rhinesuchids are morphologically transitional between early Permian eryopids and Triassic Capitosaurs and mastodonsaurs. Note the sequence from the short, heavy skull of the semi-terrestrial *Eryops* (*left*) to the large flat light (notice the large vacuities or gaps in the bone of the roof of the mouth) late Triassic *Cyclotosaurus*. MAK 010423, ATW020723.

Rhinesuchus:

Range: Late Permian of South Africa.

Phylogeny: Rhinesuchidae: *Laccocephalus* + *Uranocentradon* + *Broomistega* + *.

***Rhinesuchus whaitsi* Broom 1908**
***Horizon:* this and other species from the *Tapinocephalus*, *Cistecephalus*, and *Daptocephalus* zones, Lower and Middle Beaufort Beds, South Africa**
***Age:* Capitanian to Late Wuchiapingian / Early Changhsingian (middle to late Permian)**
***Place:* central Gondwana**
***Weight:* 100 kg**

***Rhinesuchus* from the *Daptocephalus - Dicynodon* Zone. Image © Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.**

Comments: The mouth is armed with numerous tiny teeth on the palatine (roof of mouth), even smaller teeth on the pterygoid and parasphenoid bones of the hard palate. These animals presumably fed on fish and smaller tetrapods. Other similar species (perhaps transferred to other genera) include *Rhinesuchus africanus* Lydekker and *R. nyasaensis* Haughton (from the Karoo of Nyasaland). vonZittel (1932). *Rhineceps* from the *Cistecephalus* zone is a similar (or perhaps synonymous) genus. (MAK 010423).

Links: South African Museum - An Introduction to the Fossil Wealth of the Nuweveld Mountains; paleontology; fossils; South Africa; Fossil Picture Gallery. ATW020808.

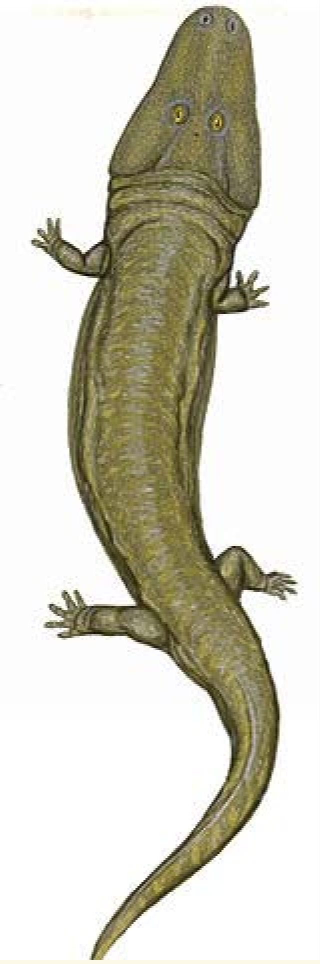
Laccocephalus:

Range: Late Permian or Early Triassic of South Africa.

Phylogeny: Rhinesuchidae: *Rhinesuchus* + *Uranocentradon* + *Broomistega* + *.

Laccocephalus Watson.
Horizon: Daptocephalus zone, Beaufort Beds, Orange Free State, South Africa
Age: ? Changhsingian
Place: central Gondwana

Comments: previously included with *Uranocentradon* in the family Uranocentrodontidae. Carroll lists this genus as early Triassic, but according to Anderson & Cruikshank (1978) it is late Permian. Perhaps it is from the early Changhsingian. (MAK 010423).



***Uranocentradon*:**

Range: Late Permian or Early Triassic.

Phylogeny: Rhinesuchidae: *Rhinesuchus* + *Laccocephalus* + *Broomistega*.+ *.

Uranocentradon senekalensis van Hoepen 1911
Horizon: Lower Lystrosaurus Zone, Beaufort Beds, Orange Free State, South Africa
Age: Latest Changhsingian or Induan
Place: central Gondwana
Known remains: several complete specimens
Length: skull about 50cm. Anderson & Anderson (1970). Overall length 375 cm. vonZittel (1932).

Comments: The skull is greatly flattened. The palatine (on the roof of the mouth) is equipped with a single row of large teeth. The pelvis is very like that of Eryops (indicating terrestrial ability), but the wrist and ankles are incompletely ossified (implying an aquatic existence). Presumably this animal was capable of crawling about on land when need be, but preferred to spend its time in water. vonZittel (1932). This was the last large Rhinesuchid. All the known specimens occur in a single locality and horizon, with specimens of *Lystrosaurus* occurring in horizons immediately above and below. Romer (1947) places *Uranocentradon* in its own family, the Uranocentrodontidae. Carroll and Winer (1977) place it in the Rhinesuchidae. The **Fossil Record II** retains the family Uranocentrodontidae. MAK

Image: *Uranocentrodon senekalensis* from Late Permian of Malawi. Life Reconstruction by Dmitry Bogdanov, Wikipedia

References: Anderson & Anderson (1970); Romer (1947); vonZittel (1932).

***Broomistega*:**

Range: Early Triassic

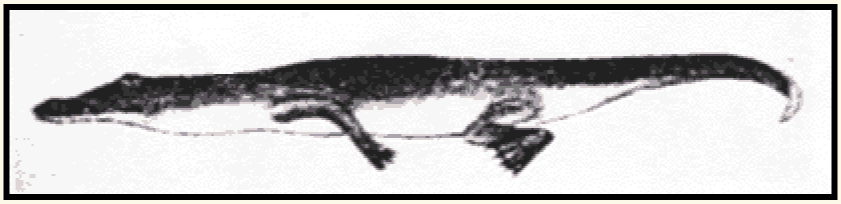
Phylogeny: Rhinesuchidae: *Rhinesuchus* + *Laccocephalus* + *Uranocentradon* + *.

Broomistega putterilli (Broom 1930) synonym: Lydekkerina putterilli Broom 1930
Horizon: Lystrosaurus Zone, Beaufort Beds, South Africa
Age: Induan
Place: central Gondwana
Length: small

Comments: Previously regarded as a species of *Lydekkerina* or a juvenile *Uranocentrodon*, this small aquatic tetrapod is now regarded as a paedomorphic rhinesuchid. This means that most of the *Lystrosaurus* Zone 'amphibians' are now paedomorphic miniature species, perhaps owing to the small size and shallowness of the ponds, lakes, and streams of this period. MAK

Links: New rhynchosaur & temnospondyls

References: Shishkin & Rubidge (2000).



Lydekkerinidae: *Chomatobatrachus*, *Lydekkerina*

Range: Triassic of South Africa & Australia.

Phylogeny: Capitosauria: (*Mastodonsaurus* + Capitosauridae) + *.

Comment: *Lydekkerina*'s short anterior pterygoid and broader contact of pterygoid and parasphenoid are advanced features relative to the rhinesuchids, although the postcranial skeleton indicates a more terrestrial lifestyle (Carroll 2009, p.214). Highly uncertain phylogenetic possition: a basal capitosaur according to Yates & Warren 2000 and Ruta & Bolt 2008, basal rhytidosteid-brachyopoid in the Ruta et al 2003b and Ruta et al 2007 supertrees, and basal sterospondyl according to Pawley 2006, Schoch et al 2007 and Schoch 2008 MAK111115

Links: Wikipedia

---

checked ATW060327. New page MAK111113

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Plagiosauroidea

Abbreviated Dendrogram

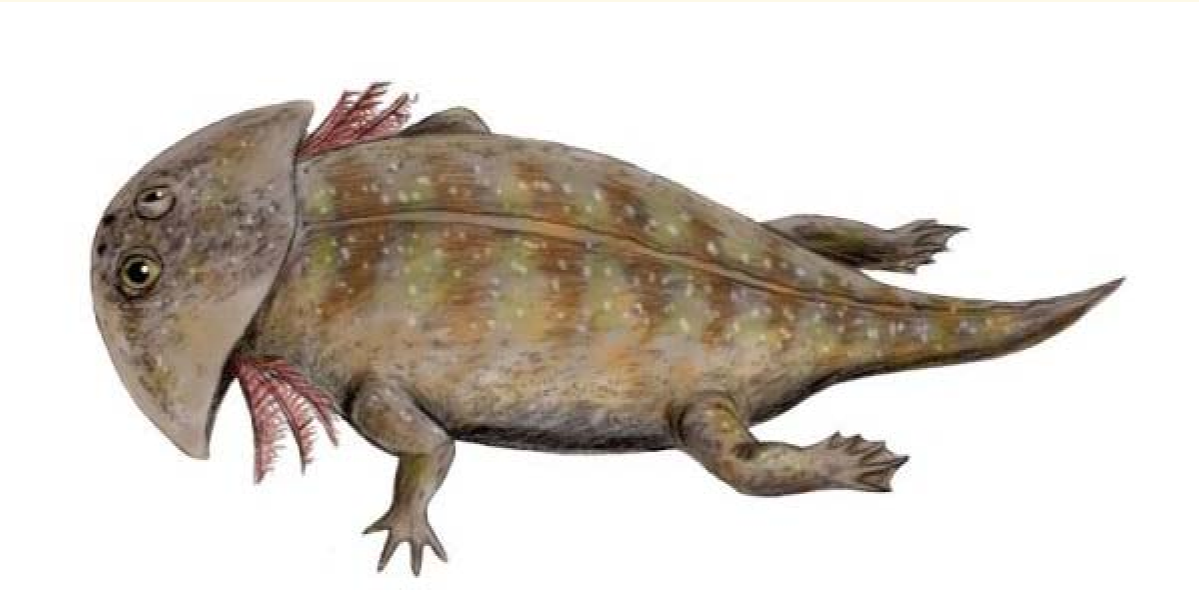
```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
   `--+--Euskelia
       |   |==Dissorophoidea
       |   |  `--LISSAMPHIBIA
       |   `--Eryopoidea
       `--Stereospondyli
           |--Rhinesuchidae
           `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   |--Plagiosauridae
               |   |   |--Plagiosaurinae
               |   |   `--Plagiosterninae
               |   |--Laidleria
               |   `--+--Rhytidosteidae
               |       `--Brachyopoidea
                `--+--Capitosauria
                   `--Trematosauria
                      |--Trematosauroidea
                      `--Metoposauroidea
```

Contents

Taxa on this Page

1. *Laidleria* X
2. Plagiosauridae X
3. PlagiosaurinaeX
4. Plagiosauroidea X
5. PlagiosterninaeX

The Weirdness of Plagiosaurs



Gerrothorax pulcherrimus, life reconstruction, by Nobu Tamura (Wikipedia)

Plagiosaurs are unreasonably difficult beasts to research. Despite the fact that *Gerrothorax* is one of the world's most-illustrated stem tetrapod, articles on the taxon are not easy to find. I am very grateful to Prof. Anne Warren of La Trobe University who has recently (too recently to be used in this version of this Note) supplied me with copies of many of the key articles in the field.

This note will largely consist of a question without even speculative answers. For example, *Laidleria*, the sister of the Plagiosauridae, has an almost flat, sharply triangular skull, with relatively close-set, dorsal eyes. The plagiosaurs are much bigger, a bit thicker, but generally adhere to the same plan. We are frequently told that this betokens a bottom - dwelling ambush predator like a ray. But rays have a unique ambush style which is completely different from anything a temnospondyl could manage.

Granted, lifting the flat head off the bottom quickly could generate the same kind of suction that assists the ray, but the plagiosaur has no obvious means of managing that trick against the considerable resistance of the water column. The neural spines of plagiosaurs are strong, but low – not the sort of arrangement one might associate with strong muscles and powerful tendons which could rapidly raise the head. further, the vertebral column (to extrapolate from Warren (1985) and Warren (1998)) seems designed to *inhibit* arching of the back. **Figure 2** is not to be taken too seriously, but represents an attempt to reconstruct the vertebral articulations, based on *Laidleria*.

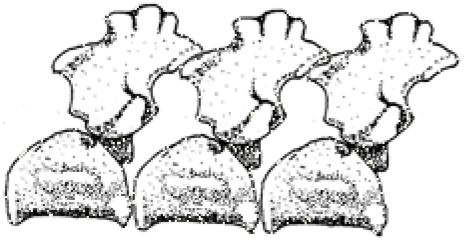


Figure 2. Attempted reconstruction of plagiosaurid vertebrae. Modified from Warren (1998).

Suppose this obstacle is overcome in some way, then is the plagiosaur to leap lithely forward at the wildly gyrating prey and snap its jaws over the struggling victim? But the plagiosaurs had doubled occipital condyles. These were combined, to be sure, with a relatively advanced atlas-axis complex. Still, quick turns to the side were no easy matter for plagiosaurs. To make matters worse, many plagiosaurs were fairly heavily armored, making quick dashes more difficult.

Likewise, a quick snap of the jaws seems impractical. The very flatness of the head leaves little room for large jaw adductors, as the small (or even absent) adductor chambers (post- or sub- temporal fenestrae) demonstrate. Nor are there tabular horns which might signal a posterior extension of the adductors. In any case, there is almost no conceivable place one could put the adductors which would give them a reasonable mechanical advantage in a flat head.

So how did creatures like plagiosaurs, *Diplocaulus* or, for that matter, galeaspids, manage to get by? It is hard to imagine an entirely obsolete ecological guild, but it is notable that there are no vertebrates today with wide, flat, relatively inflexible and immobile skulls, dorsal orbits, and terminal or subterminal mouths. Yet this was a fairly common design in Paleozoic times. We may well be dealing with a way of life that has no easy parallels in today's world. ATW010422.

Descriptions

Plagiosauroidea: *Laidleria* + *Plagiosaurus*.

Range: Early Triassic to Late Triassic

Phylogeny: Trematosauria::: (Rhytidosteidae + Brachyopoidea) + *: Plagiosauridae + *Laidleria*.

Introduction: These strange aquatic forms had a very short, wide skull with pustular ornamentation, and upwardly facing eyes in the middle of the head. Many forms had external gills, indicating a return to a fully aquatic environment. So specialized and distinct are they that have often been placed in their own suborder. MAK010417.

Characters: Very short, wide skull with pustular ornamentation; orbits closely spaced and dorsal; pterygoid denticles absent; orbits near midline; **$** frontal participates in orbit; quadratojugal dorsal to quadrate and overhangs quadrate; subtemporal fenestra reduced or absent; **$** otic notch absent; tabular horns absent; neural spines with lateral buttresses; neural spines relatively short; **$** pleurocentra extremely reduced or perhaps absent; **$** tessellated & ornamented dorsal osteoderms; some (juvenile forms?) with external gills.

Note: for image, see Laidleria.

Links: Plagiosauroidea (Mikko's Phylogeny).

References: Warren (1998); Yates & Warren (2000). ATW010725.

Plagiosauridae: *Gerrothorax*, *Plagiosternum*, *Plagiosaurus*, *Plagioscutum*, *Plagiobatrachus*.

Range: Early Triassic of Australia; Middle Triassic of Germany, and Kazakhstan; Late Triassic of Germany and France, Sweden, Spitzberg, Greenland, and Thailand

Phylogeny: Plagiosauroidea**:** *Laidleria* + ***:**Plagiosaurinae + Plagiosterninae.

Characters: Body short & broad; skull flattened ventrally, broad, short and parabolic; maxilla has some, but reduced, participation in choana; dentition with simple infolding of dentine; teeth on medial margin of choana; 4-6 palatine teeth; usually a row of larger, marginal teeth with inner row of smaller teeth & no tusks; width of interpterygoid vacuity pair more than 90% of length; lateral margin of pterygoid on subtemporal vacuity (adductor chamber?) straight in ventral view; subtemporal fenestra reduced or absent; nares closely spaced; orbits anterior to mid-length of skull; lacrimal present; nasal participates in orbital margin; prefrontal absent (?); pineal foramen anterior to center of radiation of parietal; postparietal pair large and more than 4 times wider than long; exoccipital - pterygoid suture present and visible in ventral view; ascending process of pterygoid absent; pterygoid articulates with parasphenoid & exoccipital; "palatal ramus of entopterygoid" (= pterygoid?) does not reach vomer; well-developed osseous bar formed by parotic processes of tabular & exoccipital; otic notch reduced or absent; stapes massive; occipital condyles strongly projecting; braincase and gill arches have relatively high degree of ossification; ceratobranchials ossified; possible external gills in adults; gill rakers (!?); atlas highly elongated; vertebrae platycoelous, with equally developed anterior and posterior parapophyses; adjacent vertebral (inter)centra "share" neural arches, so that each centrum has two arches; centra elongate & solid; hemal arches reduced or absent; ribs articulate with 2 consecutive arches (*Gerrothorax*); normal temnospondyl posterior extension of interclavicle absent; cleithrum very elaborate with 3 lamina, almost completely ornamented on exterior face; dermal armor including equivalent of ossified ventral ribs present (*Gerrothorax*); ornamentation reticulate or of regularly spaced pustules; frequently found with scutes and complex armor, sometimes ornamented. ATW

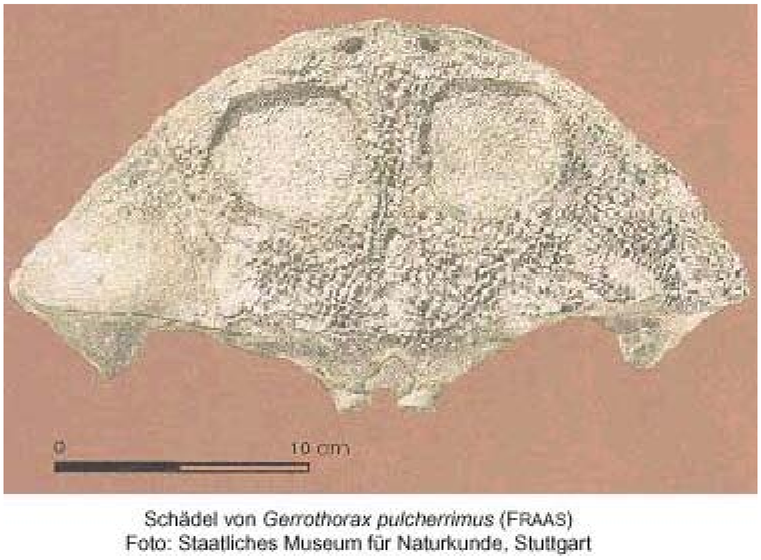
Comments: These specialised short-headed amphibians were probably bottom-living suction gulpers, adapted to a totally aquatic existence, as indicated by the presence of gills. They reach a maximum of 2.5 meters, although most were under a meter in length. *Plagiosaurus* and *Gerrothorax* were medium-large (around a meter long) of the clade Plagiosauria that lived alongside Cyclotosaurs and phytosaurs. They are best known from the Ladinian to Rhaetian of Europe, but have also been found in Greenland, Spitzberg, the Huai Hin Lat Formation (Norian) of Thailand, and the Arcadia Formation (Olenekian - Early Triassic) of Australia (*Plagiobatrachus australis* [Warren 1985]). The latter is the only record of the family from Gondwana. Plagiosaurs have been found in association with Mastodonsaurs, Capitosaurs, and Metoposaurs, but - except for the Australian record - never with Brachyopids. It can be assumed that the two groups required the same ecological niche, and hence would outcompete each other. MAK020305

Links: sh: Prehistoric Animals; Plagiosauroidea; Gerrothorax Printout- Enchanted Learning Software; gerrothorax (Swedish?); Paléontologie, licence, chapitre 7; Dinosaurios, Tutorial interactivo; amph.htm.

References: Milner 1994; Nilsson (1946); Warren (1985); Warren (1995); Warren (1998); Warren & Davey (1992); Warren & Marsicano (2000); Yates & Warren (2000).

Image: *Gerrothorax*, approx 100cm.

Note: [1] In temnospondyls, the intercentrum dominates over the pleurocentrum. In most other tetrapods, the reverse is true. In fact, the intercentrum disappears in amniotes. I assume that the presence of *two* pairs of parapophyses is related to this condition. **[2]** The relationship with *Laidleria* is not completely secure. ATW020902.



Gerrothorax pulcherrimus, from the Stubenstein (Middle Norian) of Stuttgart, SW Germany; Fleming Fjord Formation of Greenland
illustration from the Staatliches Museum für Naturkunde

Plagiosaurinae: *Gerrothorax, Plagiosaurus*

Range:

Range: Middle to Late Triassic (Ladinian to Rhaetian) of Germany, Greenland, and ?Thailand

Phylogeny: Plagiosauridae**:** Plagiosterninae + *.

Characters: Pustulate dermal ornament

Comments: these were the common plagiosaurs of the late Triassic of Europe. They flourished rioght up untiol; the end of the Triassic

Some representative species:

Plagiosaurus depressus *Jaekel*	***Gerrothorax pulcherrimus*** *Fraas*	***Gerrothorax rhaeticus*** *Nilsson*
Horizon & Locality: Knollenmergel of Halberstadt, Germany Age: Late Norian Skull width: 35 cm	Horizon & Locality: Stubenstein of Stuttgart, SW Germany; Fleming Fjord Formation of Greenland Age: Middle Norian Skull width: 30 cm	Horizon & Locality: Rhaetic of Scania, Sweden Age: Rhaetian Overall Length: 1 meter

References: Milner 1994

MAK020305

Plagiosterninae: Plagiosternum

Range: Middle to Late Triassic (Ladinian to Carnian) of Germany and Spitzberg

Phylogeny: Plagiosauridae**:** Plagiosaurinae + *.

