Reptiliomorpha: Overview

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

Contents

Tseajaia campi Vaughn 1964, an early Permian diadectomorph, length about 90cm. This was an animal on teh verge of becoming a reptile. The diadectomorphs, of which *Tseajaia* was a late but primitive representative, were animals that were very reptile like in structure and appearance, but probably were still physiologically amphibians, having to return to the water to lay their eggs. Life reconstruction, by Nobu Tamura . Wikipedia, GNU Free Documentation/Creative Commons Attribution

"Gaining Ground"

Our subtitle here is the same as the title of Dr. Jenny Clack's recent book about the origin and early evolution of the Tetrapoda. The irony of Clack's title is that she has shown, rather convincingly, that none of the early tetrapods were likely to have been terrestrial to any marked degree. She argues, convincingly, that many of the critical "terrstrial" adaptations of the early tetrapods can just as easily be interpreted as adaptations to aquatic lifestyles. Elsewhwere, we have discussed that this point may have been overstated. The particular suite of adaptations we see in early tetrapods may have succeeded, not because they were aquatic adaptations, and not because they were terrestrial adaptations, but precisely because they were both. Thus, Clack's thesis is certainly valid to the extent it states that tetrapods were primitively not evolving toward terrestriality. Rather, they were becoming better and better amphibians.

The real turn to terrestriality begins here, with the **Reptiliomorpha**. **We tentatively define this clade as one of the supporting stems of crown group Tetrapoda*. As a reminder, Tetrapoda* is defined (at various places in Palaeos, as dogs + frogs, princes + frogs, or Prof. Michael Coates + frogs. These are all equivalent definitions. Reptiliomorpha is then dogs (or princes, or Prof. Coates) > frogs.**

In the not unlikely event that living amphibians are descended from temnospondyls, then the reptilomorphs will include a few more taxa but will otherwise change little. In terms of evolutionary grade, this section covers things from the anthracosaurs through the first steps of the amniote radiation. Temporally, this spans a very limited period. This whole process was probably compressed into about 30 million years, between the middle Mississippian and the middle of the Pennsylvanian. Yet, in that brief period, the tetrapods diversified from a rather homogeneous, if peculiar, bunch of air-breathing freshwater fishes into truly terrestrial amniotes, including anapsids (the turtle lineage), synapsids (the mammal lineage), and the true reptiles.

The critical points in this process involved the acquisition of a large group of amniote adaptations, most of which are listed here. ATW040821.

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Reptiliomorpha

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Eoherpeton
      |     |--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
         `--Batrachosauria
            |--Seymouriamorpha
            `--+--Solenodonsaurus
               `--Cotylosauria
                  |--Diadectomorpha
                  `--AMNIOTA
```

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2. *Eoherpeton* X
3. Reptiliomorpha

Inroduction

During the Carboniferous and Permian periods, prehistoric amphibians evolved along a number of parallel lines towards a reptilian condition. Some of these amphibians (e.g. *Archeria*, *Eogyrinus*) were elongate, eel-like aquatic forms with diminutive limbs, while others (e.g. *Seymouria*, *Solenodonsaurus*, *Diadectes*, *Limnosceles*) were so reptile-like that until quite recently they actually have been considered reptiles, that some of them they may still turn out to be reptiles, and it is likely that to an observer they would have appeared indistinguishable from small or large reptiles.

Although the first amniote reptile probably appeared in the late or even middle Mississippian period (Middle Carboniferous), as forms like *Casineria* would seem to indicate, a number of lines of reptiliomorph amphibians and proto-amniotes continued to flourish alongside their fully reptilian (crown amniote, to use the cladistic term) descendents and relatives for many millions of years.