Characters: No ornament

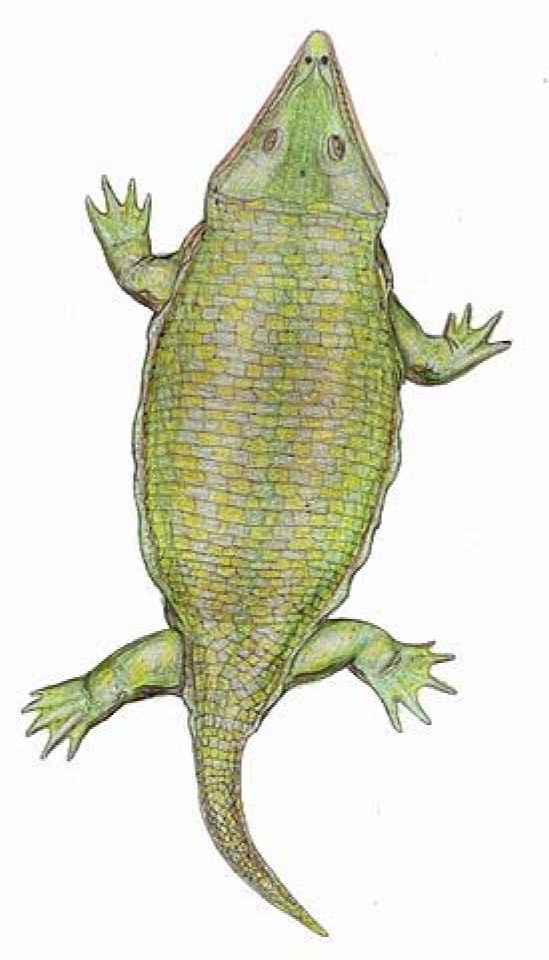
References: Milner 1994

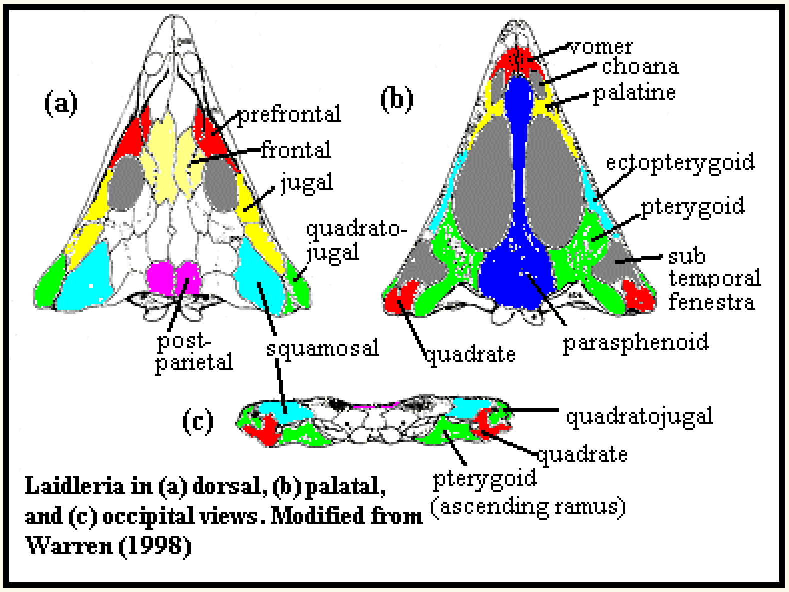
MAK020305

***Laidleria*:** *L. gracilis* Kitching, 1957

Range: Early Triassic of South Africa.

Phylogeny: Plagiosauroidea: Plagiosauridae + *. (Yates & Warren 2000)





Laidleria in (a) dorsal, (b) palatal, and (c) occipital views. Modified from Warren (1998)

Characters: 30-40 cm long. Extremely thin, flat skull forming an equilateral triangle; dentary teeth larger than corresponding maxillary teeth; dentary tusks present; maxilla excluded from choana by sutural articulation of palatine & vomer; more than 8 palatine teeth; no denticles on parasphenoid; ventral surface of pterygoid ornamented; ascending ramus of pterygoid does not contact squamosal; prefrontal and jugal in sutural contact; orbits behind mid-length of skull; quadratojugal with lateral projection; stapes robust, terminating under a solid section of skull roof, with no possible contact with a tympanum; uniform ornamentation of pits surrounded by ridges; strongly armored and "turtle-like;" no specialized scutes associated with neural spines.

Comments:

Yates and Warren 2000 make this genus the sister clade to the plagiosaurs, whereas Ruta et al 2007 place it on the Rhytidosteidae-Brachyopoid group (Rhytidostea). *Uruyiella liminea* Piñeiro et al., 2007 from the Permo-Triassic Buena Vista Formation of Uruguay is a closely related form (Piñeiro et al 2007) MAK111114

Graphic: *Laidleria gracilis* - life reconstruction by Dmitry Bogdanov, Wikipedia

Links: Plagiosauroidea, Wikipedia - Laidleria (stub) , Wikipedia - Uruyiella (stub) .

References: Warren (1998); Yates & Warren (2000). ATW010421.

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW050530, revised MAK111114

Rhytidosteids & Brachyopoids

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
    `--+--Euskelia
        |   |==Dissorophoidea
        |   |  `--LISSAMPHIBIA
        |   `--Eryopoidea
        `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   |--Laidleriidae
               |   `--+--Rhytidosteidae
               |        `--Brachyopoidea
               |           |--Chigutisauridae
               |            `--Brachyopidae
                `--+--Capitosauria
                   `--Trematosauria
                      |--Trematosauroidea
                      `--Metoposauroidea
```

Contents

Taxa on this Page

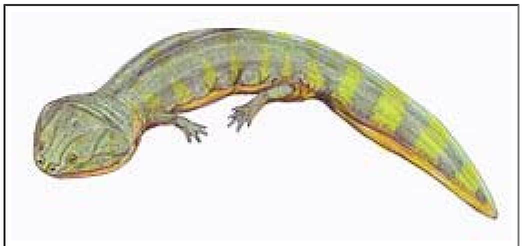
1. Brachyopidae X
2. Brachyopoidea X
3. Chigutisauridae X
4. Rhytidosteidae X

Brachyopoids

Compsocerops cosgriffi Sengupta, 1995 was a Chigutisaurid that lived during the Late Triassic of Gondwana (India); artwork by Arthur Weasley - Wikipedia

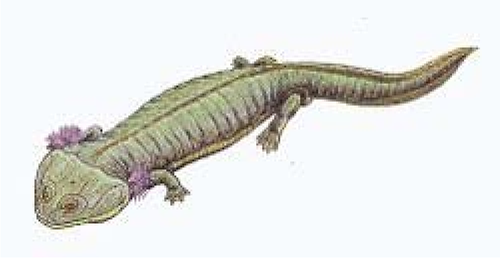
---

From **Adam Yates's blog *Dracovenator*: More temnospondyls: old big eyes from the Moenkopi (Tuesday, December 23, 2008)**:



Batrachosuchus, a classic brachyopid from the Early Triassic of South Africa. (Wikipedia)

Among the Triassic temnospondyls are the enigmatic brachyopids. Brachyopids present a classic case of the difficulty in disentangling convergence from relationship in an extinct group. Their shortened parabolic skulls bear more than a passing resemblance to another group of temnospondyls, the dvinosaurs (dinosaurs are good but a dvinosaur is devine – sorry, couldn't resist) and indeed the consensus opinion is that brachyopids are the derived descendants of earlier dvinosaurs.



Dvinosaurus, a dvinosaur from the Late Permian of Russia. (Wikipedia)

However brachyopids share some unusual derived characters with other derived temnospondyls from the Triassic known as stereospondyls. Some of these characters include: a double occipital condyle; the pterygoid bone in the palate forms a long broad suture with braincase rather than a narrow synovial contact; and lack of exposure of the opisthotic in the occiput. I took this to mean that brachyopids really were stereospondyls and share a more recent common ancestor with long snouted stereospondyls like *Paracyclotosaurus* than they do with short snouted dvinosaurs like *Dvinosaurus* (*right*), or rather that is what I found in my cladistic analysis that I performed for my PhD thesis, later published with my supervisor, Dr Anne Warren. This kind of ecophenotypic convergence seems to have happened multiple times in the evolution of crocodile snout shape (though maybe a little less than previously thought if false gavials and gavials really are sister taxa) and seeing it in temnospondyls was almost to be expected. Of course the situation isn't quite so simple, for instance some late surviving incontrovertible dvinosaurs *do* develop some of the stereospondyl synapomorphies convergently (even more disconcerting is that they develop them at the same time that the streospondyl lineage does!). So it really maybe the case that it is the unusual and apparently unrelated features of stereospondyls that are the convergences while the broad trophic adaptations such as snout shape are a true indication of relationship. It's a wonderfull and truly juicy puzzle that I once wanted to tackle myself, but I'm so thoroughly bogged down in dinosaur projects now that I can't see myself getting to it anytime soon. Furthermore the travel involved in unraveling this tangle is pretty daunting. Significant fossils are scattered all over the globe, with important specimens in many parts of the US, England, Argentina, South Africa, Australia and Russia. So for now I am happy to sit back and watch the progress from the sidelines. One researcher who has really picked up where I left off is Marcello Ruta. Marcello hasn't solved the problem yet but he has started really squeezing more phylogenetic information out of temnospondyl fossils than I ever did.

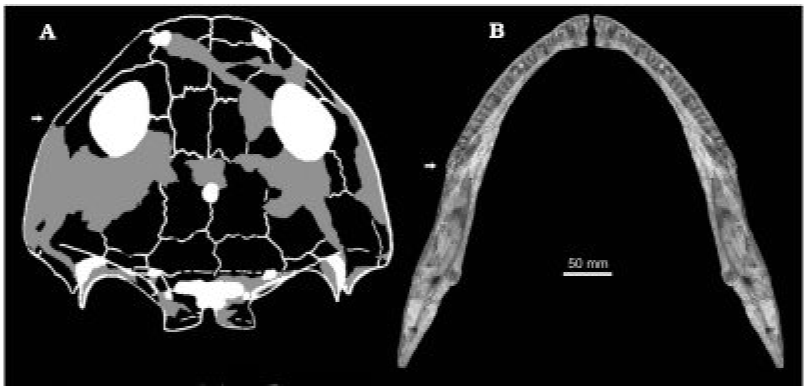
One little step on the road to understanding brachyopids has just been published by Marcello together with John Bolt of the Field Museum. They looked at *Hadrokkosaurus bradyi* a large brachyopid from the Moenkopi Formation of the US and one of the better known brachyopid names. The name *Hadrokkosaurus* means"big eyed lizard" and the skull disseminated around the world in the form of casts truly does have big goggling orbits.


The famous skull, referred to *Hadrokkosaurus*.

It comes as a surprise to many, myself included, that this famous skull isn't the holotype. Indeed the holotype doesn't even preserve orbits at all,for it is an isolated lower jaw ramus. Furthermore this lower jaw was found over 100km away from the skull. With a name like *Hadrokkosaurus* it is hard to dispute that the Welles had the skull in mind when he erected the name. However the jaw was found first and originally named *Taphrognathus*, which was unfortunately preoccupied by a conodont (*not* an arthropod for once!). Thus *Hadrokkosaurus* was created to replace *Taphrognathus*, leaving the lower jaw as the holotype specimen. This is a pity and it has created a messy taxonomic situation. Jupp and Warren suggested way back in 1986 that the lower jaw might not belong to the skull, and might not even be a temnospondyl at all! They cited the presence of an external mandibular fenestra, teeth that are partially sunk into sockets, weak surface ornamentation, a splenial bone that does not participate in the symphysis of the jaw and a surangular-prearticular contact behind the jaw joint, to suggest that the jaw is infact an archosaur (archosauriform in recent classifications). I need not remind you that a pair of roundned lower jaws fitting onto something roughly the size and shape of a dustbin lid makes for a pretty unusual archosauriform, particularly one of proterosuchian grade with subthecodont teeth. Because of the uncertainty surrounding the identity of the type jaw Anne Warren and Caudia Marsicano decided to bestow a new name upon the well-known skull, they called it *Vigilius wellesi*. The genus name means 'watchfull' or 'vigilant' and sort of echoes the original 'big eyed lizard'. The species name obviously honours Samuel Welles, the original describer of Hadrokkosaurus.

So is *Hadrokkosaurus* a weird-ass archosauriform? Definately not: Ruta and Bolt demolish any chance that these jaws belong to an archosauriform. The jaw shows some additional primitive bones (three coronoid bones, and two splenial bones) that are not found in any crown group amniotes, let alone in archosauriforms.

So its not an archosauriform what is it? Well it is without doubt a brachyopid after all. The so called un-temnospondyl like features are either artefacts of damage or misinterpretation (e.g. the so-called external mandibular fenestra) or are derived characteristics that are present in other temnospondyls (e.g. reduced ornamentation of the bone surface, subthecodont teeth and failure of the splenial to reach the symphysis). Furthermore a number of other characteristics, most obviously the honking big retroarticular process, are fairly convincing synapomorphies of Brachyopidae.

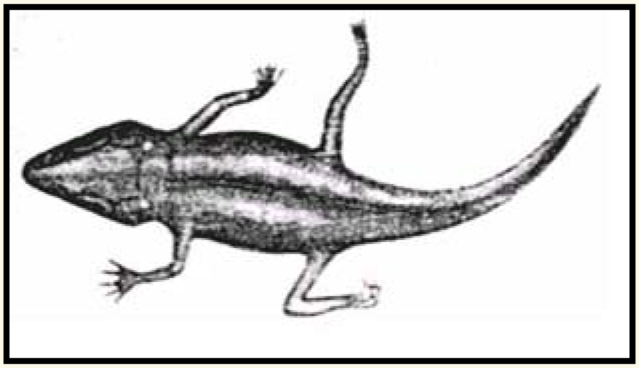


The skull of *Vigilius* (left) and the jaws of *Hadrokkosaurus* (with the right side mirrored) on the right. Taken from Ruta and Bolt 2008.

So are *Vigilius* and *Hadrokkosaurus* the same thing after all? I think they probably are, although Ruta and Bolt suggest that they may be two different brachypoids on the basis of non-matching jaw curvature. However we are dealing with different individuals of different sizes in a taxon that did not have precise occlusion in any case so slight differences in jaw curvature not convince me that they are distinct. Indeed both the lower and upper jaws seem to me to have slightly squared-off tips and angular margins that differ ever so slightly from the typical parabolic jawlines of most other brachyopids. This observation coupled with the highly reduced ornamentation of both *Vigilius* and *Hadrokkosaurus* (extreme even for brachyopids) and their occurence in the same formation leads me to suspect that the two taxa are indeed the same. We'll just have to wait to find a skull with jaws included to prove it.

Apart from clearing up the identity of *Hadrokkosaurus*, Ruta and Bolt 2008's paper is important because it demonstrates that a great deal of phylogenetic information can be gleaned from the lower jaws. They analyse lower jaw characters alone and recover a topology that has much in common with my own (there is some weirdness but what do you expect from analysing just one organ system?). In contrast my analysis included a paltry 14 lower jaw characters and probably would only be able to resolve a couple of nodes, if any at all, if run by themselves. That's a whole lot of information that shouldn't be ignored.

Descriptions



Rhytidosteidae: *Acerastia*, *Acadia*, *Deltasaurus*, *Derwentia*, *Nanolania*, *Peltostega*, *Pneumatostega*, *Rewana*, *Rhytidosteus*.

Range: Late Permian to Early Triassic worldwide.

Phylogeny: Trematosauria:::: Brachyopoidea + *.

Characters: Skull triangular, with straight sides; lacrimal absent; **$** transversely short, triangular condyles on quadrate without median sulcus [Y00]; otic notch shallow; broad cultriform process; quadrate ramus of pterygoid not "twisted"; **$** body of pterygoid, palatine ramus of pterygoid, vomers, cultriform process & anterior 2/3 of parasphenoid covered with dense field of denticles [Y00]; denticles lateral to dentary tooth row; teeth absent from coronoids; tusks on anterior ectopterygoid.

Links: Temno.htm; Lydekkerinidae/ Rhytidosteidae; Untitled Document; amphibians; TRIÁSSICO INFERIOR.

References: Yates (2000). ATW020820.

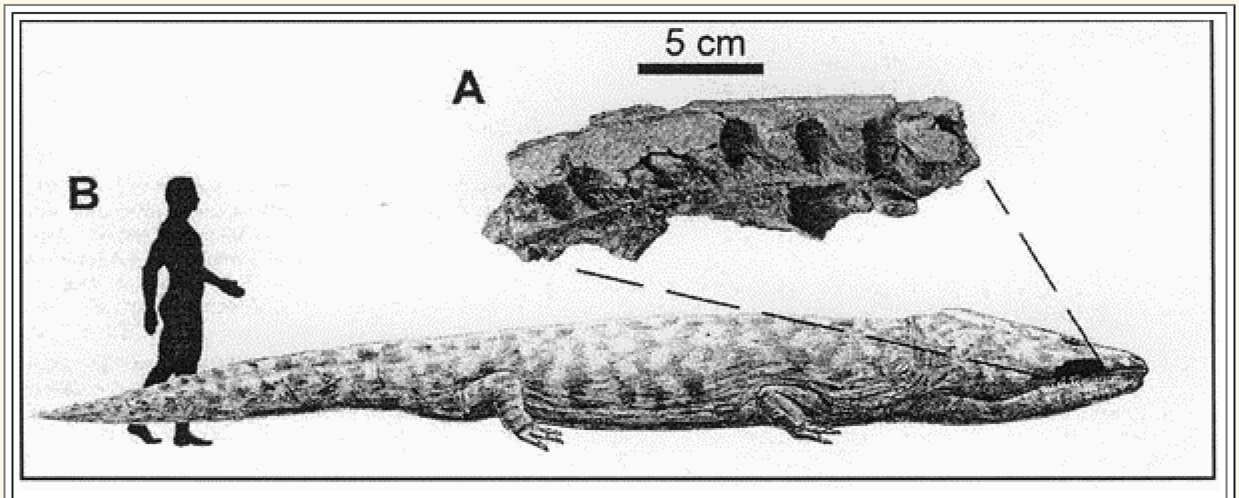
Brachyopoidea:

Range: Early Triassic to middle Cretaceous

Phylogeny: Trematosauria:::: Rhytidosteidae + *. Chigutisauridae + Brachyopidae. ATW000420.

These were short-headed semi-aquatic forms, they flourished during the Triassic. A few survived into the Jurassic and Cretaceous and grew to quite large size. MAK010417.

A giant brachyopoid



Representatives of several clades of temnospondyls reached huge size. These included the 9 meter long gavial-like Prionosuchus, an Archegosaurid from the Permian), and the 6 meter-long Mastodonsaurus (a middle Triassic Capitosaur). The illustration above

7 metre long Brachyopoid. Illustration by A. Beneteau (original url)

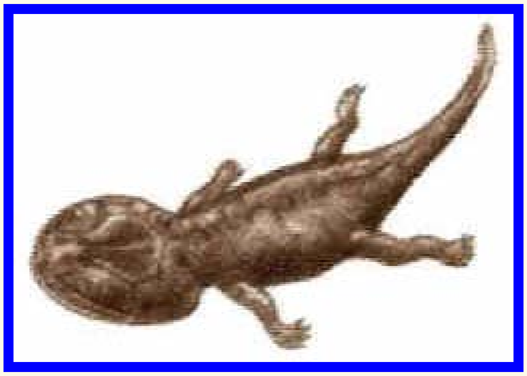
shows a giant brachyopoid from the Latest Triassic or Early Jurassic of Lesotho, estimated to have been some 7 metres in length, which dwarfs previous known giants of this clade such as *Siderops* and *Koolasuchus* (botha round 2.5 meters). A small fragment of a skull, just 22 cm long, was found in 1970 by a French Expedition near Alwynskop in Quthing District (Summary of events in Lesotho). Initially considered a mastodonsaur because of its size, it was redescribed by Steyer and Damiani, 2005 and found to be a Brachyopoidea (Brachyopidae + Chigutisauridae *sensu* Warren and Marsicano [2000]) based on its dental morphology, presence of a well-developed ectopterygoid tusk, and the concavity of the ventral margin of the skull in lateral view. (abstract)

MAK090724

Chigutisauridae: *Keratobrachyops, Koolasuchus, Siderops*. The last temnospondyls.

Range: Triassic? to middle Cretaceous.

Phylogeny: Brachyopoidea: Brachyopidae + *.



Brachyopidae: *Banksiops, Batrachosaurus, Batrachosuchoides, Batrachosuchus, Blinasaurus, Brachyops, Gobiops, Notobrachyops, Platycepsion, Sinobrachyops, Vanastega, Vigilius, Xenobrachyops*.

Range: Triassic? to Late Jurassic.

Phylogeny: Brachyopoidea: Chigutisauridae + *.

The Brachyopids were a group medium-sized tetrapods characterized by short, broad flat skulls with large eyes situated far forward. The legs are relatively small; the creature would have spent most of its life in streams and lakes, although it may have been quite capable of moving about on land. The upper margin of the mouth was armed with large fangs, indicating fish-eating habits. The different species are distinguished mainly by details of skull shape. MAK000208.

Links: A phylogeny of the Brachyopoidea (Temnospondyli, Stereospondyli) (abstract); amphibians (range data); JVP Content; Some Amphibian and Reptilian Remains (1859) (historical importance of *Brachiops*); Dinosaur museum (*Sinobrachiops* image and Chinese text); TRIÁSSICO INFERIOR. ATW031120.

Page Back | Unit Home | Page Top | Page Next

checked ATW050530

Capitosauria

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
   `--+--Euskelia
      `--Stereospondyli
         |--Rhinesuchidae
         `--+--Lydekkerinidae
            |--+--Plagiosauroidea
            |   `--+--Rhytidosteidae
            |       `--Brachyopoidea
             `--+--Capitosauria
                 |  `--+--Mastodonsaurus
                 |     `--Capitosauridae
                 `--Trematosauria
                    |--Trematosauroidea
                    `--+--Metoposauroidea
```

Contents

Taxa on this Page

1. Capitosauria X
2. Capitosauridae X
3. *Mastodonsaurus* X

Here's another of those very important groups of ancient amphibians that unfortunately at present only have scant coverage on *Palaeos*. Hopefully this will be rectified at some point. It's hasrd to imagine the Triassic period without capitosaurs lurking in rivers and waterways, they are such an integral part of the early Mesozoic landscape. Despite all looking very similar, with big flat solid heads and long stocky flattened bodies, they were actually quite a diverse group, including a number of distinct families and clades. They count among their number not only more modest sized creatures but some of the biggest amphibians to have ever lived, such as the huge *Mastondonsaurus giganteus*, which reached 6 or more meters in length. The Capitosaurs, or Mastodonsauroidea to give them a taxonomically equivalent but phylogenetically distinct name, were, along with the Trematosauriaia, the last great evolutionary radiation of temnosopondyl evolution, surviving the rigours of Pangaean droughts, giant phytosaurs, and more. Such an important and interesting group really deserve several detailed pages to summarise their phylogenetica history. For the present however, all that we can offer are a few short technical descriptions and an under construction sign. Hopefully this will be rectified in due course. MAK111116

Descriptions

Capitosauria:

Range: Early Triassic to Late Triassic.

Phylogeny: Stereospondyli::: Trematosauria + *: Lydekkerinidae + (*Mastodonsaurus* + Capitosauridae)

Introduction: The capitosaurs were a large and important group of large to huge flat-headed semi-aquatic or completely aquatic tetrapods. Some forms reached three to four or even five metres in length. They dominated the freshwater ponds, lakes and rivers of the Triassic, but were pushed to extinction by the carnivorous phytosaurs which appeared at the end of the period. MAK

Characters: Very flat skulls, small limbs, ossification reduced (obligate aquatic); some very large forms. ATW990919.

***Mastodonsaurus*:** Jaeger 1852;

Range: Middle Triassic of Europe.

Phylogeny: Capitosauria:: Capitosauridae + *.

Characters: ~6m;

Links: Mastodonsaurus; *Triassico*; Adventures in Etymology- Oplosaurus, Mastodonsaurus; Mastodonsaurus (Bullyland) (toy); amphibien keuper trias fossilien (most of jaw); fossil des monats trias (**Best on the Web**); Triassic (a bit hokey, but interesting); SITE Name- Ladram Bay to Sidmouth Parish- Sidmouth Local ...; Some Amphibian and Reptilian Remains (1859); Waldenburg Online - Bildung, Kultur & Vereine - Urweltmuseum. ATW030621.

Capitosauridae: *Cyclotosaurus, Eryosuchus, Kestrosaurus, Paracyclotosaurus, Parotosuchus*

Range: Early to Late Triassic of Russia, Australia & South Africa.

Phylogeny: Capitosauria:: *Mastodonsaurus* + *.

The capitosaurs were large aquatic tetrapods common throughout much of the Triassic The various species are distinguished by relative proportions of the snout, the ornamentation or sculpting on the skull, and the degree of closure of the otic notch.

Page Back | Unit Home | Page Top | Page Next

checked ATW060327. New page MAK111113

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Trematosauria: Metaposauroidea

Metaposaurs

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
   `--+--Euskelia
       |    `==Dissorophoidea
       |         `--LISSAMPHIBIA
       `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |  `--+--Rhytidosteidae
               |      `--Brachyopoidea
               `--+--Capitosauria
                   `--Trematosauria
                       |--Trematosauroidea
                       `--+--Metoposauroidea
                          |--Inflectosaurus
                          `--+--Latiscopidae
                             `-
-Metoposauridae
                                  |-
-Apachesaurus
                                  |-
-Arganasaurus
                                  |-
-Dunuitosaurus
                                  |-
-Koskinonodon
                                  `-
-Metoposaurus
```

Contents

Taxa on this Page

1. *Apachesaurus* X
2. *Arganasaurus* X
3. *Dunuitosaurus* X
4. *"Eupelor"* X
5. *Inflectosaurus* X

6. *Koskinonodon* X
7. Latiscopidae X
8. Metoposauridae X
9. Metoposauroidea X
10. *Metoposaurus* X

The Metoposaurs - aquatic preditors of the Late Triassic

"Buettneria" bakeri, life reconstruction, by Dmitry Bogdanov (Wikipedia)

Imagine an animal sitting at the bottom of a Triassic swampy pond or shallow lake, vaguely resembling a huge and quite flat frog, except with small hind legs and stubby tail; the whole creature some 2 meters in length. The head is almost pancake flat, the small upward facing eyes far forward and close to the snout. The scaly skin is a green or brown or mottled color to blend in with the murk, mud, and weeds among which the creature spends most of its time, completely motionless. Now and then it moves is to push off the bottom with a kick of a hind leg and a brief tail wriggle, take a gulp of air from the surface, and resume its position. Occasionally an unwary fish, or maybe a large crustacean, small amphibian, or juvenile phytosaur will swim by too close, wherupon the huge trapdoor mouth snaps open and shut and the luckless prey is gone.

If you can imagine that, you can imagine a metoposaur, or at least what I would think they might look and act like. Metoposaurs were one of the success stories of the Carnian (early part of the late Triassic) age, appearing out of nowhere to attain almost worldwide distribution (only absent in South America (South-West Pangea), perhaps because of geographical obstacles). Then, after some ten million years of success, they markedly declined, victim of the end Carnian extinction event. A few diminutive forms contuinued into the following, Norian , age, including a quite successful terrestrial type, but they too dissapeared, leaving no descendents of this short-lived but successful line.

What is very interesting about the Metoposaurs is that they weren't the only giant, flat-bodied, short-tailed, pancake-headed, bottom dwelling amphibians making life miserable for the smaller denizens of Triassic lakes, rivers and swamps. Move the eyes further towards the rear of the skull, make the body not quite as flat, you have a Capitosaur. Or, make the head very short, but still wide, so it is several times wider than long, and keep the body flat, add big feathery external gills, the result is a Plagiosaur. Why was it that three totally independent lines of temnospondyl each convergently evolved the same size and form, and how were they able to co-exist without out-competing each other?

Clearly Carnian ecosystems were rich, complex, and highly diverse; indeed the Cranian in many ways was the apex of the Triassic. I am reminded of the mighty Carboniferous coal swamps, where there were always a number of quite distinct but convergent large pike- or eel-like fish and amphibians (Xenacanthida, Rhizodontiformes, Crassigyrinidae, Colosteidae, Eogyrinidae, etc), each co-existing quite happily within specific niches, even though they would seem to follow the same lifestyle. But although both biomes show the same example of convergence among multiple aquatic clades, there the parallels ended. In the Carboniferous, a narrow, seperentine-like body was necessary to navigate the submerged logs and weeds to actively search for prey; in the Triassic, it seems like a bottom-dwelling flat-bodied ambush-predator was the way to go.

The end of the Triassic didn't mean the end of the amphibian giants. One clade, the brachyopoids continued right until the Cretaceous, and in at least one case attaining gigantic size. But they were never common or widespread except perhaps locally; the post-Triassic world was a very different place, and the time in which large amphibians dominated aquatic environments was gone forever.

MAK090808

Descriptions

Metoposauroidea: *Almasaurus, Koskinonodon*. Definition: *Almasaurus* + *Metoposaurus*. Yates & Warren (2000).

Range: Middle Triassic (Ladinian) to Late Triassic (Rhaetian). Probably cosmopolitan.

Phylogeny: Trematosauria:: (Plagiosauroidea + (Rhytidosteidae + Brachyopoidea))) + ***:** *Inflectosaurus* + (Latiscopidae + Metoposauridae)

Characters: **$** infra-orbital sulcus with a step-like flexure between orbit & naris [this appears to mean that the sensory line canal passing below the orbit makes a sharp medial or dorsal turn just anterior to the orbit, then an opposite turn anteriorly, to pass just outside each naris. However, this interpretation may be erroneous, since *Batrachosuchus* (=*Batrachosaurus*) (Plagiosauroidea) and even *Neldasaurus* (Dvinosauria) seem to have the same feature]; **$** length of posterior skull table >90% of width; **$** "gutter" bordered by ridges at margin of otic notch; exoccipital-pterygoid suture visible in ventral view; paired anterior palatal fossae; **$** keeled lateral margin of clavicle.

Links: Paleontology and Geology Glossary: M.

References: Yates & Warren (2000) [comparative remarks based on figures in Carroll (1988) from Watson (1956) and from Chase (1965), *vide* Carroll (1988)]. (ATW 000213)

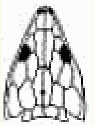
Inflectosaurus: Shishkin 1960. *S. amplus* Shishkin 1960.

Range: Early Triassic of Russia, Yarenskian Gorizont (Astrkhan)

Phylogeny: Metoposauroidea: (Latiscopidae + Metoposauridae) + * . [S02]

Characters: skull up to 70 cm [S+00]; orbits small [S+00]; pineal foramen close to middle of orbit - occiput distance [S+00]; quadrates posterior to occipital condyles [S+00]; preotic pterygoid ascending ramus strongly developed [S+00].

References: Shishkin *et al*. (2000) [S+00]; Steyer (2002) [S02]. ATW020721.



Latiscopidae [Almasauridae]: *Latiscopus disjunctus, Almasaurus habbazi*.

Range: Late Triassic (Late Carnian to Early Norian). SW USA (*Latiscopus*) and Morrocco (*Almasaurus* is known from the Lower Irohalene Member - Early Late Carnian of Morocco)

Phylogeny: Metoposauroidea**:** *Inflectosaurus* + (Metoposauridae + *)

Characters: slightly elongate and narrowly pointed muzzle,small lateral orbits, prominant dermosensory canals

Size: overall length about a meter

Comments: aquatic piscivores

References: Milner 1994 p.10,

MAK090724

Metoposauridae: Watson, 1919 *Metoposaurus*, *Koskinonodon*.

Range: Late Triassic (Carnian to Norian). Probably cosmopolitan.

Phylogeny: Metoposauroidea**:** *Inflectosaurus* + (Latiscopidae) + * **:** *Dunuitosaurus* + *Metoposaurus* + *Koskinonodon*

Characteristics: Lachrymal separated from the orbital margin by broad prefrontal-jugal suture; small widely spaced nares; continuous lateral-line loop behind the orbit [Milner 1994]

Introduction: A group of large flat-headed aquatic tetrapods. Although in appearance very like the capitosaurids in size and body proportions, the metoposaurs belong to a distinct lineage of temnospondyls. The most noticeable distinction (apart from various details of the skeleton) are the more forward position of the eyes. The metoposaurs were large mostly aquatic predators that fed on fish and small animals. As with many Triassic temnospondyls tetrapods the head was large and flat, with the eyes looking upwards. The creature probably spent a great deal of time submerged and motionless, waiting for an unwary fish or smaller tetrapod to swim past. The jaw was lined with teeth, and there were large teeth on the palate. Metoposaurs were strong swimmers, but would have been very clumsy on land, and it is likely that they ventured from water rarely, if at all.

Large numbers of fossil specimens have been found crowded together, dying when the ponds and lakes in which they lived dried up, and preserved when the mud that covered them hardened into rock. (MAK 980114)

Comments: These large successful aquatic animals are entirely limited in range to the Late Triassic, and were most common durintg the Carnian, when they achieved almost cosmopolitan distribution (they are however unknown from South America (SW Pangea) where their ecological role was taken by mastodonsaurs).

Metoposaurs were large amphibians; averaging about 2 meters in length, the largest may have reached 3 meters, rivalling the larger Capitosaurs in size. *Koskinonodon perfectum* (formerly known as *Buettneria*) had a skull 65 cm long and would have no doubt been able to hold its own against all but the largest phytosaurs. At the other end of the scale, the small, elongate, terrestrial *Apachesaurus*, with a skull less than 20 cm in length, seemed to have been survived after the larger aquatic types died out.

relationships between Metoposaur species

Attempts at working out the phylogeny of these animals remain controversial; as with temnosopondyls in general, there seems to be little agreement regarding the relationship between the different Metoposaur taxa, although the work of Sulej 2002 and 2007 has helped clarify the status of *Metoposaurus*. The following trees are presnted for comparison:

```
--+--Dunuitosaurus
  `-+--Apachesaurus
    `-+--+--B.bakeri
      |   `--M. diagnosticus
      |--Arganasaurus
```

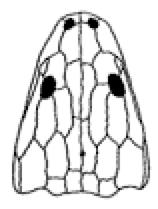
```
--+-
-Apachesaurus
  `-+-
-Metoposaurus
```