By the middle Permian these various terrestrial forms had died out, but several aquatic groups continued to the end of the Permian, and in the case of the Chroniosuchids survived the end Permian mass extinction, only to die out at the end of the Middle or even the early Late Triassic. Meanwhile, the single most sucessful daughter-clade of the Reptiliomorphs, the Amniotes, continued to flourish and to inherit the Earth MAK050702 (for Wikipedia), MAK111108

Changing Definitions

The name Reptiliomorpha was coined by Professor Gunnar Säve-Söderbergh in 1934 to designate various types of late Paleozoic reptile-like labyrinthodont amphibians. (Säve-Söderbergh 1934) However Alfred Sherwood Romer used the name Anthracosauria instead. In 1970, the German paleontologist Panchen reverted to Säve-Söderberghs definition, (Panchen 1970) but Romer's terminology is still in use, e.g. Carroll 1988 and 2002, and Hildebrand & Goslow 2001. Some cladistic also work prefer Anthracosauria. (Gauthier et al 1988)

In 1956 Friedrich von Huene included both amphibians and anapsid reptiles in the Reptiliomorpha. This included the following orders: 1. Anthracosauria, 2. Seymouriamorpha, 3. Microsauria, 4. Diadectomorpha, 5. Procolophonia, 6. Pareiasauria, 7. Captorhinidia, 8. Testudinata. (Von Huene 1956) Now we know that these groups belong to very different lineages, and similarities are the result of convergences or shared primitive features.

In 1997 Michel Laurin and Robert Reisz (1997) adapted the term in a cladistic sense. Michael Benton (2000, 2005) made it the sister-clade to Batrachomorpha. However, when considered a linnaean ranking, Reptiliomorpha is given the rank of superorder and only includes reptile-like amphibians, not their amniote descendants (Systema Naturae 2000). More recently Reptiliomorpha has been adopted as the term for the largest clade that includes – according to the technical definitions of the phylocode which only refers to species level organisms – *Homo sapiens* but not *Ascaphus truei* (a primitive frog) (International Phylogenetic Nomenclature Meeting 2003); or is, as Palaeos co-author Toby White puts it, more like dogs than frogs (i.e. mammals but not amphibians). However, given the lack of consensus of the phylogeny of the labyrinthodonts in general, and the origin of modern amphibians in particular, the actual content of the Reptiliomorpha under the latter definition is uncertain. MAK050702 and updated by editors on Wikipedia, MAK111107