```
--+-
-Metoposaurus
  `-+-
-Apachesaurus
    `-+--K.
```

```
--+--B.
howardensis
  |--+--B.
perfecta
  |   `--+-
-Dunuitosaurus
  |      `--+-
-Arganasaurus
  |         `-
--Apachesaurus
  `-+--B.
bakeri
```

`-+--*B. perfecta* |--Anaschisma `--Dictyocephalus Hunt 1989. Note: Sulej 2002 has invalidated the characteristic Hunt has used here regarding the the lacrymal bone; hence *Metoposaurus diagnosticus* would have to be a sister taxon to *Buettneria perfecta* (= *Koskinonodon*).	`-+--*B. perfecta* `- -*Dunuitosaurus* Ruta *et al* 2007	*bakeri* `--*K. perfecta* Anon (unsigned NPS website)	`--+- -*Metoposaurus maleriensis* `--+- -*M. d. diagnosticus* `-- -*M. d. krasiejowensis* Sulej 2007 (converted to dendogram).

MAK090724



Apachesaurus: *Apachesaurus gregorii* Hunt, 1993

Range: Late Triassic (Latest Carnian to Middle Norian). SW N Am. (Lower and Upper Chinle and Redonda Formations of Arizona and New Mexico, Dockum Group of Texas). This animal is rare in the Carnian, were larger forms dominate, but much more common during the Norian [Milner 1994 p.11]

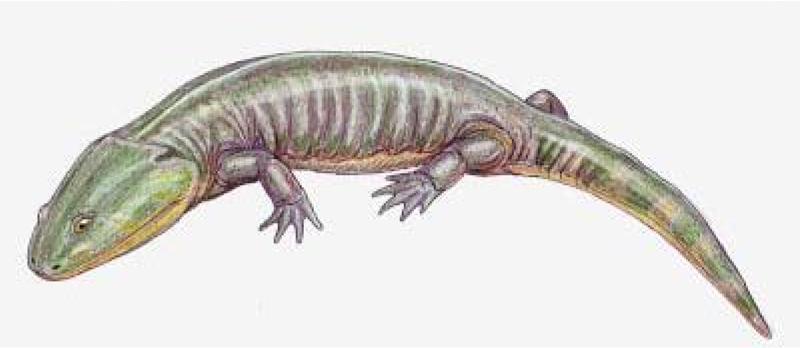
Phylogeny: Metoposauridae**:::** *
(see comments on phylogeny)

Synonyms: *Kalamoiketor pinkleyi* Branson & Mehl, 1929, *Anachisma* sp., perhaps *Dicytocephalus*.

Characters: reduction of otic notch and body size (Sulej 2007 p.124), Otic notch shallow and rounded [Hunt 1989], elongation of body, vertebral intercentra elongate with excavated articular faces, absense of pleurocentra, skull less than 25 cm [Milner 1994]

Ecological Niche: Terrestrial/Semi-aquatic insectivore/small carnivore

Notes: *Apachesaurus* is an unusual dwarf metoposaur (skull lengths of less than 20 centimeters) with a number of adaptations for a terrestrial existence (e.g. advanced pelvis). It seems that following the aridification of west equatorial Pangea, this little animal, which was pre-adapted to be less dependent on water than its larger cousins, not only survived but flourished. It is known from abundant intercentra, teeth, and other remains, as well as several partial skulls and skeletons, and other postcrania. Although Lucas 1998 mentions only a single species, and indicates this animal seems to have continued right up until the very end if the Triassic, it is not unlikely that over this extended period of time there were a number of closely related and similar species existing. A more realistic range would be latest Carnian (Adamanian faunal stage) to Early or Mid Norian

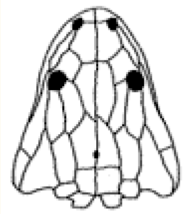


Life reconstruction of *Apachesaurus gregorii*, by Dmitry Bogdanov (Wikipedia)

Link: Petrified Forest National Park - Apachesaurus (useful reference but much shorter than their page on *Koskinonodon*); Wikipedia (includes references and useful life reconstruction (*left*), but nothing much else when I last looked)

MAK090724

Arganasaurus lyazidi (Dutuit, 1976).



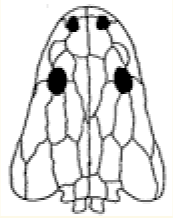
Range: Late Triassic (Upper Irohalene Member - Latest Carnian). Morocco.

Phylogeny: Metoposauridae::: *
(see comments on phylogeny)

Characters: reduction of otic notch and body size (Sulej 2007 p.124)

Notes: "Metoposaurus Grade 2" of Milner 1994. *Dunuitosaurus ouazzoui* (Dutuit, 1976) is included in this clade by of Milner 1994. Hunt 1989 considers that because of primitive features (presence of pleurocentra elements, long intercentra) that species is much more basal. *Arganasaurus* is distinctively smaller, and has a shallower otic notch, than *Dunuitosaurus* (Sulej 2007 p.123).

MAK090724



Dunuitosaurus: *Dunuitosaurus ouazzoui* (Dutuit, 1976) .

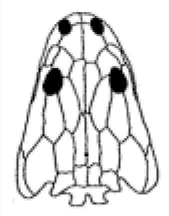
Range: Late Triassic (Lower Irohalene Member - Early Late Carnian (Otischalkian of Lucas 1998) of Morocco.

Phylogeny: Metoposauridae::: *
(see comments on phylogeny)

Characters: Pleurocentra elements, intercentra long [Hunt 1989]. Tail long (Lambert et al 2001, p.60)

Note: A fairly early form, characterised by primitive features, such as long intercentra. Other Metoposaurs have short intercentra. The long tail implies that *Dunuitosaurus* was more of an active hunter than a lurk and wait ambush predator.

MAK090808



"Eupelor" bakeri (Case, 1931)

Range: Late Triassic (Earliest Late Carnian - Otischalkian Age) N Am. (Dockum Group, Texas; Fundy Basin, Newark Supergroup, Nova Scotia). - note, the generic designation Eupelor is a provisional one, assuming that this species is not necessarily closely related to *K. perfecta*.

Phylogeny: Metoposauridae::: *
(see comments on phylogeny)

Synonyms: *Buettneria bakeri* Case, 1931, *Eupelor fraasi jonesi* (Case, 1922), *Metoposaurus fraasi jonesi* (Case, 1922), and *Metoposaurus bakeri* (Case, 1931) Hunt, 1993], Koskinonodon bakeri

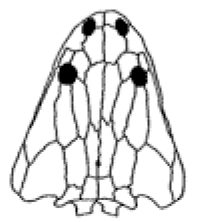
Characters: Anterior shift of lachrymal (Sulej 2007); lachrymal not close to orbit [Hunt 1989], incomplete sensory canal system [Murray 1986], elongate pits in the frontal and postorbital regions, extension of the palatal vacuities anterior to the orbits, narrower and more elongate skull, smaller adult size.

Notes: This species may be more primitive than other Metoposaurs, and it has an earlier stratigraphic range (Sulej 2007 p.123). . In a number of phylogenies it is not necessarily the sister taxon of *Koskinonodon perfecta*. Murray 1986 suggests that the elongate palatial vacuities and narrowness and small size of the skull indicate a juvenile rather than a distinct species, but other references acknowledge it as a valid species . Juvenile features could simply be a primitive neotonous or paedomorphic form. Also the incomplete lateral-line system is an advanced feature, like the elongate lachrymal entering the orbit, this feature seems to have evolved several times among metoposaurs.

According to Sulej 2007 p.126, *Buettneria bakeri* initiated a new lineage, in which the lacrimal out of the orbit margin. This was charcterised by a tendency to decreasing size and depth of the otic notch, and elongation of the interclavicle, and culminated in *Apachesaurus*.

B. bakeri also has a similar sculpture of the centrum of interclavicle to *B. perfecta*, which has lacrymal forms the margin of the orbit. In both these species the large area of the centrum is charcterised by polygonal pits. This feature distinguishes "*Buettneria*", from North America from the European and Indian species of the genus *Metoposaurus* Sulej 2002 p.125

MAK090724



Koskinonodon perfecta Case, 1922

Range: Late Triassic (Late Carnian) N Am. (Chinle Formation, Arizona and New Mexico; Dockum Group, Texas and New Mexico; Popo Agie Formation, Wyoming)

Phylogeny: Metoposauridae::: *
(see comments on phylogeny)

Synonyms: *Buettneria* Case, 1922 (Mueller, 2007) The generic name being preoccupied, it was replaced with *Koskinonodon* Branson and Mehl, 1929. Species synonymns: *Borborophaqus wyomingensis* Branson & Mehl, 1929, *Buettneria calgariensis* Green, 1954, *Buettneria howardensis* Sawin, 1945, *Buettneria major* Branson and Mehl, 1929, *Buettneria perfecta* Case, 1922, *Eupelor fraasi jonesi* Colbert and Imbrie, 1956, *Eupelor fraasi fraasi* Colbert and Imbrie, 1956, *Eupelor browni* Colbert and Imbrie, 1956, *Koskinonodon princeps* Branson & Mehl, 1929, *Metoposaurus browni* Roy Chowdhury, 1965, *Metoposaurus jonesi* Case, 1920, *Metoposaurus fraasi jonesi* Roy Chowdhury, 1965, *Metoposaurus fraasi fraasi* Roy Chowdhury, 1965

Characters: Elongation of lachrymal, shortening of prefrontal, reduction of interclavicle, centre (Sulej 2007), lachrymal entering the margin of the orbit. These featrures are all continued in *Metoposaurus* (Sulej 2002). The implication being that this form is either ancestral to *Metoposaurus* (Sulej 2007 p.127) or evolved *Metoposaurus*-like features in parallel.

Size: average skull length of about 65 centimeters. Assuming the same proportions as *Metoposaurus diagnosticus* (see illustration) that gives an overall length of about 3 meters, making it among the largest of the metoposaurs.

Skeleton of *Koskinonodon* (Buettneria), Dinosaur Exhibit at the American Museum of Natural History. (Wikipedia) What's wrong with this mount? That's right, the tail is too long! When skeletons of this species were first found, the tail was incomplete. Not knowing how much tail to add, and because the long, serpentine tail looks sexier, it was given a big tail at least in some reconstructions. Compare also the overlong tail of early reconstructuction of *Tyrannosaurus rex*. In life *Koskinonodon* almost certainly had a shorter tail, like the closely related *Metoposaurus* (see sketch of *Metoposaurus* skeleton).

Comments: A large and common animal, better known as *Buettneria*, The weak axial skeleton and intact lateral line system of the skull indicates that *Koskinonodon* was a fully aquatic amphibian. The teeth are sharp and conical, indicating a diet of fish and other small aquatic animals. The upward facing eyes indicaye an ambush predator, lying in wait in the soft mud at the water bottom and attacking suddenly from below. (NPS website)

Sulej 2007 considers *B. howardensis* a distinct species of *Buettneria*, and places this species at the bottom of his non-cladistic phylogenetic diagram (Sulej 2007 p.124). Anon (unsigned NPS website) identifies it with *Koskinonodon perfecta*

Link: Petrified Forest National Park - Koskinonodon (a detailed page and useful reference)

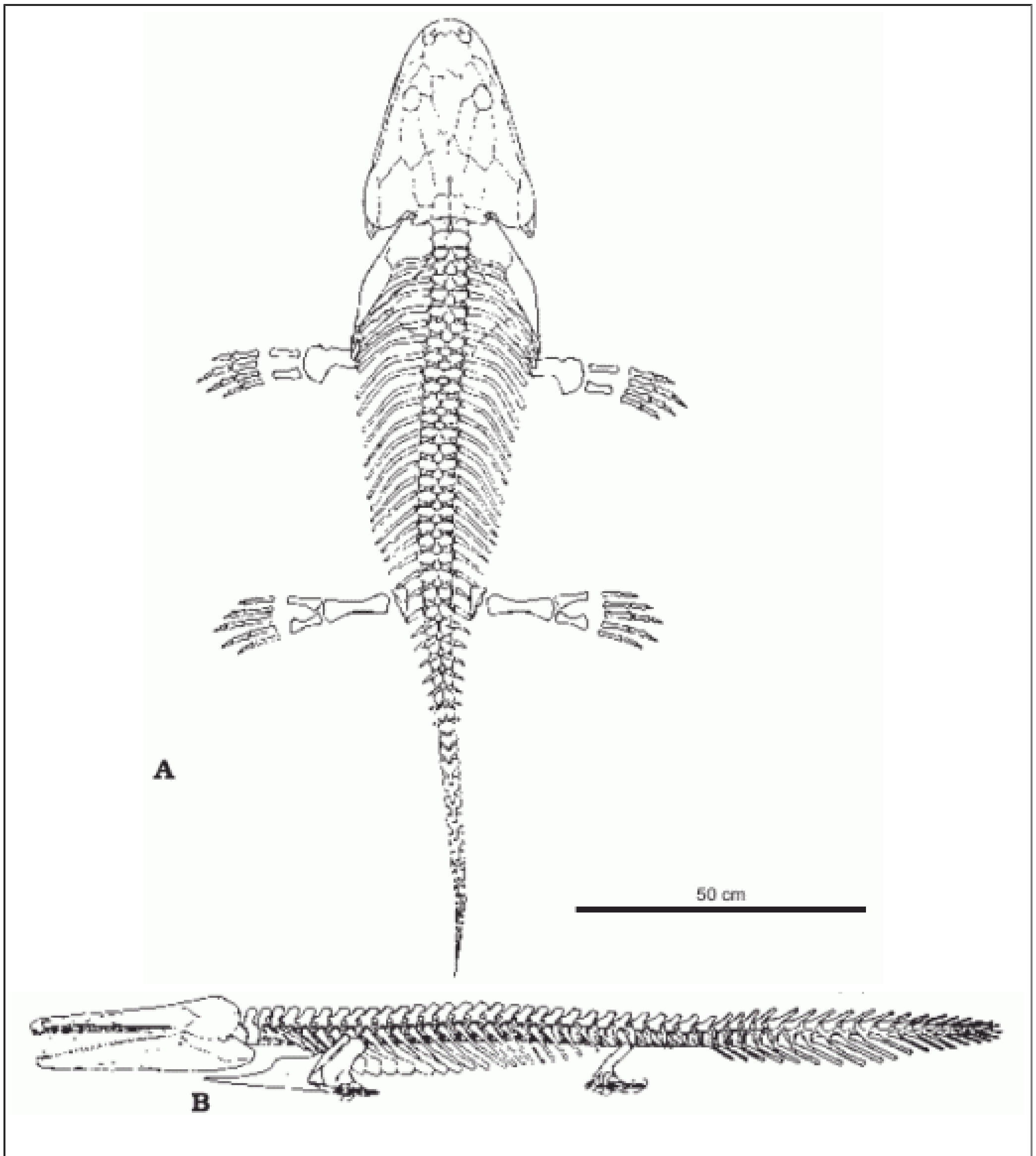
MAK090724

Metoposaurus Lydekker, 1890

Range: Late Triassic (Late Carnian to Early Norian). Europe and India.

Phylogeny: Metoposauridae::: * : *Metoposaurus maleriensis* + *Metoposaurus diagnosticus*
(see comments on phylogeny)

Characters: Lachrymal enters orbital margin as with *Koskinonodon* Sulej 2002 p.539; interclavicle with relatively long posterior part; small centre consisting of isometric pits; the glenoid of scapula directed posterolaterally; the braincase weakly ossified; the humerus, scapula, and fibula relatively slender. Sulej 2007 p.128



Metoposaurus diagnosticus krasiejowensis. Dorsal (A) and Lateral (B) view of skeleton.. Overall length 1.75 meters. Illustration from Sulej 2007 p.122

Comments: The German *Metoposaurus* has traditionally been distinguished from the American *Buettneria* (now *Koskinonodon*) on a certain detail of the bones around the eye socket. In *Koskinonodon* the lachrymal enters orbital margin (this being a specialized feature), whereas (Fraas 1889, Romer 1947) it was always thought that with *Metoposaurus* this was not the case. *Metoposaurus* therefore was given a more basal position in all phylogenies, for example Hunt 1989. But in a restudy of the European material, as well as of specimens from Krasiejów in Poland, Sulej 2002 has shown that in all European metoposaurs the lacrymal does actually enters the orbital margin, and in this regard these specimens do not differ from those of *Buettneria perfecta* (*Koskinonodon*) from North America. Sulej suggests that the metoposaur skulls studied by Fraas were poorly preserved and so he may have based his interpretation of the shape of the Metoposaur lacrimal largely on the much better preserved *Cyclotosaurus* fossils, to which he compared it.

In contrast to the lacrimal topography of *Metoposaurus* and *Koskinonodon*, in *Buettneria bakeri* (here "*Eupelor*"), *Apachesaurus gregorii*, *Dutuitosaurus ouazzoui*, and *Arganasaurus lyazidi* the lacrimal is excluded from the orbital margin. (Sulej 2002 p.539)

MAK090724

Metoposaurus maleriensis: Roy Chowdhury, 1965

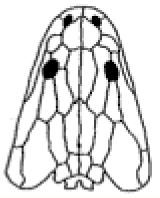
Synonyms: *Buettneria maleriensis* (Roy Chowdhury, 1965) Sengupta, 2002

Range: Late Triassic (Maleri Formation - Early Late Carnian (Otischalkian) of India. (Lucas 1998 p.366)

Phylogeny: *Metoposaurus* **:** *Metoposaurus diagnosticus* + *

Comments: Identified with *Koskinonodon perfecta* by Anon (unsigned NPS website), referred to *Metoposaurus* by Sulej 2007, who presents this species as more primitive than *Metoposaurus diagnosticus*

MAK090724



Metoposaurus diagnosticus (Meyer, 1842) Lydekker, 1890

Synonyms: Synonyms to this species include *Metopias diagnosticus* Meyer, 1842; *M. stuttgartiensis* Fraas, 1913 (nomen dubia) ; *M. heimi* Kuhn, 1932; and *Buettneria perfecta* Case, 1922 in part].

Range: Late Triassic (Late Carnian to Early Norian). Europe.

Phylogeny: *Metoposaurus* **:** *Metoposaurus maleriensis* + * **:** *M. d. diagnosticus* + *M. d. krasiejowensis*

Characters: Clavicles have long common margin anterior to the interclavicle [Hunt 1989] (only metoposaur with clavicles united in this way); Lachrymal enters orbit (Differs from *Apachesaurus*; *Arganasaurus*; *Dutuitosaurus*; and *Koskinonodon bakeri* in the position of the lacrimal which enters the orbital margin); area of rounded pits in middle of interclavicle small (Differs from *Koskinonodon* and *Apachesaurus* in the smaller area with sculpture formed by the isometric pits of the interclavicle.) (Sulej 2002)

Notes: A common European genus, which is distinct from the American and Gondwanan forms. It is a monotypic genus with a single species *Metoposaurus diagnosticus* with two subspecies. This animal flourished across a wide area during the Carnian, before dying out at the end of the age.

Reference: Sulej 2002

Comment: The type of *Metoposaurus stuttgartiensis*, from the early Norian Lehrbergstuff of Stuttgart-Sonnenberg, Germany, is the only known Norian metaposaur from Europe. Although too fragmentary to be diagnostic, I wouldn't be surprised if this turned out to be a distinct species. Like *Apachesaurus*, it was a relatively small animal [Milner 1994]

MAK090724

Metoposaurus diagnosticus diagnosticus (Meyer, 1842)

Range: Late Triassic (Early Late Carnian). Western Europe.

Phylogeny: *Metoposaurus diagnosticus* + * **:** *M. d. krasiejowensis* + *

Notes: the western subspecies

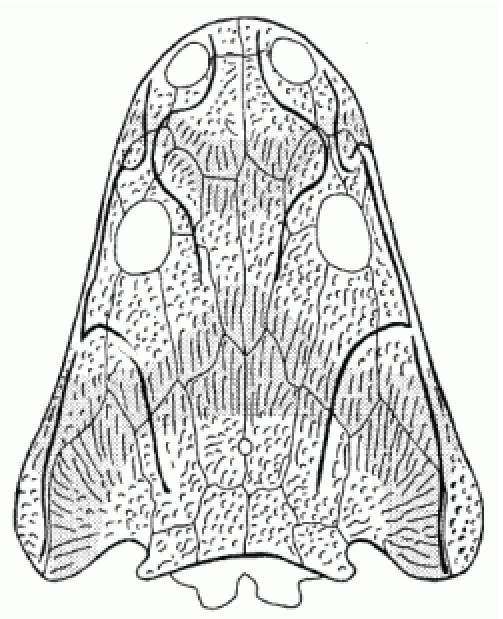
Reference: Sulej 2002

Metoposaurus diagnosticus krasiejowensis. Sulej, 2002

Range: Late Triassic (Otischalkian (Lucas 1998) /Early Ischigualastian (Langer 2005) / Early Late Carnian - Drawno Beds - Silesia in Poland). Eastern Europe

Phylogeny: *Metoposaurus diagnosticus* **:** *M. d. diagnosticus* + *

Characters: Differs from *Metoposaurus diagnosticus diagnosticus* in the much shorter pre-pineal part of parietal, and the larger expansion angle of sutures separating the parietal from the supratemporal (Sulej 2002 p.545)



Metoposaurus diagnosticus krasiejowensis. Zones of intense growth shaded. Illustration from Sulej 2002 p.545

Notes: the eastern subspecies, a more advanced species than *M. d. diagnosticus* The age of the Krasiejów spinicaudatan assemblage probably lies within the middle-late Carnian, which would mean that the two subspecies of M. diagnosticus are not chronosubspecies but geographic races. (Sulej 2007 pp.127-8).

Reference: Sulej 2002, Sulej 2007

MAK090724

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW040722, last modified MAK090808

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next
Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Temnospondyli: Trematosauroidea

Thoosuchinae

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
   `--+--Euskelia
       |   |==Dissorophoidea
       |   |  `--LISSAMPHIBIA
       |   `--Eryopoidea
       `--Stereospondyli
          |--Rhinesuchidae
          `--+--Lydekkerinidae
             |--+--Plagiosauroidea
             |   `--+--Rhytidosteidae
             |       `--Brachyopoidea
             `--+--Capitosauria
                 `--Trematosauria
                    |--Trematosauroidea
                    |  |--Thoosuchinae
                    |  |  |--Prothoosuchus
                    |  |  `--Thoosuchus
                    |  `--Trematosauridae
                    `--Metoposauroidea
```

Contents

Taxa on this Page

1. *Prothoosuchus* X
2. Thoosuchinae X
3. *Thoosuchus* X
4. Trematosauria X
5. Trematosauroidea X

Trematosauroidea: Ghosts from Gondwana?

According to Yates & Warren (2000), whom we have no reason to doubt, the middle part of the temnospondyl story goes something like this. Temnospondyls thrived throughout the Permian, during which they had a world-wide distribution. Whatever disaster overtook life on Earth at the end of the Permian killed off just about all of the temnospondyls in a fairly short space of time. Somewhere in Gondwana, a relict population held out. In the earliest Triassic (Induan), these forms radiated from Gondwana to repopulate the Earth. The two major branches of this renaissance were the Capitosauria (*e.g.*, lydekkerinids, capitosaurs, and mastodonsaurs) and the **Trematosauria**, including the **Trematosauroidea** and all other post-Permian temnospondyls.

Not surprisingly, some of the most basal temnospondyls we see are the trematosauroids. Its not surprising that we *see* them, because they are big and easy to find. Its not surprising that we see them *early* because they are the only stem tetrapods to have developed truly marine forms. We would thus anticipate that they would radiate fast and far. In fact, the odd thing is that we don't see them even earlier than the Oleneckian, some 2 My after the dawn of the Triassic.

At least this is what Damiani (2001) states. Damiani's paper is, in some ways, a paper of classic quality. In other respects, it is rather frustrating. In fairness, Damiani did not set out to study the Trematosauria. Quite the contrary. He aims at a comprehensive revision of the Capitosauria, or what he believes would be better termed the "Mastodonsauroidea." However, in order to delineate his group, he necessarily takes in some trematosaurian genera, including ***Thoosuchus***, *Angusaurus*, and *Trematosaurus*. So far as the Capitosauria are concerned, he has certainly produced a definitive reorganization of the clade. However, some of the details relating to the taxa of interest to us on *this* page are unclear. See, for example, the comments set out as notes under the entries for*Thoosuchus* and *Yarengia*.

Another bone we would pick with Damiani relates to the bones he picked. That is, how can we possibly assess the phylogenetic position of the Capitosauria when the *only* other Triassic forms in the cladogram are trematosauroids? The problem can be summarized in the following, highly abbreviated, cladograms:

Yates & Warren (2000)

```
Stereospondyli
|--Capitosauria
|  |--Lydekkerinidae
|  `--+--Mastodonsaurus
|     `--+--Benthosuchus
|        `--Capitosauridae
`--Trematosauria
   |--Trematosauroidea
   `--+--Metoposauroidea
      `--+--Plagiosauroidea
         `--etc.
```

Damiani (2001)

```
Stereospondyli
|--Lydekkerinidae
`--+--Mastodonsauroidea
   |  |--Benthosuchus
   |  `--Mastodonsaurus deeply nested
   |       in a mess of capitosaurids
   `--Trematosauroidea
```

The differing position of the Lydekkerinids is obviously of some interest. To Yates & Warren, they are the sister of all Capitosauria. To Damiani, they end up being the sister group of *all* other Triassic temnospondyls. *Benthosuchus* is also of considerable importance. It has historically been regarded as a trematosaur of some kind and differs from them in only a few characters. Damiani asserts that it is the sister of all other capitosaurs and *Mastodonsaurus*. But how can we have any confidence in Damiani's findings about either group if we do not know the branch point leading to all other Triassic temnospondyls? And, if we are unsure about the positions of either lydekkerinids or *Benthosuchus*, how much confidence can we have in the rest of the arrangement?

At its most abstract -- but also most fundamental -- level, the problem is that you need a clade to make a cladogram. Unless Yates & Warren (and many others) are very far off base, the study taxa do not constitute a clade. Somewhere between the granddaddy stereospondyl and *Trematosaurus* there is a branch leading to hundreds of other species of stereospondyl, including metoposaurs, plagiosaurs, batrachosaurs and many, many others.

Absent a clade, it is a bit of a strain to talk about consistency, and that may be why Damiani does not use any tests of consistency. A consistency index measures how many times a character flips from one state to another in the cladogram. If a large chunk of the clade is missing, as here, there is no way to measure consistency. This is not simply a choice of statistical measures. The whole point of a parsimony-based cladogram is to be parsimonious – that is, to minimize the total number of character state changes. That's not possible unless you haveenough taxa to fairly sample the changes which occurred in the clade. If one arbitrarily hacks off branches, there is no valid measure of parsimony. We don't get a phylogenetic tree, but a paraphyletic topiary shaped by the choice of test taxa.

In the last analysis, we can confidently buy into Damiani's cladogram of the Capitosauridae, excluding *Benthosuchus*.

This clearly leaves a monophyletic group, although it may unreasonably exclude lydekkerinids. This means that Damiani is likely correct in placing *Mastodonsaurus* deeply among the capitosaurids. Hence he *may* be correct in changing the name to Mastodonsauroidea. However, lacking valid information on the position of the two key sister taxa (lydekkerinids and *Benthosuchus*), it is more difficult to accept the higher-level placement of this clade. Since we can't yet be confident in the placement of *Benthosuchus*, it is too early to accept Mastodonsauroidea (= *Benthosuchus* + *Mastodonsaurus*) as a useful taxon. ATW020722.

Descriptions

Trematosauria: *Trematosaurus* > *Parotosuchus*.

Range: Early Triassic to middle Cretaceous.

Phylogeny: Stereospondyli::: Capitosauria + *: (Trematosauroidea + Luzocephalidae) + (Metoposauroidea + (Plagiosauroidea + (Rhytidosteidae + Brachyopoidea))).

Characters: Interorbital space > 50% of skull width at mid-orbit; foramen on stapes absent; no sharp rimmed depression on posteroventral surface of parasphenoid (reversal); denticle patches absent from coronoids.

References: Yates & Warren (2000). ATW000213.

Trematosauroidea: *Thoosuchus* + *Trematosaurus* [YW00] *Vybrosaurus*?

Range: Early Triassic (Olneckian) [D01]

Phylogeny: Trematosauria:: Luzocephalidae + *: Thoosuchinae + (*Yarengia* + Trematosauridae).

Introduction: Large, gharial-like forms with elongated rostrums, probably specialized for catching fish. Inkeeping with Yates & Warren (2000) the short-lived northern Pangean Thoosuchinae (formerly considered basal capitosauroids) are transferred from the Capitosauroidea to the Trematosauroidea. They could perhaps be considered primitive members of this lineage.

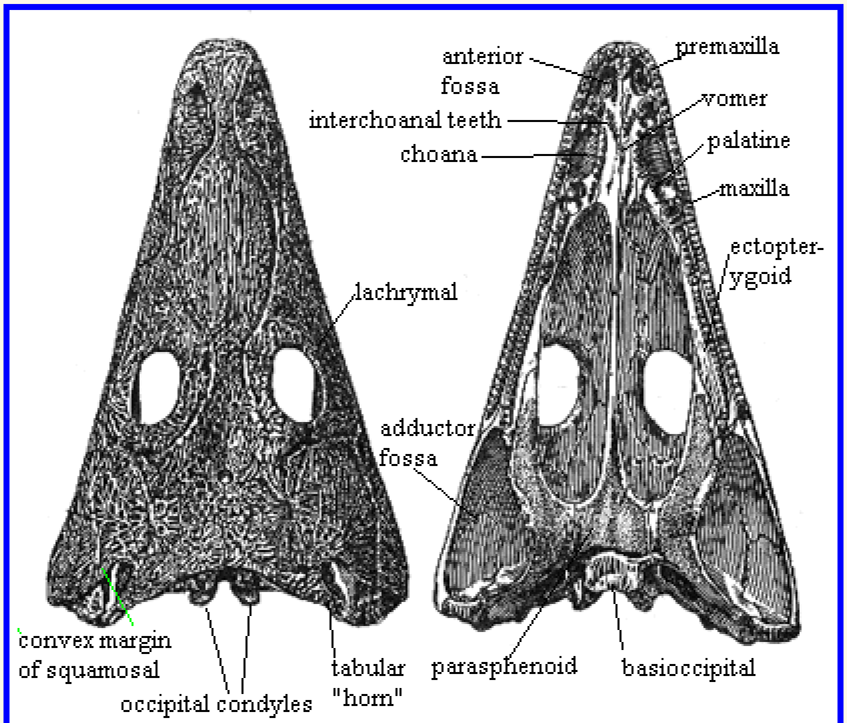
Characters: Specialized long-nosed marine fish-eaters. Skull generally wedge-shaped, tall and narrow [S+00]; long snout formed by extended frontals, narials and premaxillae; nares long & narrow [D01]; orbits well-separated [S+00]; frontal excluded from orbit [S+00]; lateral projection of postorbital reduced or absent [S+00]; postorbital, prepineal growth zone present [D01] **[1]**; tabular horns and otic notch reduced or absent [S+00]; squamosal minimally embayed; sensory canal present on occiput [D01]; *pterygoid oblique ridge* reduced [S+00]; *glenoid fossa* below level of dorsal surface of dentary [D01]; **$** parasphenoid plate extends posteriorly to cover exoccipital condyles in ventral (?probably means palatal) view [YW00]; **$** parasphenoid cultriform process laterally compressed so that sides meet to form midline ventral keel [YW00][D01]; cultriform process underplated by a posterior extension of the vomers [D01]; pterygoid - parasphenoid suture extends back to underlie anterior part of middle ear cavity [S+00]; labial wall of adductor fossa arched dorsally (in lateral view) [D01]; ectopterygoid enters margin of interpterygoid vacuity [D01]; **$** paired anterior palatal fossae [YW00] [S+00]; posterior *Meckelian foramen* long, exceeding 50% length of *adductor fossa* [D01]; pterygoid denticle fields well-developed [S+00]; ectopterygoid tusks absent in adults [D01] (*contra*, [S+00]); retain primitive paired pleurocentra in vertebrae; well-developed lateral line system [D01] [S+00]; at least some forms marine(!).

Notes: [1] Temnospondyls usually show a pattern of ornamentation on dermal skull bones consisting of a pattern of ridges and pits. In some cases, the pits seem to be stretched out into grooves. These are thought to represent regions of localized growth. A marked zone of this sort is characteristic of trematosauroids. Damiani (2001) lists it as a synapomorphy of the clade. However, Damiani did not include *any* trematosaurians in his study other than trematosauroids (*i.e.* no metoposaurs, plagiosaurs, rhytidosteids, etc.). As a result, the status of his trematosauroid synapomorphies is unclear. They may, instead, represent characteristics of all Trematosauria. Against the background of Yates & Warren (2000) it seems likely that Damiani is correct -- if nothing else, both Yates and Damiani did much of their critical work in Prof. Warren's lab at the same time. However, out of an abundance of caution, I have not flagged these characters as synapomorphies of Trematosauroidea on the basis of Damiani's study alone.

Links: Abstracts for PaleoBios 14(1-4) (include Lonchorhynchinae?); Trematosauroidea; Steyer (2002).

References: Carroll (1988); Damiani (2001) [D01]; Pough et al. (1999); Shishkin *et al*. (2000) [S+00]; Yates & Warren (2000) [YW00]. ATW030126.

Thoosuchinae: (= Thoosuchidae) *Thoosuchus*, *Prothoosuchus*.



Thoosuchus yakovlevi skull in dorsal and palatal views

Range: Early Triassic (Early Olneckian) [D01] of Russia.

Phylogeny: Trematosauroidea: (*Yarengia* + Trematosauridae) + *: *Prothoosuchus* + *Thoosuchus*.

Characters: lacrimals present; orbits posterior to midpoint of skull; skull table not elongated; sensory sulci on skull roof; convex squamosal margin which bulges and narrows otic notch in ventral view [YW00]; deep otic notch; tabular well developed; tabular horns extend to posterolateral margin of skull; quadratojugal does not contribute to mandibular condyle [D01]; doubled occipital condyle, without contribution from basioccipital; anterior palatal fossae separated by median ridge; vomer, palatines, and maxilla all contribute to margin of choana; parasphenoid extends posteriorly to partially cover base of occipital condyles in ventral view (note that figure does not show this condition, & instead suggests that the basioccipital partially covers the condyles); some muscular crests on posterior of parasphenoid; premaxillary teeth unspecialized; vomer without denticles; ectopterygoid without tusks, with >3 rows of teeth; posterior coronoids with teeth (?); dermal bones ornamented with ridges enclosing pits.

Links: Thoosuchus; bone_clones_thoosuchus; Comparative Vertebrate Anatomy - Lecture Notes 1; TIKHVINSKOYE

Image: modified from More Thoosuchus yakovlevi, citing Ryabinin (1925).

References: Damiani (2001) [D01]; Yates & Warren (2000) [YW00]. ATW020719.

Prothoosuchus: Getmanov 1989. *P. blomi* Getmanov 1989, *P. samariensis* Getmanov 1989.

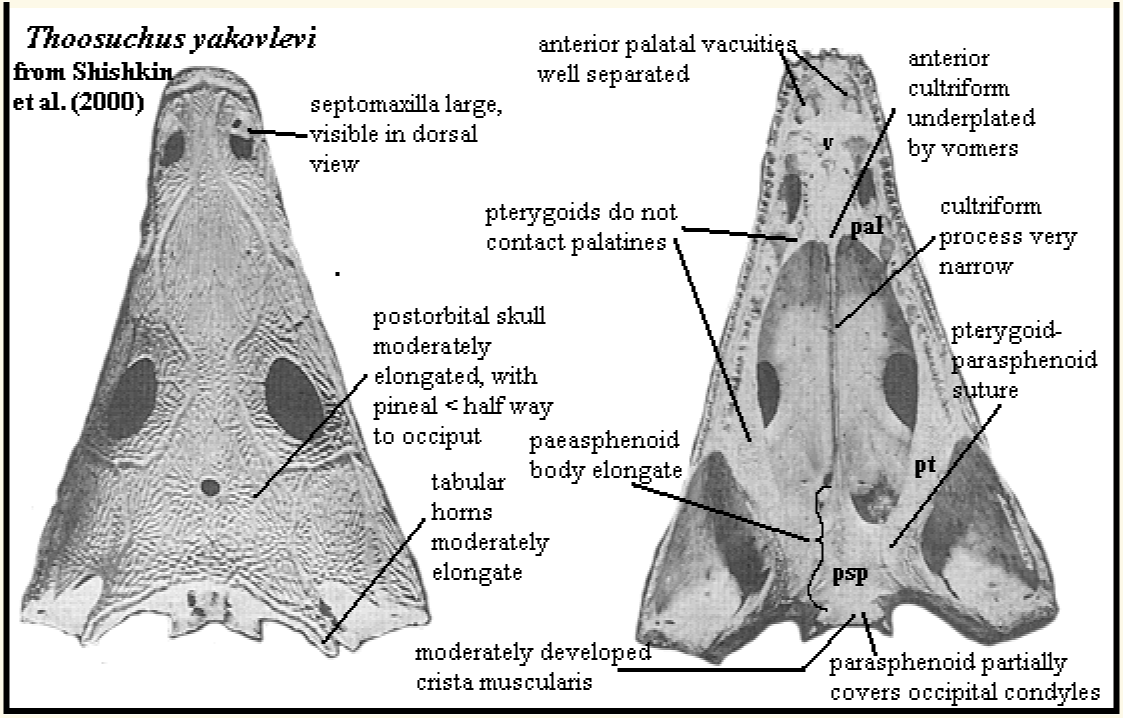
Range: Early Triassic of Russia.

Phylogeny: Thoosuchinae: *Thoosuchus* + *.

Characters: pineal foramen close to posterior margin of orbits [S+00]; parasphenoid cultriform process relatively broad [S+00].

References: Shishkin *et al*. (2000) [S+00]. ATW020720.

Thoosuchus: Efremov 1940. *T. yakovlevi* Ryabinin 1927, *T. tardus* Getmanov 1989, *T. tuberculatus* Getmanov



1989.

Range: Early Triassic of Russia.

Phylogeny: Thoosuchinae: *Prothoosuchus* + *.

Characters: septomaxilla large and exposed on dorsal surface [S+00]; orbits broadly separated [S+00]; skull roof moderately elongated behind orbits [S+00]; pineal foramen in anterior 1/3 of orbital - occipital distance [S+00]; lateral projection of postorbital weak or absent [S+00]; posterior squamosal margin convex, narrowing otic notch [YW00] **[1]**; tabular horns moderately elongated [S+00]; parasphenoid plate elongate, with moderate *cristae muscularis* [S+00]; cultriform process very narrow [S+00]; pterygoid does not contact palatine [S+00]; anterior palatal vacuities broadly separated [S+00]; lower jaw with pronounced retroarticular process [S+00]; well-developed posterior Meckelian foramen [S+00]; surangular medial process weak [S+00]; tooth rows between choanae meet at acute angle [S+00].

Notes: [1] in Yates & Warren's (2000) study, this is the only character state which separates *Thoosuchus* from the Trematosauridae. Damiani (2001) states that they differ because *Thoosuchus* has a deep otic notch. Yates & Warren score this character as unknown for trematosaurids. Damiani also states that they differ because the occipital condyles in *Thoosuchus* are anterior to the quadrate condyles. In the image, this simply does not appear to be the case. However, compare the illustration of the *same* specimen from Ryabinin's original paper under Thoosuchinae.

Links: TIKHVINSKOYE; Thoosuchus; Thoosuchus Skull - Thoosuchus spp; TRIÁSSICO vertebrados (Spanish).

References: Damiani (2001); Shishkin *et al*. (2000) [S+00]; Yates & Warren (2000) [YW00]. ATW020720.

Page Back | Unit Home | Page Top | Page Next

checked ATW050530

Temnospondyli: Trematosauroidea: Trematosauridae

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
|--Edopoidea
`--+--Dvinosauria
    `--+--Euskelia
       |   |==Dissorophoidea
       |   |  `--LISSAMPHIBIA
       |   `--Eryopoidea
       `--Stereospondyli
          |--Rhinesuchidae
          `--+--Lydekkerinidae
             |--+--Plagiosauroidea
             |   `--+--Rhytidosteidae
             |       `--Brachyopoidea
             `--+--Capitosauria
                `--Trematosauria
                   |--Trematosauroidea
                   |   |--Thoosuchinae
                   |   `--+--Yarengia
                   |      `--Trematosauridae
                   |         |--Luzocephalidae
                   |         `--+--Angusaurus
                   |            `-
-Trematosaurus
                   `--Metoposauroidea
```

Contents

Trematosaurus brauni, life reconstruction, by Dmitry Bogdanov (Wikipedia)

Taxa on this Page

1. *Angusaurus* X
2. Luzocephalidae X
3. Trematosauridae X
4. *Trematosaurus* X
5. *Yarengia* X

Descriptions

Yarengia**:** Shishkin 1960. *Y. perplexa* Shishkin 1960.

Range: Early Triassic (Early Olneckian) of Russia (Archangel'sk).

Phylogeny: Trematosauroidea:: Trematosauridae + *.

Characters: exoccipital with reduced subotic process and elongated base [S+00]; **$** parasphenoid body elongated, constricted (?) in the midline and indented on rear margin [D01]; parasphenoid plate ornamented [S+00]; pterygoid - parasphenoid suture elongate [D01] and underlies tympanic cavity [S+00]; parasphenoid *crista muscularis* curved in a unique fashion [D01]; "ornament on pterygoid predominates over shagreen" [S+00]; anterior palatal vacuities fused [S+00]; interchoanal tooth rows meet at acute angle [S+00].

Note: [1] known from an isolated basicranium. **[2]** Damiani (2001: 441) lists several other characters of unreasonable obscurity. He states that *Yarengia* is a mastodonsauroid (= capitosaurian) based on "a well-developed *crista muscularis* of the parasphenoid which presumably would have been confluent in the midline, and the presence of a *crista obliqua* of the pterygoid." The prominent *crista muscularis* is a character shared with the trematosauroids. The "confluence" character is found in other Mesozoic temnospondyls (Damiani, 2001: 454) and is thus probably a synapomorphy of a clade more inclusive than Mastodonsauroidea. While absent in *Thoosuchus* and *Angusaurus*, the state of this character is not known in *Trematosaurus*. The oblique ridge of the pterygoid is a character which, as Damiani notes, is also present in some trematosaurids (2001: 456). Even more significantly, *Yarengia* has an elongated pterygoid-parasphenoid suture, a synapomorphy of the Trematosauridae. Accordingly, pending more complete specimens, *Yarengia* is treated as a trematosauroid, as Shishkin originally proposed.

References: Damiani (2001) [D01]; Shishkin *et al*. (2000) [S+00]. ATW020720.

Trematosauridae: *Aphaneramma*, *Erythrobatrachus*, *Lyrocephaliscus*, *Mahavisaurus*, *Microposaurus*, *Platystega*, *Stoschiosaurus*, *Tertrema*, *Tertremoides*, *Trematosaurus*, *Trematosuchus*, *Wantzosaurus*. Defined [S02] as *Wantzosaurus* + *Lyrocephaliscus*.

Range: Early Triassic (Olneckian) [D01] to Late Triassic [S02] of Australia, Europe (Spitsbergen), South Asia (Pakistan) & Madagascar [S02].

Phylogeny: Trematosauroidea:: *Yarengia* + *: Luzocephalidae + (*Angusaurus* + *Trematosaurus*).

Characters: orbits broadly separated [S+00]; strong postorbital extension of skull table [S+00]; pineal foramen in posterior 1/2 of orbit - occiput distance [S+00]; squamosal posterior margin straight or concave [YW00] **[1]**; **$** otic notch reduced to an embayment [D01]; occiput deep [S+00]; **$** occipital condyles level with or posterior to quadrate condyles [D01]; parasphenoid plate elongate [S+00]; parasphenoid without *crista muscularis* [S+00]; parasphenoid plate extending posteriorly to cover the pedicel of exoccipital condyles (in ventral view) [S02]; parasphenoid, cultriform process laterally compressed and knife-edged [S+00] [S02$]; $ suture between pterygoid and parasphenoid elongated antero-posteriorly [D01]; pterygoid usually does not contact palatine [S+00]; pterygoid, ascending ramus, does not contact squamosal [S02]; anterior palatal vacuities well-separated [S+00]; retroarticular process elongate [S+00]; elongate posterior Meckelian foramen [S+00]; interchoanal tooth rows reduced or absent [S+00].

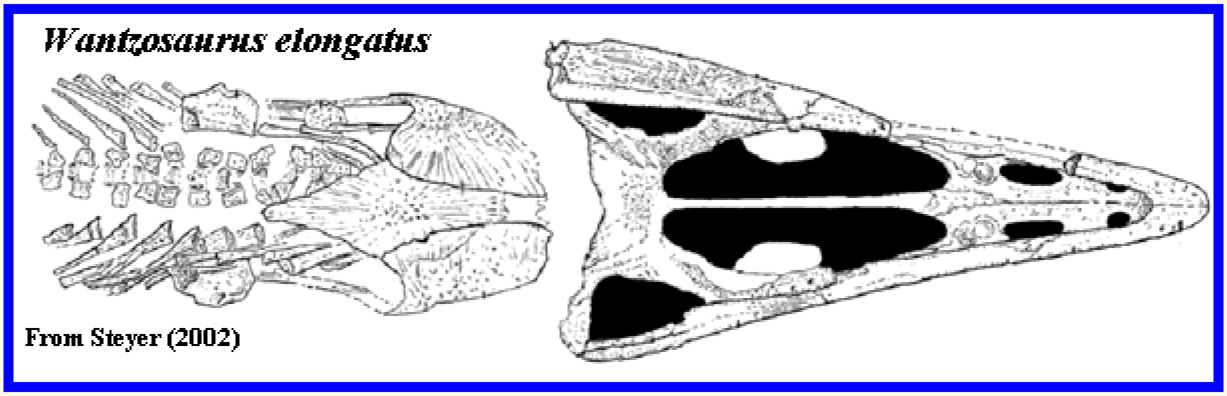


Image: (right) *Tertrema*, © 1999, Palaeontological Museum, University of Oslo, Norway, courtesy of Dr. Hans Arne Nakrem.

Notes: [1] In Yates & Warren's (2000) study, this is the only character separating *Thoosuchus* from the Trematosauridae. *See also* related comments set out as a note under *Thoosuchus*.

Links: Abstracts for PaleoBios 14(1-4); amphibians; Trematosauroidea

References: Damiani (2001) [D01]; Shishkin *et al*. (2000) [S+00]; Steyer (2002) [S02]; Yates & Warren (2000) [YW00]. ATW030905.

Luzocephalidae: *Luzocephalus*.

Range: Early Triassic (Induan).

Phylogeny: Trematosauridae: (*Angusaurus* + *Trematosaurus*) + *. [S02]

Characters: Pterygoid unornamented and without denticles; ascending ramus of pterygoid does not contact squamosal (palatoquadrate fissure); main body of pterygoid broadly contacts lateral margins of parasphenoid; ectopterygoid with at least 3 rows of teeth, but tusks absent; vomeral fangs joined by transverse tooth row; posteroventral parasphenoid without rimmed depressions; parasphenoid denticles extend transversely onto ectopterygoid; palatine with elongate posteromedial process and >8 teeth; medial margin of choana with tooth row; prefrontals postfrontals articulate; maxilla - quadratojugal contact reduced or absent; orbits located about half-way along skull; orbits widely spaced; postorbital skull length 70-90% of width; straight or concave margin of squamosal in dorsal view; squamosal & tabular articulate on skull roof; otic notch wide, shallow embayment; extensive sensory sulci on skull; skull ornamentation of small pits enclosed by ridges.

Note: [1] Could well be a Lydekkerinid. [S+00] **[2]** The monophyly of this taxon seems to be in doubt. Several species of *Luzocephalus* have been referred to other families.

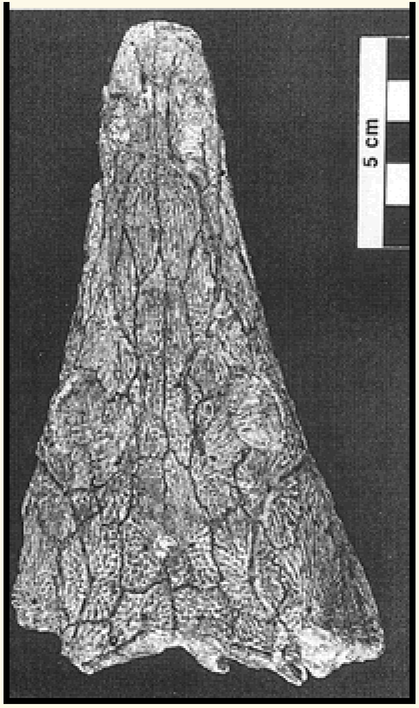
References: Shishkin *et al*. (2000) [S+00]; Steyer (2002) [S02]; Yates & Warren (2000). ATW030905.

Angusaurus: Getmanov 1989. *A. dentatus* Getmanov 1989, *A. succedaneus* Getmanov 1989, *A. tsylmensis* Novikov 1990 (?= *Trematosaurus* [S02]), *A. weidenbaumi* (= *Trematosaurus w.* = *Thoosuchus w.*) Kuzmin 1935.

Range: Early Triassic of Russia.

Phylogeny: Trematosauridae:: *Trematosaurus* + *.

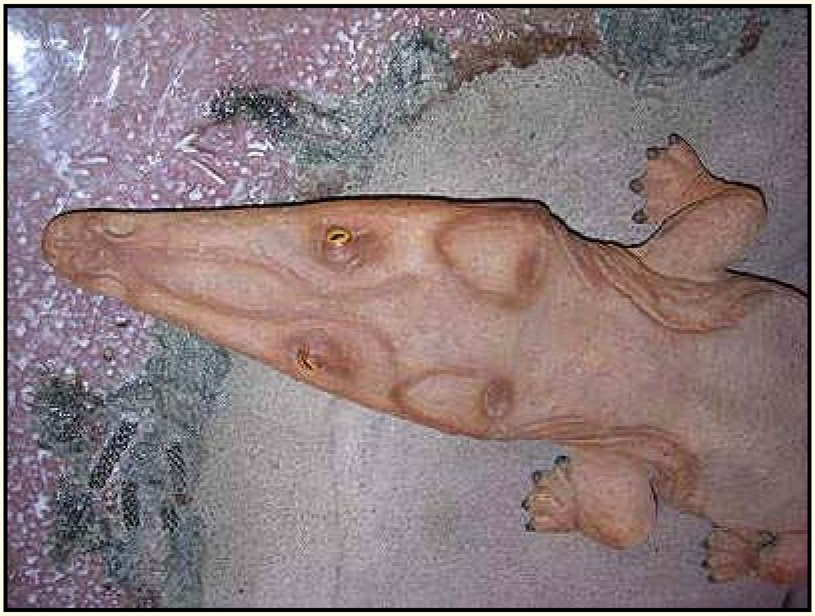
Characters: skull up to 20 cm [S+00]; pineal foramen in middle of orbit -



occiput distance [S+00]; quadratojugal does not participate in jaw condyle [D01]; elongate retroarticular process [S+00]; surangular medial process well-developed [S+00]; interchoanal tooth row strongly reduced [S+00].

Image: from Shishkin *et al*. (2000).

References: Damiani (2001) [D01]; Shishkin *et al*. (2000) [S+00]; Steyer (2002) [S02]. ATW020905.



Trematosaurus**:** *T. brauni* Burmeister, 1849; *T. madagascariensis* Lehman, 1966 (possibly a juvenile of *T. brauni* [S02]); *T. sobeyi* ??, 1915. *T. kannemeyeri* is a junior synonym of *Aphaneramma rostratum* [S02].

Range: Early Triassic (cosmopolitan)

Phylogeny: Trematosauridae:: *Angusaurus* + *.

Characters: skull triangular [S02]; prenarial region short [S02]; quadratojugal participates in jaw condyle (derived) [D01].

Image: from **Palherp - Treffen der deutschsprachigen Paläoherpetologen**

References: Damiani (2001) [D01]; Steyer (2002) [S02]. ATW030911.

Page Back | Unit Home | Page Top | Page Next

checked ATW060327

Temnospondyli: Dendrogram

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
`--+--Edopoidea
   `--+--Dendrerpeton
      |--Dvinosauria
      `--+--Euskelia
         |    |==Dissorophoidea
         |    |  `--LISSAMPHIBIA
         |    `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |  `--+--Rhytidosteidae
               |     `--Brachyopoidea
               `--+--Capitosauria
                  `--Trematosauria
                     |--Trematosauroidea
                     `--Metoposauroidea
```

Contents

Dendrogram

The following dendrogram follows the cladistic analysis of Yates and Warren 2000. Alternative phylogenies are discussed elesehwere MAK111114

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI ToL
|--Edopoidea X
|  |--Edops •X
|  `--Cochleosauridae •X
`--+--Dendrerpeton •X
   `--+--Euskelia MH
      |  |--+==Dissorophoidea •X MH
      |  |  `--LISSAMPHIBIA
      |  `--Eryopoidea  •X
      `--Limnarchia X
         |--Dvinosauria X
         `--Stereospondylomorpha X
            |--Archegosauroidea •X
            `--Stereospondyli X
```

```
|--Lapillopsidae •X
`--+--Rhinesuchidae X
   |  |--Rhinesuchus •X
   |  |--Laccocephalus •X
   |  |--Uranocentradon •X
   |  `--Broomistega •X
   `--+--Capitosauria X
      |  |--Lydekkerinidae •X
      |  `--+--Mastodonsaurus •X
      |     `--Capitosauridae •X
      `--TrematosauriaX
         |--Trematosauroidea X MH
         |  |--Thoosuchinae X
         |  |  |--Prothoosuchus •X
         |  |  `--Thoosuchus •X
         |  `--+--Yarengia •X
         |     `--Trematosauridae X
         |        |--Luzocephalidae •X
         |        `--+--Angusaurus •X
         |           `--Trematosaurus •X
         `--+--Metoposauroidea •X
            |  `--Inflectosaurus •X
            `--+--Plagiosauroidea X MH
               |  |--Plagiosauridae •X
               |  `--Laidleria •X
               `--+--Rhytidosteidae •X
                  `--Brachyopoidea X
                     |--Chigutisauridae •X
                     `--Brachyopidae •X
```

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW050530, revised MAK111114

Page Back	Unit Home	Unit Dendrogram	Unit References	Taxon Index	Page Next
Unit Back	Vertebrates Home	Vertebrate Dendrograms	Vertebrate References	Glossary	Unit Next

Temnospondyl References

Abbreviated Dendrogram