Descriptions

Reptiliomorpha: dogs > frogs.

Range: from the Early Carboniferous.

Phylogeny: Tetrapoda* : Lepospondyli + * : Anthracosauroidea + (Gephyrostegidae + Batrachosauria)

Characters: Domed skull, retaining kinesis (skull roof loosely attached to cheek); skull usually with fine radiating grooves;

tabular large & attached to parietal; deep otic notch in quadrate; some with slight, impedance-matching stapes; pleurocentrum dominant element of vertebrae; well-developed limbs; 5 digits; usually terrestrial.

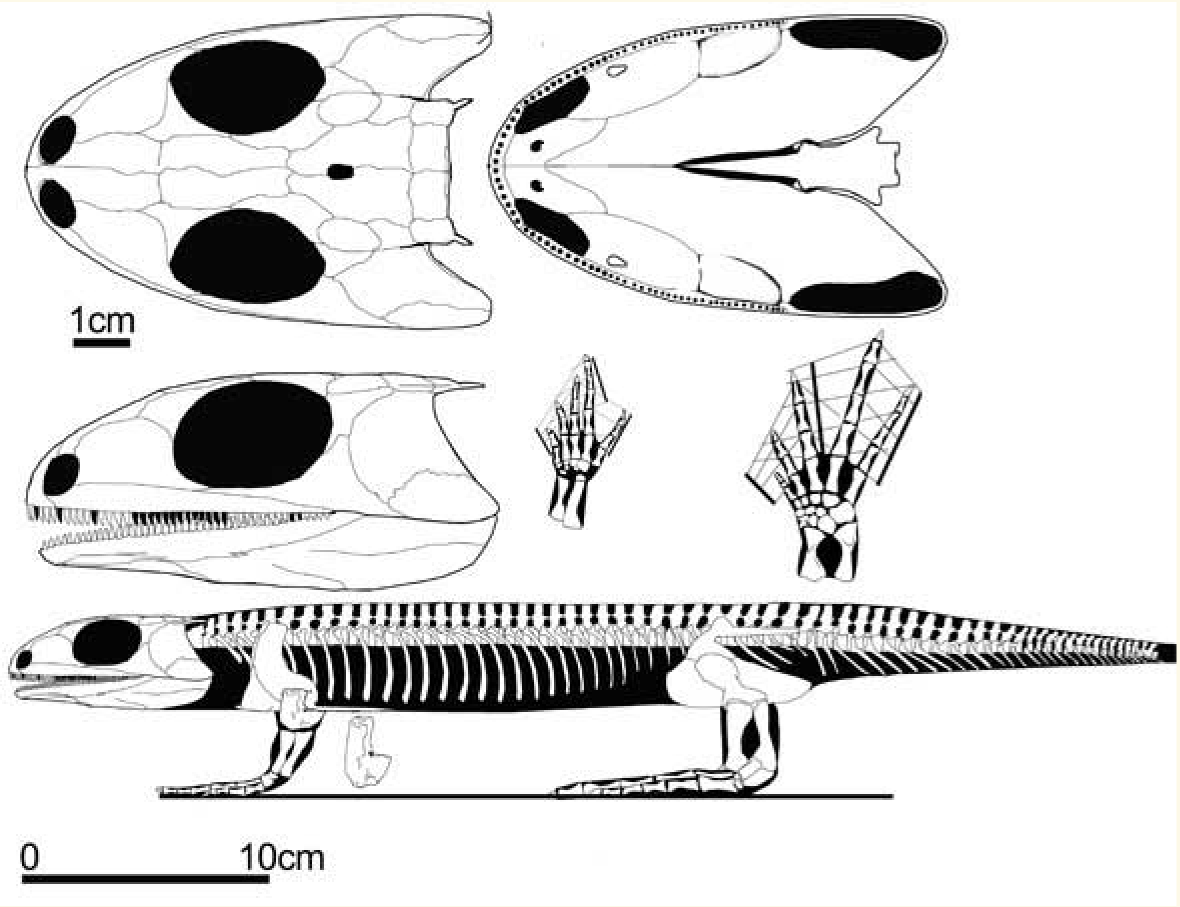
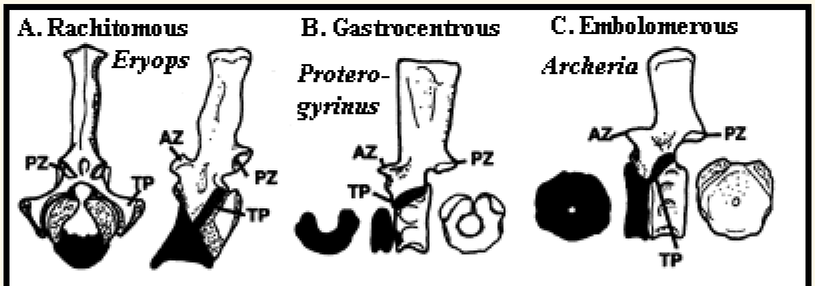


Image: *Silvanerpeton miripedes* Clack 1994 Visean of Scotland, about 40 cm long, from David Peters, Reptile evolution, references Clack 1994, Ruta & Clack2006 MAK111107

Links: lecture9.

Note: A reminder that we are referring to the crown group Tetrapoda*, *i.e.* frogs + dogs. Reptiliomorpha is one stem from the tetrapod node by definition. The other stem really ought to be called something other than Lepospondyli, since we really don't know if the traditional lepospondyls included the ancestor of modern amphibians. ATW021214.

Anthracosauroidea: *Eldeceeon, Silvanerpeton*



Three types of vertebral structure from Paleozoic tetrapodomorphs. From Clack (2002).

Range: Carboniferous to Triassic.

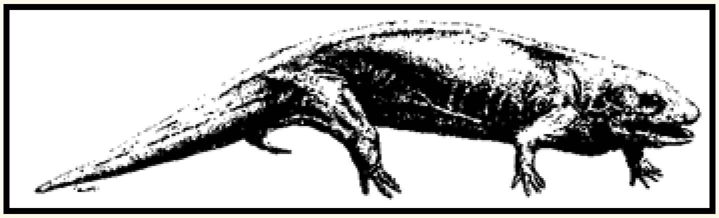
Phylogeny: Reptiliomorpha **:** (Gephyrostegidae + Batrachosauria) + * **:** *Eoherpeton* + (Chroniosuchia + Embolomeri).

Characters: "Kinetic line," i.e. abrupt angle between skull table and cheek without interdigitating suture & possibly mobile (primitive) [C02]; tabular contacts parietal [C02]; tabular horn or process common [C02]; intertemporal present (primitive) [C02]; "otic notch" present; posttemporal fossae absent; stapes massive [C02]; still has sarcopterygian skull hinge; moveable joint at basicranial articulation (primitive) [C02]; closed palate without vacuities (primitive) [C02]; vertebrae gastrocentrous, with pleurocentrum dominant element [C02]; lozenge-shaped interclavicle; 5-toed hand [C02]; ilium with 2 dorsal blades [C02]; amphibian ankle; 2-3-4-5-3 (almost reptilian) phalangeal count.