```
TETRAPODA
|--+--LEPOSPONDYLI
|  `--REPTILIOMORPHA
|
TEMNOSPONDYLI
`--+--Edopoidea
   `--+--Dendrerpeton
      |--Dvinosauria
      `--+--Euskelia
         |   |==Dissorophoidea
         |   |  `--LISSAMPHIBIA
         |   `--Eryopoidea
         `--Stereospondyli
            |--Rhinesuchidae
            `--+--Lydekkerinidae
               |--+--Plagiosauroidea
               |   `--+--Rhytidosteidae
               |       `--Brachyopoidea
               `--+--Capitosauria
                  `--Trematosauria
                     |--Trematosauroidea
                     `--Metoposauroidea
```

Contents

References

Anderson, HM & JM Anderson (1970), *A preliminary review of the biostratigraphy of the Uppermost Permian, Triassic, and Lowermost Jurassic of Gondwanaland*. **Paleontol. Afr.** 13(suppl.): 1-22.
Uranocentradon.

Anderson, JM & ARI Cruikshank (1978), *The Biostratigraphy of the Permian and Triassic, Part 5, a review of the classification and distribution of Permo-Triassic Tetrapods*, **Paleontol. Afr.** 21: 15-44.
Laccocephalus.

Anon, Petrified Forest National Park - Koskinonodon;
Koskinonodon

Berman, D.S.; and Reisz, R.R. (1980). "A new species of Trimerorhachis (Amphibia, Temnospondyli) from the Lower Permian Abo Formation of New Mexico, with discussion of Permian faunal distributions in that state". Annals of the Carnegie Museum 49: 455–485.
Trimerorhachis

Bolt, JR & S Chatterjee (2000), *A new temnospondyl amphibian from the Late Triassic of Texas*. **J. Paleontol.** 74: 670-683.

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp.
Laccocephalus; Metoposauroidea; Overview, Rhinesuchidae, Trematosauroidea

Carroll, RL (2009), *The Rise of Amphibians : 365 million years of evolution*, John Hopkins University Press, Baltimore
Dvinosauria - phylogenetic relationships, *Dvinosaurus*, *Eugryinus*, *Isodectes*, *Tupilakosaurus*

Carlson, K. J. (1987). "Perryella, a new temnospondylous amphibian from the Lower Permian of Oklahoma". Journal of Paleontology 61 (1): 135–147.
Perryella

Case, E.C. (1935). "Description of a collection of associated skeletons of Trimerorhachis". University of Michigan Contributions from the Museum of Paleontology 4 (13): 227–274.
Trimerorhachis

Colbert, E.H. (1955). "Scales in the Permian amphibian Trimerorhachis". American Museum Novitates 1740: 1-17. **pdf**
Trimerorhachis

Damiani, RJ (2001), *A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli)*. **Zool. J. Linn. Soc.** 133: 379-482.
Angusaurus, Thoosuchinae, *Thoosuchus*, Trematosauridae, Trematosauroidea, *Trematosaurus*, *Yarengia*.

Damiani, R., C.A. Sidor, J.-S. Steyer, R.M.H. Smith, F.R. O'Keefe, H.C.E. Larsson, A. Maga, O. Ide. The vertebrate fauna of the Upper Permian of Niger—V, The primitive temnospondyl Saharastega moradiensis. Journal of Vertebrate Paleontology 26: 559-572.
Comments on early temnospondyl phylogeny, *Saharastega*

Englehorn, J.; Small, B.J; and Huttenlocker, A. (2008). "A redescription of Acroplous vorax (Temnospondyli: Dvinosauria) based on new specimens from the Early Permian of Nebraska and Kansas, U.S.A.". Journal of Vertebrate Paleontology 28 (2): 291–305. doi:10.1671/0272-4634(2008)28[291:AROAVT]2.0.CO;2.
Dvinosauria - phylogenetic relationships

Falcon-Lang, H. J. 1999. Fire ecology of a Late Carboniferous floodplain, Joggins, Nova Scotia. *Journal of the Geological Society, London* 156, 137-148., Assorted basal temnospondyls

Fraas, E. 1889. Die Labyrinthodonten der Schwäbischen Trias. *Palaeontographica* 36, 1–158.
Metoposaurus

Holmes, R. 2000. Palaeozoic temnospondyls; Pp. 1081-1120 in H. Heatwole and R. L. Carroll (eds.) *Amphibian Biology*, Volume 4. Surrey Beatty and Sons Ltd., Australia. Dvinosauria - phylogenetic relationships

Holmes, R. B., Carroll, R. L. & Reisz, R. R. 1998. The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the lower Pennsylvanian locality of Joggins, Nova Scotia, and a review of its relationships. *Journal of Vertebrate Paleontology* 18, 64-79.,
Assorted basal temnospondyls

Hunt, A.P. 1989. Comments on the taxonomy of North American metoposaurs and a preliminary phylogenetic analysis of the family Metoposauridae, in Lucas, SG and Hunt, AP, eds., Dawn of the age of dinosaurs in the American Southwest, pp. pp.292-300 Albuquerque, New Mexico Museum of Natural History;
Metoposauridae.

Hunt, A.P. 1993. Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from western North America. In: M. Morales (ed.) Aspects of Mesosoic Geology and Paleontology of the Colorado Plateau. Museum of Northern Arizona Biulletin 59, 67-97.
Metoposauridae

Jupp R, Warren AA (1986) The mandibles of the Triassic temnospondyl amphibians. *Alcheringa* 10: 99–124.

Hadrokkosaurus

Lambert, David, Naish, Darren, and Wyse, Elizabeth, 2001 *Dorling Kindersley Dibnosaur Encyclopedia* DK Publishing, New York.
Dunuitosaurus

Langer, M. C., 2005, Studies on continental Late Triassic tetrapod biochronology. II. The Ischigualastian and a Carnian global correlation, Journal of South American Earth Sciences 19 (2005) 219–239,
Metoposaurus.

Laurin, M. & Soler-Gijón, R. 2001. The oldest stegocephalian from the Iberian Peninsula: evidence that temnospondyls were euryhaline. *Comptes Rendu de l'Academie des Sciences Paris, Science de la vie* 324, 495-501.,
Assorted basal temnospondyls

---- . & Soler-Gijón, R. 2006. The oldest known stegocephalian (Sarcopterygii: Temnospondyli) from Spain. *Journal of Vertebrate Paleontology* 26, 284-299.,
Assorted basal temnospondyls

Michel Laurin and Jean-Sébastien Steyer, 2000, Phylogeny and Apomorphies of Temnospondyls, Tree of Life Web project,
Comments on early temnospondyl phylogeny

Lucas, Spencer G., 1998, *Global Triassic tetrapod biostratigraphy and biochronology*. **Paleogeog. Palaeoclimatol., Palaeoecol.** 143: 347-384.
Metoposaurus

Lucas, Spencer G., 2006, Global Permian tetrapod biostratigraphy and biochronology, in Lucas, S. G., Cassinis, G. & Schneider, J. W. (eds) 2006. *Non-Marine Permian Biostratigraphy and Biochronology*. Geological Society, London, Special Publications, 265, 65–93.
Chenoprosopus

Mehl, M. G., 1913, A description of *Chenoprosopus milleri:* In: Permo-Carboniferous Vertebrates from New Mexico, Edited by E. C. Case, S. Williston and M. G. Mehl, Publications, Carnegie Institution of Washington, n. 181, p. 11-16.

Chenoprosopus

Milner, AR (1980), *The Tetrapod assemblage from Nyrany, Czechoslovakia*, **in** AL Panchen (ed.), **The Terrestrial Environment and the Origin of Land Vertebrates**. Academic Press: pp.439-496.
Cochleosauridae; Edopoidea.

Milner, A. R. 1990. The radiations of temnospondyl amphibians. 321–349. In Taylor, P. D. and Larwood, G. P. (eds). *Major evolutionary radiations*. Clarendon Press, Oxford, 437 pp.
Dvinosauria - phylogenetic relationships

Milner, A. R. 1993. Biogeography of Palaeozoic tetrapods; pp. 324–353 in J. A. Long (ed.), Palaeozoic Vertebrate Biostratigraphy and Biogeography. Belhaven Press, London.,
Edopoid Geographical distribution

Milner, A.R. 1994, Late Triassic and Jurassic amphibians: fossil record and phylogeny, pp.5-22 in Fraser & Sues (eds.) In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, Cambridge University Press, Cambridge.
Plagiosauridae, Latiscopidae, Metoposauridae.

Milner, A. R. 1996. A revision of the temnospondyl amphibians from the Upper Carboniferous of Joggins, Nova Scotia. *Special Papers in Palaeontology* 52, 81-103.,
Assorted basal temnospondyls

Milner, A. R. & Sequeira, S. E. K. 1994. The temnospondyl amphibians from the Visean of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 84, 331-361.,
Assorted basal temnospondyls, *Balanerpeton*

Milner, A. C. & Sequeira, S. E. K. 1998. A cochleosaurid temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio, U.S.A. *Zoological Journal of the Linnean Society* 122, 261-290.

Edopoidea, Assorted basal temnospondyls

Milner, A. R.; and Sequeira, S. E. K. (2004). "Slaugenhopia texensis (Amphibia: Temnospondyli) from the Permian of Texas is a primitive tupilakosaurid". Journal of Vertebrate Paleontology 24 (2): 320-325. doi:10.1671/1974.
Kourerpeton, *Slaugenhopia*, Tupilakosauridae

Mueller, B.D. (2007). "Koskinonodon Branson and Mehl, 1929, a replacement name for the preoccupied temnospondyl Buettneria Case, 1922". Journal of Vertebrate Paleontology 27 (1): 225. ;
Koskinonodon.

Müller, AH (1968), ***Lehrbuch der Paläozoologie***, **vol.II part 1 (Vertebrates)**.
Rhinesuchidae.

Murry, P.A. 1986. Vertebrate paleontology of the Dockum group, western Texas and eastern New Mexico. In *The Beginning of the Age of Dinosaurs. Faunal Change across the Triassic-Jurassic Boundary* (K. Padian, Ed.), pp. 109-137. Cambridge Univ. press, Cambridge, UK.
Metoposauridae.

Nilsson, T. (1946), *A new find of* ***Gerrothorax rhaeticus*** *Nilsson a plagiosaurid from the Rhaetic of Scania*. **Lunds Univ. Årsskr.** N.F.(2) 42(10).
Plagiosauridae.

Olson, E.C. (1979). "Aspects of the biology of Trimerorhachis (Amphibia: Temnospondyli)". Journal of Paleontology 53 (1): 1–17. JSTOR 1304028.
Trimerorhachis

Pawley, Kat, 2006, The Postcranial Skeleton of Temnospondyls (Tetrapoda: Temnospondyli), Phd thesis, La Trobe University, **online**
Dvinosauria - phylogenetic relationships

Pawley, K. (2007). "The postcranial skeleton of Trimerorhachis insignis Cope, 1878 (Temnospondyli: Trimerorhachidae): a plesiomorphic temnospondyl from the Lower Permian of North America". Journal of Paleontology 81 (5): Journal of Paleontology. doi:10.1666/pleo05-131.1.
Trimerorhachis

Graciela Piñeiro, Claudia Marsicano, and Nora Lorenzo (2007). "A new temnospondyl from the Permo-Triassic Buena Vista Formation of Uruguay". Palaeontology 50 (3): 627–640. doi:10.1111/j.1475-4983.2007.00645.x.

Laidleria

Pough, FH, CM Janis & JB Heiser (1999), **Vertebrate Life** (5th ed.), Prentice Hall, 733+ pp.
Trematosauroidea.

Rieppel, O., 1980, The edopoid amphibian *Cochleosaurus* from the Middle Pennsylvanian of Nova Scotia: Palaeontology, v. 23, n. 1, p. 143-149.,
Cochleosaurus florensis

Robinson, J., Ahlberg, P. E. & Koentges, G. 2005. The braincase and middle ear region of *Dendrerpeton acadianum* (Tetrapoda: Temnospondyli). *Zoological Journal of the Linnean Society* 143, 577-597.,
Assorted basal temnospondyls

Romer, A. S. 1947, Review of the Labyrinthodontia, Bulletin of the Museum of Comparative Zoology, v.99, pp.1-368
Metoposaurus

Ruta, M. & Bolt, J. R. 2006. A reassessment of the temnospondyl amphibian*Perryella olsoni* from the Lower Permian of Oklahoma. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 97 (2): 113-165. doi:10.1017/S0263593300001437.
Dvinosauria - phylogenetic relationships, *Perryella*

Ruta M, Bolt JR (2008)The brachyopoid *Hadrokkosaurus bradyi* from the early Middle Triassic of Arizona, and a phylogenetic analysis of lower jaw characters in temnospondyl amphibians. *Acta Paleontologia Polonica* 53: 579-592
Hadrokkosaurus

Ruta, M., Coates, M. I. & Quicke, D. L. J. 2003a. Early tetrapod relationships revisited. *Biological Reviews* 78, 251-345.,
Assorted basal temnospondyls, Comments on early temnospondyl phylogeny

Ruta, M., Jeffery, J. & Coates, M. I. 2003b. A supertree of early tetrapods. *Proceedings of the Royal Society of London* B 270, 2507-2516.,
Assorted basal temnospondyls, Dvinosauria - phylogenetic relationships

Marcello Ruta, Davide Pisani, Graeme T Lloyd and Michael J Benton, 2007, A supertree of Temnospondyli: cladogenetic patterns in the most species-rich group of early tetrapods, *Proc. R. Soc. B* 2007 274, 3087-3095 doi: 10.1098/rspb.2007.1250
Dvinosauria - phylogenetic relationships, Laidleria

Romer, AS (1947) **Vertebrate Paleontology**, (3rd ed.1966) Univ. Chicago Press.
Uranocentradon.

Marcello Ruta, Davide Pisani, Graeme T. Lloyd and Michael J. Benton, A supertree of Temnospondyli: cladogenetic patterns in the most species-rich group of early tetrapods, Proc. R. Soc. B (2007) 274, 3087–3095
Comments on early temnospondyl phylogeny, Dvinosauria - phylogenetic relationships

Schoch, R. R. 2001. Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 220, 335-367.
Edopoidea

Schoch, Rainer R. 2008, The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy, , Palaeodiversity 1: 189–226
Lydekkerinidae

Schoch, R.R., Fastnacht, M., Fichter, J., and Keller, T. 2007. Anatomy and relationships of the Triassic temnospondyl Sclerothorax. *Acta Palaeontologica Polonica* 52 (1): 117–136.
Lydekkerinidae

Scotese, C. R. 2001. Atlas of Earth History, Volume 1, Paleogeography. Paleomap Project, Arlington, Texas, 52 pp.
Edopoid Geographical distribution

Scott, A. C. 2001. Roasted alive in the Carboniferous. *Geoscientist* 11 (3), 4-7.,
Assorted basal temnospondyls

Sequeira, S. E. K. 1996. A cochleosaurid amphibian from the Upper Carboniferous of Ireland. *Special Papers in Palaeontology* 52, 65-80.
Edopoidea

Sequeira, S. E. K. 1998. The cranial morphology and taxonomy of the saurerpetontid Isodectes obtusus comb. nov. (Amphibia: Temnospondyli) from the Lower Permian of Texas. In D. B. Norman, A. C. Milner and A. R. Milner (eds.): A study of fossil vertebrates. Zoological Journal of the Linnean Society 122(1-2):237-259
Isodectes

Sequeira, S. E. K. 2004. The skull of *Cochleosaurus bohemicus* Fric, a temnospondyl from the Czech Republic (Upper Carboniferous) and cochleosaurid interrelationships. *Transactions of the Royal Society of Edinburgh* 94, 21-43.
Edopoidea

Sequeira, S. E. K. & Milner, A. R. 1993. The temnospondyl amphibian *Capetus* from the Upper Carboniferous of the Czech Republic. *Palaeontology* 36, 657-680.,
Assorted basal temnospondyls, *Capetus*

Shishkin, MA, IV Novikov & YM Gubin (2000), *Permian and Triassic temnospondyls from Russia* **in** MJ Benton, MA Shishkin, DM Unwin & EN Kurochkin (eds.), **The Age of Dinosaurs in Russia and Mongolia**, Cambridge Univ. Press, pp. 35-59.
Angusaurus, *Dvinosaurus*, *Inflectosaurus*, Luzocephalidae, *Prothoosuchus*, *Thoosuchus*, Trematosauridae, Trematosauroidea, *Tupilakosaurus* *Yarengia*.

Shishkin, MA & Rubridge, BS (2000), *A relict rhinesuchid (Amphibia: Temnospondyli) from the Lower Triassic of*

South Africa. **Palaeontology** 43: 653-670.
Broomistega.

Sidor, C. A., O'Keefe, F. R., Damiani, R., Steyer, J. S., Smith, R. M. H., Larsson, H. C. E., Sereno, P. C., Ide, O. & Maga, A. 2005. Permian tetrapods from the Sahara show climate-controlled endemism in Pangaea. *Nature* 434, 886-889.
Edopoidea, Assorted basal temnospondyls, Saharastega

Steyer, JS (2000), *Ontogeny and phylogeny in temnospondyls: a new method of analysis*. **Zool. J. Linn. Soc.** 130: 449-467.
Temnospondyli.

Steyer, JS (2002), *The first articulated trematosaur "amphibian" from the Lower Triassic of Madagascar: implications for the phylogeny of the group*. **Palaeontology** 45: 771-793. **WWW**.
Angusaurus, *Inflectosaurus*, Luzocephalidae, Trematosauridae, *Trematosaurus*.

J. Sébastien Steyer and Ross Damiani, 2005, A giant brachyopoid temnospondyl from the Upper Triassic or Lower Jurassic of Lesotho. Bulletin de la Société Géologique de France, 176 (3): 243-248.
giant brachyopoid

Steyer, J. S., Damiani, R., Sidor, C. A., O'Keefe, R., Larsson, H. C. E., Maga, A. & Ide, O. 2006. The vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae), and the edopoid colonization of Gondwana. *Journal of Vertebrate Paleontology* 26, 18-28.
Edopoidea, Comments on early temnospondyl phylogeny, Edopoid Geographical distribution, Nigerpeton, Assorted basal temnospondyls, Saharastega

Sulej, T., 2002: Species discrimination of the Late Triassic temnospondyl amphibian Metoposaurus diagnosticus. *Acta Palaeontologica Polonica*: Vol. 47, #3, pp. 535-546
Metoposaurus.

Sulej, T. 2007. Osteology, variability, and evolution of Metoposaurus, a temnospondyl from the Late Triassic of Poland. Palaeontologia Polonica 64, 29–139.
Metoposaurus.

von Zittel, KA (1932), **Textbook of Paleontology**, CR Eastman (transl. and ed), 2nd edition, vol.2, Macmillan & Co.
Rhinesuchus; *Uranocentradon*.

Warren, AA (1985), *Triassic Australian plagiosauroid*. **J. Paleontol.** 59: 236-241.
Plagiosauridae.

Warren, AA (1995), ***Plagiosternum granulosum*** *E. Fraas: a plagiosaurid temnospondyl from the Middle Triassic of Crailsheim, Germany*. **Stuttgarter Beiträge zur Naturkunde Ser. B** #229. 8 pp.
Plagiosauridae.

Warren, AA (1998), ***Laidleria*** *uncovered: a redescription of* ***Laidleria gracilis*** *Kitching (1957), a temnospondyl from the* ***Cynognathus*** *Zone of South Africa*. **Zool. J. Linn. Soc.** 122: 167-185.
Laidleria; Plagiosauridae; Plagiosauroidea.

Warren, A.A. (1999). "Karoo tupilakosaurid: a relict from Gondwana". Transactions of the Royal Society of Edinburgh Earth Sciences 89: 145–160.
Slaugenhopia

Warren, AA & L Davey (1992), *Folded teeth in temnospondyls -- a preliminary study*. **Alcheringa** 16: 107-132.
Plagiosauridae.

Warren, AA & C Marsicano (2000), *A phylogeny of the Brachyopoidea (Temnospondyli, Stereospondyli).* **J. Vert. Paleontol.** 20: 462-483.
Dendrogram, Plagiosauridae, *Hadrokkosaurus*, giant brachyopoid

Werneburg, R.; Steyer, J. S.; Sommer, G.; Gand, G.; Schneider, J. W.; and Vianey-Liaud, M. (2007). "The earliest tupilakosaurid amphibian with diplospondylous vertebrae from the Late Permian of southern France". Journal of Vertebrate Paleontology 27 (1): 26–30. doi:10.1671/0272-4634(2007)27[26:TETAWD]2.0.CO;2.

Tupilakosauridae

Williston, S.W. (1915). "Trimerorhachis, a Permian temnospondyl amphibian". The Journal of Geology 23 (3): 246–255.
Trimerorhachis

Williston, S.W. (1916). "The skeleton of Trimerorhachis". The Journal of Geology 24 (3): 291–297.
Trimerorhachis

Yates, AM (1999), *The Lapillopsidae: a new family of small temnospondyls from the Early Triassic of Australia*. **J. Vert. Paleontol.** 19: 302-320.
Dendrogram; Stereospondyli.

Yates, AM (2000), *A new tiny rhytidosteid (Temnospondyli: Stereospondyi) from the Early Triassic of Australia and the possibility of hidden temnospondyl diversity*. **J. Vert Paleontol.** 20:484-489.
Rhytidosteidae.

Yates, AM & AA Warren (2000), *The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli*. **Zool. J. Linnean Soc.** 128: 77-121.
Dendrogram; *Laidleria*; Limnarchia; Luzocephalidae; Metoposauroidea, Overview, Plagiosauridae; Plagiosauroidea; Temnospondyli; Thoosuchinae; *Thoosuchus*, Trematosauria, Trematosauridae, Trematosauroidea., *Hadrokkosaurus*

Page Back **Unit Home** **Page Top** **Page Next**

checked ATW050530, last modified MAK111114

Lissamphibia: Overview

Abbreviated Dendrogram

```
TEMNOSPONDYLI
|
Lissamphibia
|--Gymnophiona
|  |--Eocaecilia
|  `--+--Rhinatrematidae
|     `--Caeciliidae
`--+--Urodela
   |  |--Karaurus
   |  `--Sirenidae
   `--Anura
```

Contents

---

checked ATW060209

Lissamphibia

Abbreviated Dendrogram	Contents
see below	Overview Lissamphibia References