Note: In the figure, the intercentrum is shaded. The rachitomous type is dominated by the intercentrum, and the pleurocentra appear as paired, dorsolateral elements cushioning the notochord.. It is highly flexible and permits simultaneous twisting and bending -- appropriate for aquatic mobility, but likely to collapse on land. In the gastrocentrous vertebra, the emphasis is on supporting the arch. The neural arch sits firmly on the intercentrum and the pleurocentrum is reduced to a small, spacer element. This configuration allows less mobility, but assists the spine to bear the weight of the body on land. The embolomerous vertebra is characteristic of the secondarily aquatic embolomeres. The intercentrum reappears as a major structural unit, and both centra form complete disks. This conformation with successive small disks, recovers some of the flexibility of the rachitomous vertebra, while maintaining considerable strength and stability.

References: Clack (2002) [C02]. ATW020620.

Eoherpeton: *E. watsoni* Panchen 19??

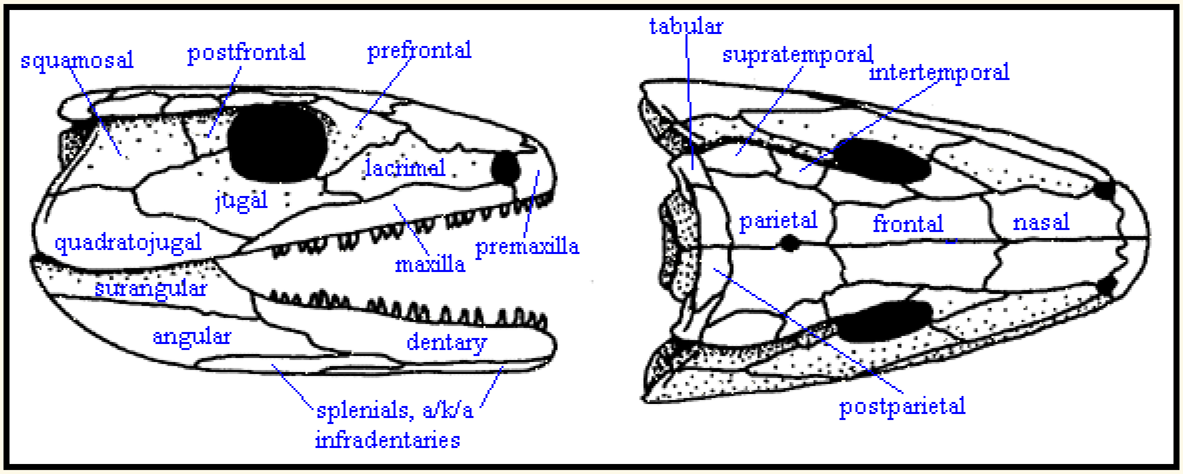


Range: Early Carboniferous (Namurian) of Europe (Scotland).

Phylogeny: Anthracosauroidea : Chroniosuchia + Embolomeri + *.

Characters: otic notch absent?

Image: (upper) *Eoherpeton* by Mike Coates; (lower) *Eoherpeton skull*, right lateral and dorsal view, from Smithson, TR (1985b), *The morphology and relationships of the Carboniferous amphibian* ***Eoherpeton watsoni*** *Panchen*. **Zool. J. Linn. Soc.** 85: 317-410; *vide* Clack (2002),



Links: EMBOLOMERI; Crassigyrinus scoticus.

Note: *Eoherpeton* has been variously classified as a gephyrostegid, an embolomere, and an anthracosaur *i.s.* It may also be none of the above. By way of explanation, this is one of these awkward areas in which we must recall our principles, even if we don't stand by on them. If Reptiliomorpha is defined as a stem group (dogs > frogs), then Anthracosauroidea must logically be a crown group (*Gephyrostegus* + *Pholiderpeton*). There is no guarantee that *Eoherpeton* falls in this group, particularly since the gephyrostegids are not very well known. It is included here among the anthracosauroids only by convention. ATW020621, MAK981010.