```
TEMNOSPONDYLI
|
LISSAMPHIBIA
|--Gymnophiona
|  |--Eocaecilia
|  `--+--Rhinatrematidae
|     `--Caeciliidae
`--+--Urodela
   |  |--Karaurus
   |  `--Sirenidae
   `--Anura
```

Taxa on This Page

1. Anura
2. Caeciliidae
3. *Eocaecilia* X
4. *Karaurus* X
5. Lissamphibia
6. Gymnophiona
7. Rhinatrematidae
8. Sirenidae
9. Urodela

Rubber Eels and Bad Music

A concertina is a sort of retarded accordion -- if one can imagine anything less intellectually stimulating than an accordion. Historically, the concertina was favored by traveling Irish musicians. It is unclear whether this was because the concertina is easily transported, or because, having taken up the instrument, the musicians themselves were forced to keep moving by angry mobs of outraged listeners. Possibly the latter applies, since concertina *locomotion* is a style of movement also used in tight spots by limbless terrestrial vertebrates. As practiced by snakes, for example, concertina movement involves curving the back of the body so that it presses outward against both walls of a burrow or any other narrow channel. The snake extends the anterior part of the body. The anterior is then folded so that it presses against the sides, and the posterior is hauled up. In dorsal view it looks as if the body fold stays in one position and the snake moves *through* it. See limbless mobile robots. Progress is relatively slow and energetically expensive, but it works well enough to allow snakes to climb trees (even those which are likewise limbless).

The snake-like terrestrial caecilians are perfectly capable of this kind of locomotion, and it is part of their normal behavioral repertoire. However, they are also highly specialized for a different style of concertina locomotion: *internal* concertina movement. This trait allows caecilians to move through spaces so narrow that there is no room for maneuver at all. Rather than folding the body against the walls of a channel, caecilians seem to laterally expand a section of the body wall so that it is fixed against the perimeter, while stretching forward with more anterior sections. Fig. 1. Figure 1 should not be taken too seriously. Not only is it constrained by my customary lack of artistic talent, but it suggests, wrongly, that the compressed section is limited to a few body segments. In fact, the whole post-cranial body may initially be compressed, with the anterior end then moving forward like a compressed spring. However, such an image is also misleading, since it suggests an elastic recoil, which does not seem to occur.

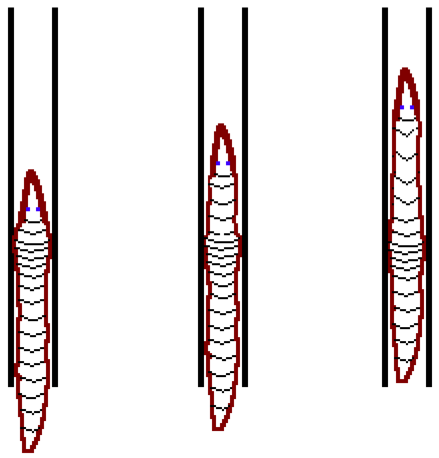


Fig. 1. Internal concertina locomotion

This series of motions, however they may be portrayed in mechanical detail, is routine behavior for an earthworm (the caecilian's favorite prey), but just how does a vertebrate manage the trick? Caecilians are unique in that their vertebral column is very loosely attached to the body wall. Thus, the spine can move independently of the skin for quite remarkable distances. But how does this translate into translation, so to speak, of the entire body?

Much of the job of unraveling this knot has fallen to Dr. James C. O'Reilly. O'Reilly was, until 2001, a Darwin post-doctoral fellow in Prof. Elizabeth Brainerd's Biomechanics Lab at the University of Massachusetts -- the same people who brought us Nat Kley, whose work is discussed at Scolecophidia **[1]**. Oddly enough, O'Reilly has proposed two quite different mechanisms for this behavior. These are not inconsistent explanations, but it is not yet clear how they work together. In Summers & O'Reilly (1997), Dr. Adam Summers (who was then O'Reilly's predecessor as Darwin Fellow in Prof. Brainerd's lab) and O'Reilly injected *Dermophis mexicanus* with stationary lead markers and monitored its movement in narrow channels with X-ray cinematography. They concluded that*Dermophis* was engaged in more or less routine concertina movement, but inside its own skin. That is, the vertebral column was deformed in a series of S-curves within the body cavity, and the caecilian was pushing its head forward, even against considerable resistance, using the force of the vertebrae against the body wall which was, in turn, fixed against the side of the channel.

This sounds reasonable, at least for this rather weird and unreasonable organism, but is it the whole story? For good and sufficient experimental reasons, O'Reilly & Summers fixed the channel width at 120% of body width. Yet *Dermophis* is capable of concertina movement in channels of 100% body width -- with no room to maneuver at all. It is not intuitively obvious that the described form of internal concertina movement would work as well in such minimum width channels.

Thus, in a later paper (which actually came off the presses about the same time due to the usual vagaries of publication delay) O'Reilly *et al.* (1997) proposed a rather different, hydrostatic mechanism. The hydrostatic mechanism is based on the detailed anatomy of the body wall. It appears that *Dermophis* has two sets of helical fibers of opposite chirality (a left handed and a right handed helix) embedded in the body wall. The two sets offibers are linked with the vertically oriented *transversus* muscles and paralleled by the *obliquus* muscles. When the muscles contract, the angle between the two sets of fibers is reduced and the body

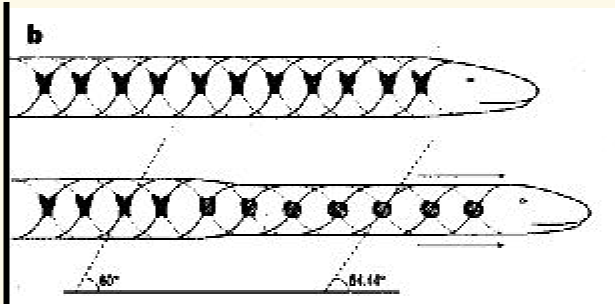


Fig. 2. Hydrostatic locomotion in Dermophis mexicanus, after O'Reilly etal. (1997)

becomes a rigid cylinder. [2] Fig. 2. This mechanism not only moves the head forward, but creates powerful forces for digging through compacted earth.

In fact, the two modes: mechanical and hydrostatic, probably work together. The hydrostatic device is powerful. It explains how the caecilian elongates and generates digging forces -- but it doesn't really explain net forward motion. The proportional extension of the body should be approximately equal to ratio of the cosines of the angles, or 16%. Assuming half the body is extended, and that *all* of the gain is maintained on relaxation, the center of mass moves a rousing 4% of body length. O'Reilly et al. measure the cycle time as about 4 minutes in their experimental system. So this is not exactly orbital velocity. In fact (if my math has not failed me somewhere) it implies a speed of one body length in a bit over an hour and a half.

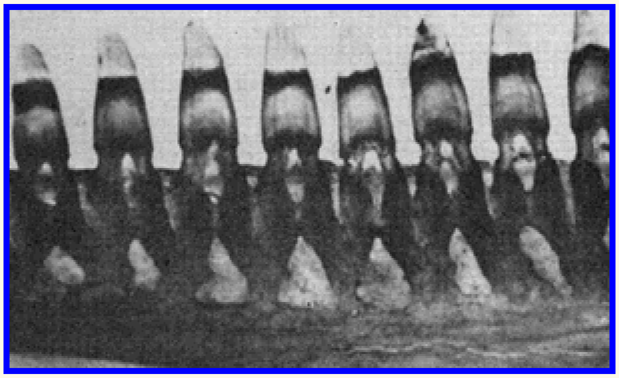
Clearly, relativistic effects can be ignored. If the animal is to actually get anywhere, it must be using something a bit speedier, if less powerful. The hydrostatic mechanism may be for digging, and the more orthodox internal concertina for movement. ATW 001107

---

[1] O'Reilly now has his own lab at the University of Miami and has taken *Dr*. Nat Kley with him as a post-doctoral student. (1/02). Back

[2] As the authors explain, the force is generated by the body wall, not by the pressurized body fluids. The rigidity and thrust are inherent properties of the helix-antihelix framework, if I understand the argument correctly (and I may not). Back.

Descriptions



Lissamphibia: frogs, caecilians, newts, salamanders.

Range: from the Early Triassic.

Phylogeny: Microsauria : Lysorophia + * : Gymnophiona + (Urodela + Anura).

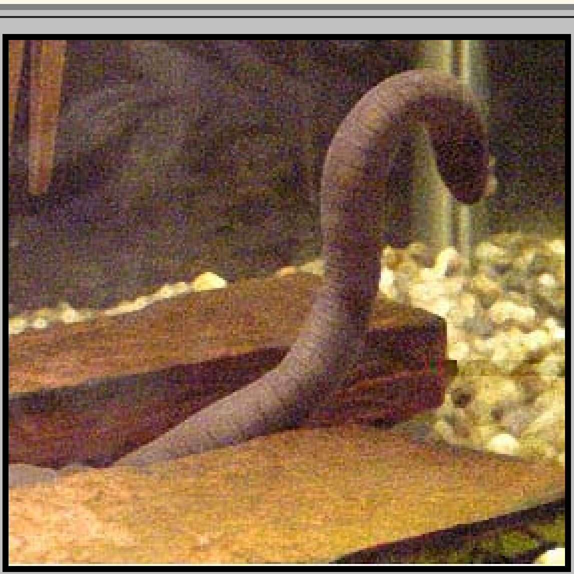
Characters: very open skull with braincase as major support in Anura & Urodela; distinctive *m. levator bulbi*; green visual rods; plectrum-operculum complex (analogous to auditory stapes); *papilla amphibiorum* for hearing; pedicellate teeth, bicuspid or multicuspid, with basal uncalcified zones; spool-shaped vertebrae; unified centrum; buccal pump ventilation (lungs for oxygen uptake only, dump CO2 through skin); glandular skin with respiratory exchange; mucous glands; scales absent; most have aquatic larvae with external gills.

Notes: Possible sister of Lysorophia. Carroll (1988) argues convincingly that this group is within Lepospondyli. However he may no longer hold this position as to urodeles and anurans.

Links: Class Lissamphibia; superordo Lissamphibia (Dutch); Living Amphibians; CHAOYANGIA & LISSAMPHIBIA; Lissamphibia after Milner, 1994, Laurin & Reisz, 1997; 209 lec s02/20908s02.pdf; LissamphibPec;

Systematics of the Amphibia; Biology 356; Evolución (Spanish); Herpetology 101 - Suite101.com; Amphibians. ATW021017.

Gymnophiona (= Apoda)**:** Caecilians.



Typhlonectes natans courtesy of Seth Morris and Rebecca Herndon of the Caecilians Web Site.

Range: Fr lwJ.

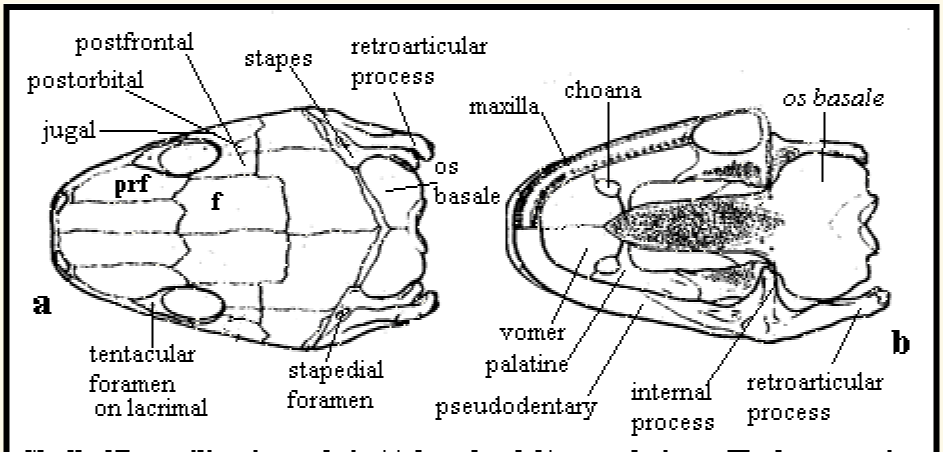
Phylogeny: Lissamphibia **:** (Urodela + Anura) + * **:** *Eocaecilia* + (Rhinatrematidae + Caeciliidae).

Characters: Amphibian vertebrate "blind worms." Possibly sister group of urodeles. Strong, flattened, integrated skull; palate and lower jaw bear medial tooth rows; teeth generally recurved; tongue rather immobile and not protrusible; eyes covered, reduced or absent; **$** protrusible tentacles between eyes and nares; **$** tentacular fossa present near or within anterior margin of orbit; eye muscles exapted to manipulate tentacle; tentacle probably chemosensory as well as tactile; eye may be attached to tentacle and become protrusible (O'Reilly et al. (1996)); skull fully roofed; solid lateral wall of braincase (os basale) formed by fusion of otic capsule and parasphenoid; jaw articulation anterior to occiput; conspicuous dermal annuli (rings) around body; amphicoelous vertebrae hour-glass shaped, with longitudinal ventral keel; vertebrae with distinct anterior diapophysis and parapophysis; short, 2-headed ribs present on almost all vertebrae; **$** dermal scales around annuli; tail much reduced or absent; *internal* concertina locomotion, moving internally over own annuli in many terrestrial forms; regular molts of microsquamose covering in some forms; but skin also glandular and may produce potent toxins in mucous secretions; limbless; lack bone marrow (?); fossorial (damp soils) or aquatic; terrestrial forms may be powerful diggers; feed on worms, insects, perhaps vegetation (?!); may have aquatic larval stage; larvae (or embryos) have conspicuous external gills; lateral line present in some larvae; water may be absorbed through skin; lungless species known.

Links: Caecilians Web Site (Gymnophiona) - Rubber Eels (**Best on the Web**); Gymnophiona = Caecilia = Apoda; Anat & Embryol - Abstr 197: 69-75; Reptiles - Belize Biodiversity Information System; caecilian; Amphibian Species of the World; Biology 356; Herpetology- Amphibian Diversity- Gymnophiona (nice summary of phylogeny and diversity); ADW- Gymnophiona- Classification; Gymnophiona - Caecilians (mostly just images); Gymnophiona [Apoda] (Mikko's Phylogeny); Gymnophiona; Gymnophiona- Herpetology (links only); ichthyophis glutinosus gymnophiona amphibien apode; Mitochondrial Evidence on the Phylogenetic Position of Caecilians ....

References: Jared *et al.* (1999); O'Reilly *et al.* (1996); O'Reilly *et al.* (1997); Summers & O'Reilly (1997); Wilkinson & Nussbaum (1997).

Eocaecilia: *E. micropodia* Jenkins & Walsh 1993.



Skull of Eocaecilia micropoda in (a) dorsal and (b) ventral views. The lower portion of (b) shows the lower jaw elements. Modified from Jenkins & Walsh (1993).

Range: Early Jurassic of North America (Arizona)

Phylogeny: Gymnophiona **:** (Rhinatrematidae + Caeciliidae) + *.

Characters: Mouth slightly subterminal; 2 upper rows of teeth, palatine-vomeral and maxillary; lower jaw from pseudodentary & pseudoangular; large "retroarticular process" on lower jaw; internal process on pseudoangular; maxilla & palatine separate; tentacular foramen present along anterior orbit; orbit large; complete primitive set of circumorbital bones: prefrontal, lacrimal, jugal, postorbital & postfrontal; quadratojugal present (but not figured?); **$** stapes large, with anterior foramen, expanded at both ends, contacting braincase (antero-medially) and os basale (postero-medially?); stapes articulates at joint (?) with retroarticular process; exoccipitals, parasphenoid & otic capsules fused (*os basale*); paired occipital condyles?; glenoid tubercle on 1st cervical (similar to microsaurs & salamanders); intercentra present; short 2-headed ribs on all vertebrae except caudals; limb remnants.

Links: Biology 356; Herpetology: Amphibian Diversity: Gymnophiona; E V (Dutch); Molecular Evidence for the Early History of Living Amphibians (*Eocaecilia* falsifies some ideas based on molecular phylogenies); Geometry.Net - Science- Herpetology (interesting note under #59);

References: Jenkins & Walsh (1993).

Notes: Most of these characteristics are diagnostic of Gymnophiona. The complete set of circum-orbital bones, the quadratojugal and (especially) separate palatines mark this as a more plesiomorphic form. Jenkins & Walsh argue that these characteristics are further evidence of lissamphibian monophyly. ATW030328.

Rhinatrematidae: *Epicrionops, Rhinatrema*

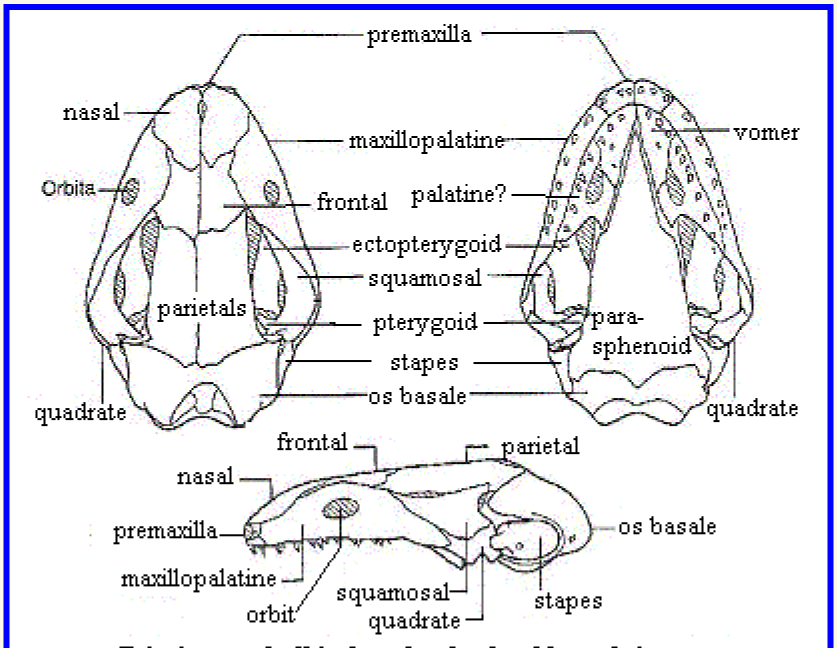
Range: R of SAm.

Phylogeny: Gymnophiona :: Caeciliidae + *.

Characters: small (<32 cm); skull *zygokrotaphic*; mouth terminal (other families are ventral); tentacle adjacent to orbit; prefrontal fused with palato-maxilla; true tail with caudal vertebrae, caudal muscles & dermal annuli; terrestrial, with aquatic larvae.

Image: *Epicrionops* skull, materially relabelled from home2

Links: AmphibiaWeb Species List- Rhinatrematidae; Gymnophiona (Spanish); A comparative study of locomotion in the caecilians Dermophis ...; Rhinatrematidae (Japanese); Untitled Document. ATW021031



Epicrionops skull in dorsal, palatal and lateral views.

Dermophis oaxae: copyright 1998 by Marvalee H. Wake. From the Digital Library Project of the University of California at Berkeley.

Caeciliidae: = Caeciliaidae? *Boulengerula, Brasilotyphlus, Caecilia, Dermophis, Gegeneophis, Gegenophis, Geotrypetes, Grandisonia, Gymnophis, Herpele, Hypogeophis, Idiocranium, Indotyphlus, Leutkenotyphlus, Microcaecilia, Mimosiphonops, Oscaecilia, Parvicaecilia, Praslinia, Schistometopum, Siphonops, Sylvacaecilia.* Probably paraphyletic, and including Typhlonectidae.

Range: from the Late Paleocene of South America, Africa & India (Gondwana except Australia & Antarctica)

Phylogeny: Gymnophiona :: Rhinatrematidae + *.

Characters: Stegokrotaphic skull; mouth subterminal; tail absent; terrestrial (mostly burrowers) and aquatic; some viviparous; no aquatic larva (but see Taxonomy).

Links: Gymnophiona; Taxonomy; Amphibians of Panamá; AmphibiaWeb Species List: Caeciliidae; AmphibiaWeb (**Best on the Web**); Blindwühlen (German);

Gymnophiona (Spanish); Untitled Document; A comparative study of locomotion in the caecilians Dermophis ....;

Note: Some with *very* odd reproductive patterns. ATW021119.

Urodela: Salamanders.

Range: fr J.

Phylogeny: Lissamphibia **::** Anura + * **:** *Karaurus* + Sirenidae.

Characters: main skull support is braincase; as in frogs, otic capsule attaches to jugal (?); maxilla separated from squamosal & quadrate by long gap; primitively, squamosal, quadrate & pterygoid form suspensorium similar to teleosts; hyoid apparatus protrudes tongue (muscles on ceratohyal pull forward and thrust anterior hyoid, with tongue, out of mouth); loss of post-orbital dermal bone permits expansion of mandibular adductor onto surface of braincase, especially prominent otic capsule; no otic notch, tympanum, or slender stapes; stapes structural link between braincase and cheek; body elongated; only extant tetrapod* group retaining horizontal septum dividing dorsal and ventral body wall muscles; ~equal limbs. protrusible tongue common; trade-off between protrusible tongue and buccal pump (thus some species. with protrusible tongue lack lungs). Locomotion involves fish-like lateral bending with limb movements. Pedomorphosis common with retention of external gills, larval tooth & bone patterns, lateral line system. Several convergent species. adapted to caves with loss of eyes. Largest genome of any tetrapod, largely repetitive DNA.

Links: Index of ... URODELES/; Ensatina; Batrachosauroididae ...from the late Cretaceous; JEB -- Summaries: Reilly 199 (5): 1219. 010719.

***Karaurus*:** *K. sharovi* Ivachnenko 1978.

Range: Late Jurassic of Kazakhstan.

Phylogeny: Urodela **:** Sirenidae + *.

Image: from Mathematical.com

Links: karaurus; Transitions among amphibians; Biology 356. ATW030202.

Sirenidae: (obviously there is much more to Urodela than *Karaurus* and Sirenidae, but we don't cover that yet) *Habrosaurus*, *Pseudobranchus*, *Siren*

Range: from the Late Cretaceous of North America only.

Phylogeny: Urodela **::** *Karaurus* + *.

Characters: Premaxillae separated, paired; premaxillae with long posterior processes extending lateral to nasals; septomaxillae absent; maxillae small; nasals ossify from single, medially-positioned anlage; lacrimals absent; small eyes; eyelids absent; quadratojugal absent; exoccipital not involved in origin of *m. levator mandibulae anterior superficialis* (origin on lateral skull); pterygoids small; columella present, detached; otic operculum absent; *basilaris* complex is present in inner ear; recessus amphibiorum oriented horizontally; otic sac [?] bulbar & partially vascularized; amphibian periotic canal lacks fibrous connective tissue; periotic cistern large, protrudes into fenestra [what fenestra?]; parasphenoids lack foramina for internal carotid; angular fused with dentary; teeth lack distinct crown and pedicel; replacement of

vomerine teeth proceeds laterally in parallel to the maxillary teeth; large external gills; one pair *(Pseudobranchus)* or three pairs *(Siren)* of gill slits; first hypobranchial & first ceratobranchial separate; second ceratobranchial includes four elements; lungs present; body long, slender & eel-like; vertebral centra amphicoelous; ribs are bicapitate; spinal-nerve foramina present in neural arches except those exiting between atlas & first trunk vertebra; finlike tail; forelimbs small; scapula & coracoid not fused; digits 4/0; **$** hind limbs absent; pelvic girdle absent; *mm pubotibialis* & *puboischiotibialis* present & separate; dermal glands for moisture seal during daily torpor or estivation; kidney, anterior glomeruli well developed; ciliated epithelium absent from cloacal tube & anterior cloacal chamber of females; epidermal lining present in anterior cloacal chamber of females; evaginations absent from dorsolateral walls of male cloacal tube; anterior ventral glands absent from cloacae of females; Female cloacal chamber without spermathecae; glands secreting into the dorsal walls of the female cloaca absent; anterior ventral glands absent from male cloacae; posterior ventral glands absent from male cloacae; Kingsbury's glands absent from male cloacae; dorsal pelvic glands absent in males; lateral pelvic glands absent in males; glands secreting into the male cloacal orifice are absent; parental care of eggs is by females; omnivorous; do not metamorphose, retaining larval (aquatic) appearance; often nocturnal; inhabit shallow water in swamps, ditches and ponds, with muddy substrates and dense vegetation; assumed to be external fertilizers (cloacal glands absent).

Note: believed to be living sister to all other living salamanders, but not particularly close relative.

Links: Sirenidae (ToL); Family Sirenidae (ADW); AmphibiaWeb Species List- Sirenidae; Armmolche (German); Herpbreeder.dk (important site for links to on line research papers, but sirenids represented only by 2 Brainerd lab papers on ventilation); Siren - MavicaNET (good selection of links). ATW030726

Anura: Frogs. Defined as last common ancestor of living frogs and all its descendants.

Range: fr P? J.

Phylogeny: Lissamphibia **::** Urodela + *.

Characters: **$** prefrontal absent; **$** lens with two *m. protractor lentis*; **$** hyobranchial elements fused into hyoid plate; **$** 9 presacral vertebrae; **$** atlas with single centrum; **$** urostyle formed from caudal vertebral segments; **$** radius and ulna fused; **$** hind limb longer than forelimb; **$** tibia and fibula fused (specializations for jumping); **$** elongate ankle bones (tibiale and fibulare = astragalus and calcaneum); **$** skin with large subcutaneous lymph spaces; larvae usually suspension feeders & very different from adult morph; **$** presence of keratinous beaks and denticles on larval mouthparts; **$** a single median spiracle in the larva (a characteristic of the Type 3 tadpole);

Links: Netfrog--The Interactive Frog Dissection--Title Page; Order Anura; Amphibians of Canada -- Browse Species; Salientia; Amphibian Families; Amphibians of Central Europe - Whose tadpole is it?; Exploratorium: Frogs; LBL ITG Whole Frog Project; Anura; Order Anura; Anura. ATW020814

checked ATW040209

Lissamphibian References

Abbreviated Dendrogram