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Reptiliomorpha: Embolomeri

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |   |--Embolomeri
      |   |   |--+--Proterogyrinus
      |   |   |  `--Pholidogaster
      |   |   `--Eogyrinidae
      |   |       |--Diplovertebron
      |   |       `--Pholiderpeton
      |   `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
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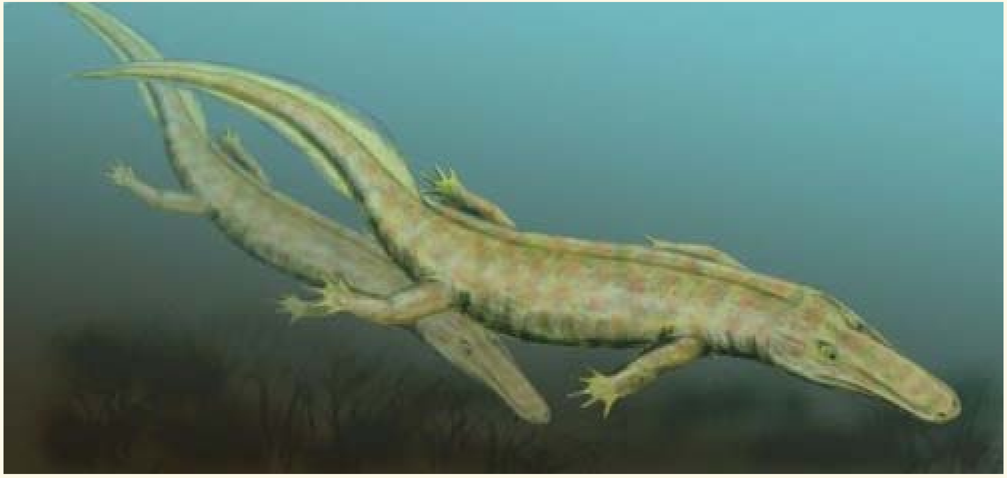
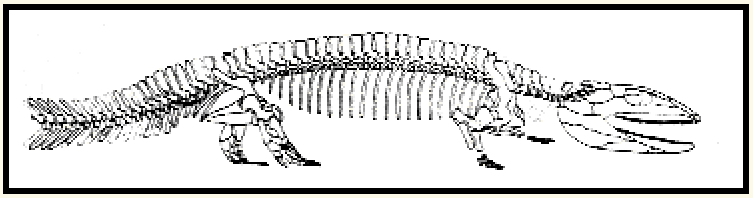
1. *Diplovertebron* X
2. Embolomeri X
3. Eogyrinidae X
4. *Pholiderpeton* X
5. *Pholidogaster* X
6. *Proterogyrinus* X



Archeria crassidiscus (Cope, 1884), Eogyrinidae Early Permian of Texas, life reconstruction, by Arthur Weasley (Larger image (*Wikimedia*))

Descriptions



Embolomeri: *Archeria*, *Pholiderpeton*, *Proterogyrinus*.

Range: Early Carboniferous to Early Triassic (*fl.* Late Carboniferous) of North America, Europe (Scotland) & Russia.

Phylogeny: Anthracosauroidea **:** Chroniosuchia + * **:** (*Proterogyrinus* + *Pholidogaster*) + Eogyrinidae.

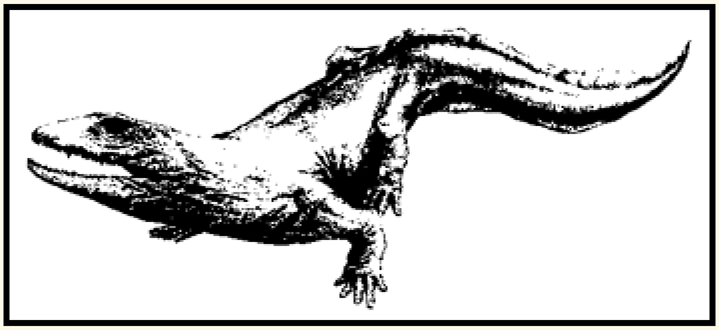
Characters: Specialized, long-bodied, piscivorous marine anthracosaurs; short skull table with *kinetic line* [C02]; prominent *tabular horn* [C02]; cheek extends well posterior to occiput [C02]; very loose junction between quadrate and quadrate ramus of pterygoid [C02]; elongated trunk (*e.g.* 40 vertebrae); both pleurocentra and intercentra developed as cylinders; some with caudal fin (i.e. caudal supraneural radials as in fish) [C02].