```
TEMNOSPONDYLI
|
Lissamphibia
|--Gymnophiona
|  |--Eocaecilia
|  `--+--Rhinatrematidae
|     `--Caeciliidae
|
`--+--Urodela
   |  |--Karaurus
   |  `--Sirenidae
   `--Anura
```

Contents

Overview
Lissamphibia
References

References

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp.
Lissamphibia.

Jared, C, CA Navas & RC Toledo (1999) *An appreciation of the physiology and morphology of the caecilians (Amphibia: Gymnophiona)*. **Comp. Biochem & Physiol. A** 123: 313-328.
Gymnophiona.

Jenkins, FA & DM Walsh (1993), *An Early Jurassic caecilian with limbs.* **Nature** 365: 246-250.
Eocaecilia.

O'Reilly, JC, RA Nussbaum & D Boone (1996), *Vertebrate with protrusible eyes*. **Nature** 382: 33. H.
Gymnophiona.

O'Reilly, JC, DA Ritter & DR Carrier (1997), *Hydrostatic locomotion in a limbless tetrapod*. **Nature** 386:269-272.
Gymnophiona.

Summers, AP & JC O'Reilly (1997), *A comparative study of locomotion in the caecilians **Dermophis mexicanus** and **Typhlonectes natans** (Amphibia: Gymnophiona)*. **Zool. J. Linnean Soc.** 121-65-76.
Gymnophiona

Wilkinson, M & RA Nussbaum (1997), Comparative morphology and evolution of the lungless caecilian Atretochoana eiselti (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). Biol. J. Linn. Soc. 62: 39-109.
Gymnophiona.

---

checked ATW040109

Lepospondyli: Overview

Abbreviated Dendrogram

```
REPTILOMORPHA
|
`-LEPOSPONDYLI
  |--Microsauria
  `--+--Lysorophia
     `--+--Adelogyrinidae
        `--+--Nectridia
           `--Aïstopoda
```

Contents

Introduction

The lepospondyls consist of four to six groups of mostly small aquatic tetrapods. Generally, they include Nectridia, Aïstopoda, Adelogyrinidae, Microsauria, Lysorphia, and possibly a few other types. All are limited to the Carboniferous and/or Cisuralian (Early Permian). Lepospondyls are one of a very few large vertebrate taxa whose phylogenetic position and definition *both* remain vague. In fact, of the 50-odd groups in which we have arbitrarily divided the chordates, only the anapsids (turtle lineage) are more loosely constrained.

Even with anapsids, it is easy to give a reasonable a phylogenetic definition: for example, turtles > turtle doves. That isn't possible with lepospondyls. It's quite possible that they are not a good clade. That is, the descendants of the last common ancestor of all lepospondyls may also include the Lissamphibia (living amphibians), some or all reptiliomorphs, or even the entire amniote clade. Things have settled down a bit in the last few years, and the following table lists the main recent contenders.

Phylogeny

```
Tetrapoda
|--Temnospondyli
|   `--Lissamphibia
`--Reptiliomorpha
   |--Lepospondyli
   `--Amniota
```

```
Tetrapoda
|--Temnospondyli
`--Reptiliomorpha
   |--Lepospondyli
   |   `--Lissamphibia
   `--Amniota
```

```
Tetrapoda
|--Temnospondyli
|   `--frogs & salamanders
`--Reptiliomorpha
   |--Lepospondyli
   |   `--caecilians
   `--Amniota
```

Possible definition	*Diplocaulus* > *Diplodocus*	frogs > philosophers	caecilians > Sicilians
Reference	Ruta *et al*. (2003)	Vallin & Laurin (2004)	Carroll (2001)

In addition, there are variants of each possibility, depending on how the lepospondyls and amniotes are nested within the various reptiliomorph groups. The degree of apparent high-level agreement is somewhat illusory. For example, among lepospondyl groups, the Microsauria are probably paraphyletic. That is, all the other types probably derive from microsaurs.

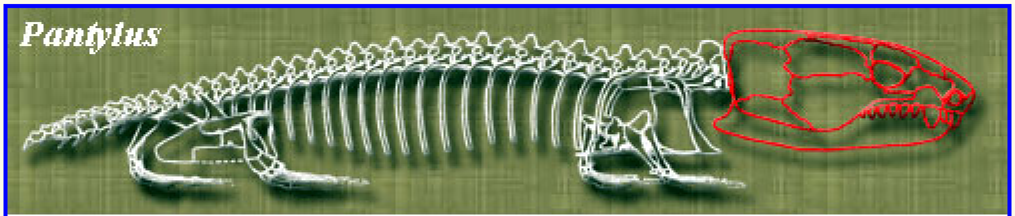
Nevertheless, this is a considerable improvement over the situation in the early 1990's. At that time, there was some feeling that the lepospondyls might be a series of unrelated groups scattered along the line from Tetrapoda to Amniota. That may still be the case, but most recent papers have allowed that the Lepospondyli may be paraphyletic (including Lissamphibia and possibly Amniota) but are not polyphyletic. Whether this consensus survives remains to be seen. *Westlothiana* (*see* image at the Dinosauromorpha site) has been very helpful as a sort of key transition critter between the reptiliomorph-amniote line and the lepospondyls. However, if it should turn out to be something different, the whole scheme could fall apart.

Juvenile and adult seymouriamorphs

The reason we engage in this pessimistic and dire speculations is that this region of phylospace is warped. Like some peculiar non-Euclidian fold in the universe of physics, this is a region in which the fundamental laws of cladistics may not hold. To see why, we must consider the peculiar difficulties raised by the recent discovery that the stem tetrapods were probably aquatic, or only minimally terrestrial. *See, e.g.*, Clack (2002). If true (and we are decidedly undecided), no one seems to have considered the next question: if all of the stem tetrapods were aquatic, then how on earth (so to speak) did the transition to terrestrial life take place? If everyone from *Acanthostega* through the colosteids, baphetids, *Greererpeton*, etc. was aquatic, then we have no reason to suppose that the early reptiliomorphs and temnospondyls were any different. These animals are all designed along the same general plan. But, if this plan – which included four legs, with feet and digits, a *bona fide* neck, moderately strong vertebral column, sacrum, lungs, and so forth -- was *not* sufficient to make a good terrestrial animal, how do we explain terrestrial life before the acquisition of the full amniote suite of terrestrial adaptations?

The answer seems to lie in a developmental anomaly acquired by derived temnospondyls and derived reptiliomorphs: two groups which seem to have, independently, adopted a terrestrial component to their lifestyle. This shared characteristic consists of a prolonged juvenile stage followed by a change to a markedly different adult form. That is, temnospondyls and many, or perhaps all, reptiliomorphs have markedly different juvenile and adult forms. *See* Steyer (2000) for a discussion of the temnospondyl case. Compare, for example, the images here showing the very different construction of the related seymouriamorphs *Discosauriscus* (juvenile) and *Seymouria* (subadult).

It is particularly clear in the case of seymouriamorphs that the juvenile form is essentially aquatic, while the adult morph is almost certainly terrestrial. We will adroitly leap to the conclusion that this, in fact, is the way in which the transition to land was actually made. Now, if true, it follows that evolution is going to have an unusually free hand. The juvenile reptiliomorph is specialized for growth and development in water until some critical point is reached. Then, like a teen-ager getting a driver's license, it rather abruptly begins to concentrate on sex and terrestrial mobility, often accompanied by a radical change of diet, complexion, and degree of cooperation. Needless to say, these are very different lifestyles, and probably caused no end of worry for their Viséan reptiliomorph parents, too. More to the point, this functional separation means that quite different selective pressures will come to bear on the juveniles and adults. And, the more terrestrial the adult, the more diverges from the aquatic juvenile and, hence, the greater the differential selective pressure on pre-amniotes tending to separate the juvenile and adult morphs yet further. As with teen-agers, it's a positive feedback system limited only by the fact that the same genome and life cycle have to contain both morphs.



A microsaur from the Cisuralian of Texas. Image from the Virtual Museum of Fossils (Valdosta State University).

Take it one step further. Metamorphosis offers significant adaptive advantages for juveniles and adults, but the process itself is awkward, metabolically expensive, and risky. There are excellent actuarial reasons why automobile insurance is expensive for young drivers; and most of these factors apply to tetrapods as well as teens: inexperience, inappropriate reflexes, and a surfeit of hormones -- to mention but a few. So, while some selective pressures tend to drive the juvenile and adult forms apart, equally compelling factors offer a rich evolutionary reward for species which can eliminate this awkward and hazardous transition phase by doing away with one or the other morph -- an option sadly unavailable to insurers. Thus, the inexorable logic of metamorphosis is a trichotomy of tetrapods: (1) amphibians with two dissimilar life stages, (2) generally aquatic *pedomorphic* forms, and (3) strongly terrestrial *peramorphic* species. While the details of development are not always easy to reconstruct in organisms extinct for 300 Ma, this is roughly what we see: a primary radiation of true amphibians (temnospondyls and early reptiliomorphs), followed closely by the evolution of peramorphic terrestrial animals (amniotes and their close relatives), and a group of strongly pedomorphic, generally aquatic species -- the lepospondyls.

But here's the problem. How can we do good cladistics on animals which may have more than one morph? This is particularly true of the pedomorphic lepospondyls, because they have jettisoned the adult form. For all we know, the adult form of some microsaur might look exactly like an early amniote. Microsaurs don't have definitive adult forms, and amniotes generally don't have an aquatic juvenile form. In short, the usual rules of cladistics don't necessarily apply. It's hard to say how seriously metamorphosis will throw things off. However, so far as we know, no one has even looked at the problem from the vantage point of cladistics, and it certainly suggests one reason for the inconsistent results in this area. The tendency of the pedomorphic lepospondyls to cluster based on juvenile characters may very well mask a very complicated relationship between lepospondyls (especially microsaurs) and the reptiliomorphs.

ATW061003

Page Back | **Unit Home** | **Page Top** | **Page Next**

checked ATW060209

Page Back	Unit Home	Unit Dendrogram	Unit References	Taxon Index	Page Next
Unit Back	Vertebrates Home	Vertebrate Dendrograms	Vertebrate References	Glossary	Unit Next

Lepospondyli

Abbreviated Dendrogram

```
REPTILOMORPHA
|
`-LEPOSPONDYLI
  |--Microsauria
  `--+--Lysorophia
     `--+--Adelogyrinidae
        `--+--Nectridia
           `--Aïstopoda
```

Contents

Taxa on This Page

1. Adelogyrinidae X
2. Aïstopoda X
3. Lepospondyli X
4. Lysorophia X
5. Microsauria X
6. Nectridia X

Descriptions

Lepospondyli:

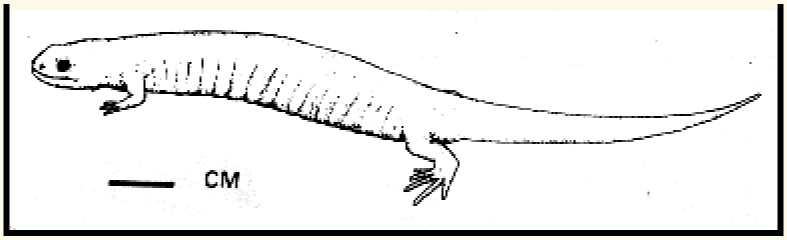
Range: from the Early Carboniferous.

Phylogeny: Batrachosauria **:** Seymouriamorpha + * **:** Microsauria + (Lysorophia + (Adelogyrinidae + (Nectridia + Aïstopoda)))

Characters: Possibly paraphyletic group united mostly by relatively small size and lack of labyrinthodont dentition. Single, spool-shaped vertebral centrum. May be stem group for Lissamphibia, rather than temnospondyls. Others eliminate this taxon altogether.

Links: Amphibia [Lepospondyli after Laurin & Reisz, 1997]; Amphibians. ATW030204

Microsauria:



Range: C–P of NAm. and Eur.

Phylogeny: Lepospondyli **:** (Lysorophia + (Adelogyrinidae + (Nectridia + Aïstopoda))) + *.

Introduction: The microsaurs ("small lizards") are a diverse group of small prehistorical amphibians of the Carboniferous and Permian periods. Some were terrestrial and lizard-like, others aquatic and newt-like. There were even specialised burrowing forms. Included as part of the "lepospondyl" group, they may be more closely related to temnospondyls. (MAK 931010)

Characters: Single bone in temporal series (tabular). All have limbs, usu. small. Many terrestrial and lizard-like with deep skulls, elongate.

Lysorophia: *Lysorophus, Cocytinus*.

Range: Pennsylvanian to Cisuralian of North America (Eastern U.S.)

Phylogeny: Lepospondyli **::** (Adelogyrinidae + (Nectridia + Aïstopoda)) + *.

Characters: fenestrate skulls, parietal foramen absent **[2]**; postfrontal, postorbital, supratemporal, jugal, quadratojugal, ectopterygoid, coronoids, and postsplenial absent **[2]**; anteriorly sloping suspensoria; parasphenoid broad, with poorly differentiated *cultriform process* **[2]**; short mandibles (each bearing a lateral mandibular fenestra); dentition not *labyrinthodont* **[2]**; denticles and fangs on the vomer and palatine absent **[2]**, parasymphysial fangs absent **[2]**; extensive, well-ossified hyobranchial skeletons; elongate bodies, vertebral centra composed of a single, cylindrical ossification **[2]**; neural arch halves sutured at midlines and to centra; anterior surface of *atlantal* centrum broader than its posterior surface **[2]**; distinct atlantal *odontoid process* present **[2]**; greatly reduced limbs; dermal sculpture absent **[2]**,

Notes: **[1]** Highly derived relative to other Paleozoic amphibians. Most closely related to Microsauria, based on morphology of the craniovertebral articulation. **[2]** synapomorphies shared with Lissamphibia

Links: link; Phylogeny of Stegocephalians; ATW040114.

Adelogyrinidae: *Adelogyrinus, Adelospondylus, Dolichopareias, Palaeomolgophis*.

Range: Early Carboniferous (Visean to Serpukhovian) of Europe.

Phylogeny: Lepospondyli **:::** (Nectridia + Aïstopoda) + *.

Characters: Long trunk, but with limb girdles; orbits very far forward; solid skull roof. (*Crassigyrinus* originally thought to be in this group).

Links: link. ATW021021.

Nectridia: *Ctenerpeton, Diplocaulus, Keraterpeton, Sauropleura, Scincosaurus*.

Range: lwC–upP (lwP?) of Eur., NAm, and NAfr.

Phylogeny: Lepospondyli **::::** Aïstopoda + *.

Introduction: The Nectridia were a group of small to medium-sized paleozoic amphibians, mostly aquatic, usually included within the lepospondyl group. Most forms resemble modern newts, with elongate flatened tails. A few late specialised forms

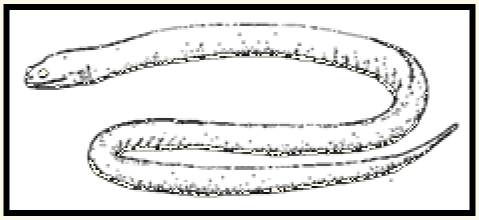
however developed strange boomerang-shape heads. These remarkable heads probably served as hydrofoils to provide lift in slow-moving streams. The Nectridia were a surprisingly succesful group during the Early Permian, but may have been unable to cope with the increasingly arid conditions at the end of the Permian, and died out without leaving any descendants.

The nectridians are best known from *Diplocaulus* and similar small to medium sized (length to 50 or 100 cm) members of the Keraterpontidae, the most extreme members of the Nectridean group, characterised by skulls possessing large backward or sideways directed "horns" or perhaps more accurately, hydroplanes. Keraterpontidae would have fed on small fish and aquatic invertebrates, and were themselves preyed upon by larger amphibians and freshwater sharks. (MAK 981010)

Characters: Primitively, skull table narrow and moveable on jugal; tabular horns in some forms (Keraterpetontidae); primitively, skull table narrow and moveable on jugal; some skull kinesis (Diplocaulids lose kinesis – very large tabular horns); body laterally compressed, fan-shaped, symmetrical neural and hemal arches; little flexibility in trunk; elongate in tail (not trunk); trunk limbs interdigitate through neural spines; limbs small; secondarily aquatic.

Links: Diplocaulus - Paleontology and Geology Glossary; lect11.html; TMMSH - Exhibits - Scratching the Surface - Diplocaulus; Diplocaulus ????????; Chamworks Dinosaurs & Such: Diplocaulus sp.; DIPLOCAULUS; Timelines | American Museum of Natural History.

Aïstopoda: *Ophiderpeton* (see image)



Range: Early Carboniferous to Early Permian of North America & Europe.

Phylogeny: Lepospondyli :::: Nectridia + *.

Introduction: The aïstopods were a small group of specialised limbless amphibians. In appearance and quite probably in movement too, they resembled snakes. Their bodies were extremely elongated, the torso containing up to 200 vertebrae, or even more, while the tail was short and primitive. The skull was very specialised, with fusion and loss of bones in the snout, cheek, and top of the head. In advanced forms the skull became a series of struts that supported the braincase against the lower jaw, just as in snakes. The evolutionary relationships to other groups are not known with confidence, but it seems that they diverged quiet early from other lineages. Aïstopod vertebrae are very similiar in structure to nectridan vertebrae, and the two groups are usually connected within the lepospondyls.

Characters: 5-100 cm; very elongate; some with snake-like kinetic, fenestrated crania; orbits large and located far anteriorly; jaws with wide gape; no limbs or limb girdles; up to 230 vertebrae; vertebrae *holospondylous* and deeply *amphicoelous*; only 1 vertebral ossification per segment; rib heads **K**-shaped; vertebral column with well-defined cervical, thoeacic and caudal regions; tail not flattened (as in aquatic forms).

Links: link, image; NRC Research Press: Canadian Journal of Earth Sciences (abstract); OBERSEMINAR – VORTRAG. (German: good short discussion, but the comments on lifestyle are very speculative); Aistopoda (Mikko's Phylogeny); Dino Land Travels Database Redpath Museum- Aïstopods; Nathis Fauna Amphibiën - Primitieve Terapoden (Dutch). ATW040705.

Page Back Unit Home Page Top Page Next

checked ATW060209

Lepospondyli: References

Abbreviated Dendrogram

```
REPTILOMORPHA
|
`-LEPOSPONDYLI
  |--Microsauria
  `--+--Lysorophia
     `--+--Adelogyrinidae
        `--+--Nectridia
           `--Aïstopoda
```

Contents

Overview
Lepospondyli
References

References

Clack, JA (2002), **Gaining Ground: the Origin and Evolution of Tetrapods**. Indiana Univ. Press, 369 pp.
Lepospondyli.

Ruta, M, MI Coates & DLJ Quicke (2003), Early tetrapod relationships revisited. **Biol. Rev.** 78: 251-345.
Lepospondyli

Steyer, JS (2000), *Ontogeny and phylogeny in temnospondyls: a new method of analysis*. **Zool. J. Linn. Soc.** 130: 449-467.
Lepospondyli.

Vallin, G & M Laurin (2004), *Cranial morphology and affinities of Microbrachis, and a reappraisal of the phylogeny and lifestyle of the first amphibians*. **J. Vert. Paleontol.**, 24: 56-72.
Lepospondyli.

---

checked ATW060209