Image: *Proterogyrinus scheeleri* from Holmes (1984).

Note: see figure and note under Anthracosauroidea.

Links: Phylogenetic position of the Embolomeri; Biology 356; Phylogeny of stegocephalians; Embolomeri.

References: Clack (2002) [C02]. ATW020128.

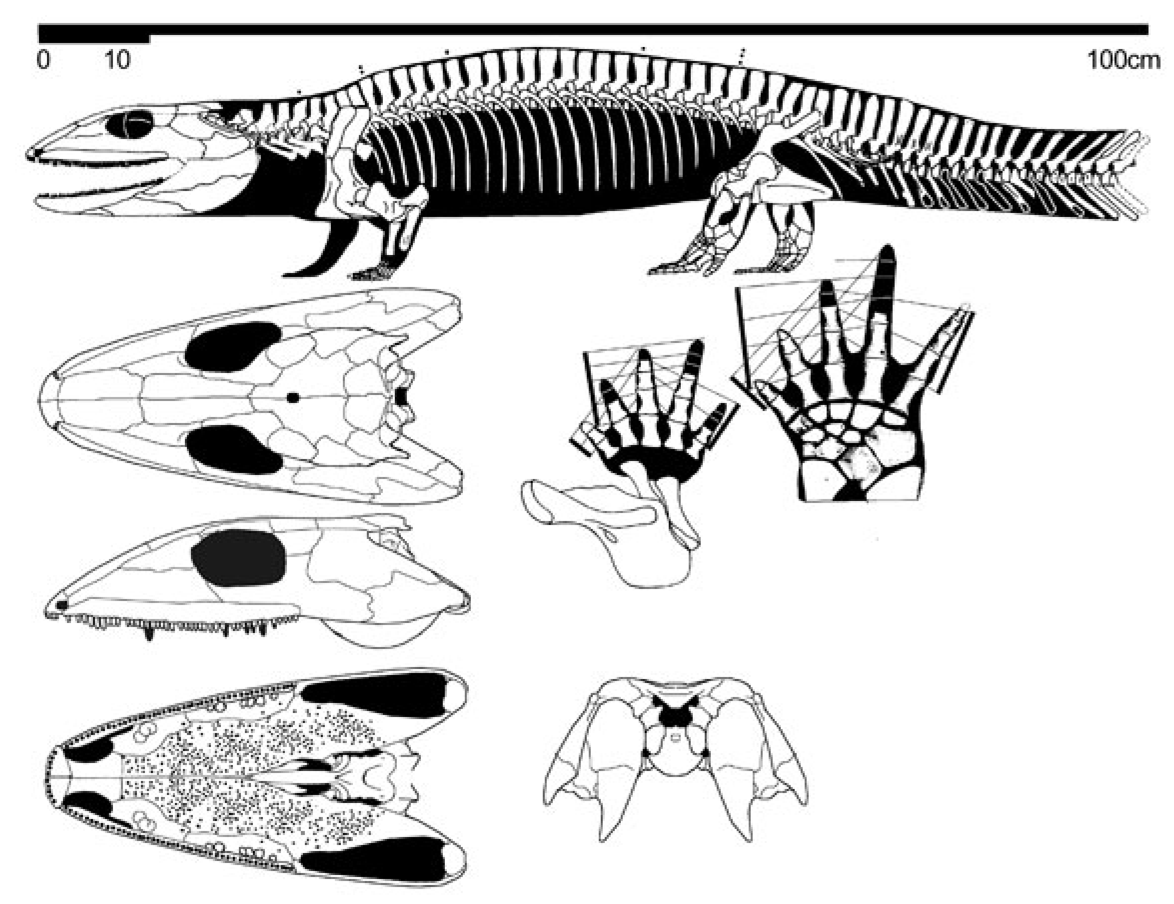


Proterogyrinus: *P. pancheni* Smithson 1986; *P. scheeleri* Romer 1970.

Range: Early Carboniferous of North America & Europe (Scotland).

Phylogeny: Embolomeri **::** *Pholidogaster* + *.

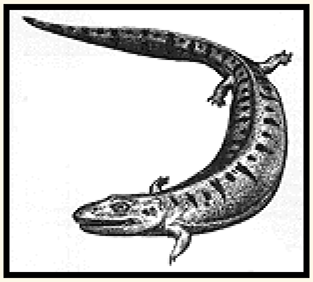
Characters: kinetic line present; neck short; 32 presacral vertebrae; vertebrae not fully embolomerous (see figure at Anthracosauroidea); tail laterally flattened; phalangeal formula 23453;



Note: **[1]** *Proterogyrinus* was a primitive semi-aquatic embolomere able to manage well both on land and in the water. It had well-developed limbs and a short neck and relatively short trunk, with 32 presacral vertebrae. The tail is flattened to aid in swimming. As with lobe-fined fish (osteolepiforms), there is a line of weakness between the skull table (the flat area at the back of the skull) and the cheek area, which allowed the skull to flex during jaw-opening. A notch at the back of the skull may have contained an eardrum, but the large bladelike stapes of primitive anthracosaurs are quite different to the narrow rod-like structure of animals with an ear adapted to detected sound in air. *P. pancheni* is the Scottish form, known from both the Dora Bone Bed near Cowdenbeath, Fife and the Lothian Region. *P. scheeleri* (see figure above, at Embolomeri) was recovered from the Bickett Shale, Bluefield Formation from Greer, West Virginia, USA. Both are of Serpukhovian age, although the American form is somewhat older. MAK981010. **[2]** note the still somewhat fish-like tail in the figure at Embolomeri. Clack (2002) compares this structure to *Eusthenepteron* and *Acanthostega* to make the argument that the transformation proceeded from anterior to posterior -- *hox* order. However, the argument is at least as strong that the transformation proceeded from distal to proximal (*BMP* or *Shh* order?). ATW020621

Images: Top: *Proterogyrinus pancheni* life reconstruction by Mike Coates, Right. *Proterogyrinus scheeleri* by David Peters, Reptile evolution MAK111107

Links: Transitional Vertebrate Fossils FAQ: Part 1B; Historický vývoj (Czech). ATW020621.



Pholidogaster: *P. pisciformes* Huxley.

Range: Early Carboniferous (late Visean to early Serpukhovian) of Scotland (Ironstone at Gilmerton, near Edinburugh) Euramerica

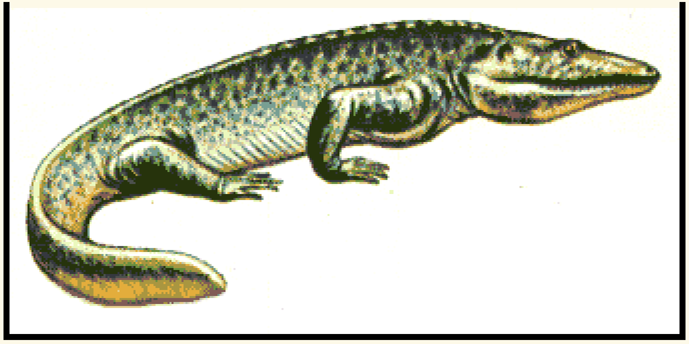
Phylogeny: Embolomeri **::** *Proterogyrinus* + *.

Size Adult Length over 1 metre long

Comments: Trunk very long and slender, the limbs are small and feeble. The pectoral arch apparently far back. There is a strong ventral (belly) armour of scutes.

Eogyrinidae: *Palaeoherpeton*, *Pteroplax*

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

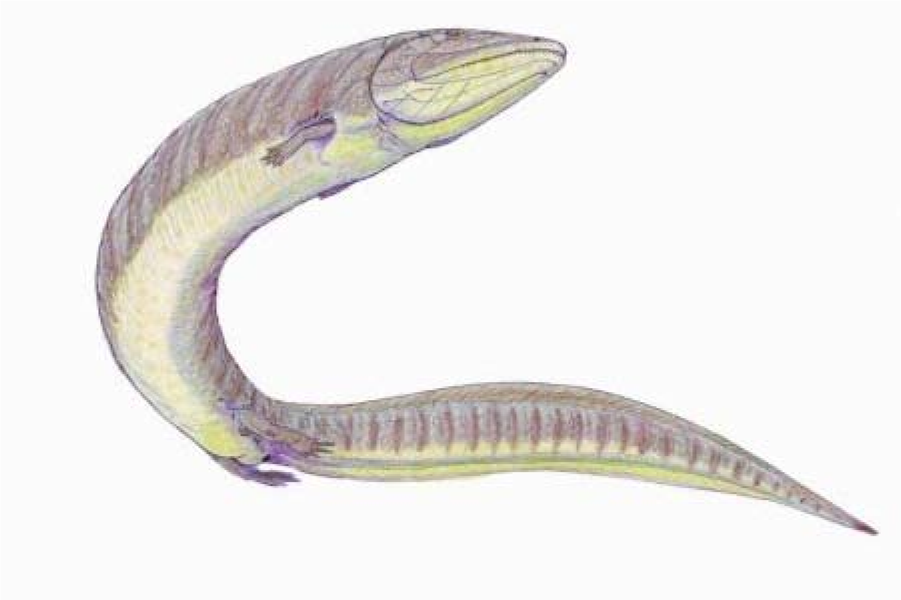


Phylogeny: Embolomeri **:** (*Proterogyrinus* + *Pholidogaster*) + * **:** *Diplovertebron* + *Pholiderpeton*.

Image: *Diplovertebron* (~60 cm).

Note: The eogyrinids were one of a number of lineages of relatively large, long-bodied tetrapods that frequented late Carboniferous rivers and watercourses. MAK981014.

Links: Class:Amphibia. ATW020621.



Pteroplax cornutus Hancock and Atthby 1868, life reconstruction, by Dmitry Bogdanov . Wikipedia, GNU Free Documentation/Creative Commons Attribution

Diplovertebron: *D. punctatum* Fritsch 1885

Range: Late Carboniferous (Moscovian? Bashkirian?) of Europe & North America.

Phylogeny: Eogyrinidae **:** *Pholiderpeton* + *.

Image: a rather imaginative reconstruction from Une page Web sur la période jurassique / A web page about jurassic period.

Links: Yale Peabody Museum: The Mural, Carboniferous & Devonian; Old, old reasons for hatred; Carbonifero (Italian); La galerie de la page jurassique : la faune aquatique et terrestre (French); ERA PALEOZÓICA (Spanish). ATW020621.

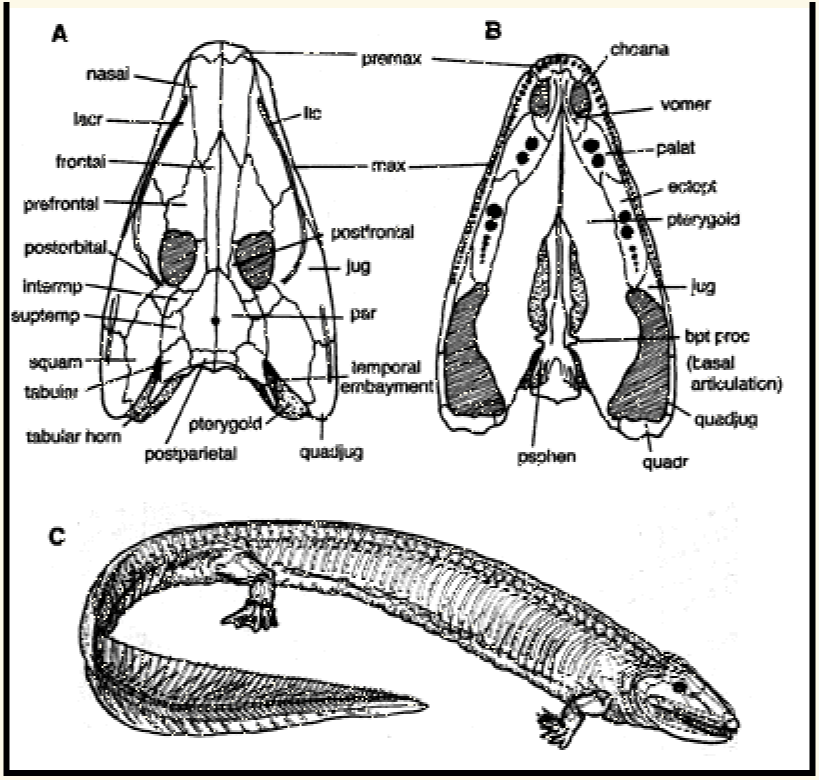
Pholiderpeton: (= *Eogyrinus*) *P. atheyi* Watson 1926, *P scutigerum* Huxley ??

Range: Late Carboniferous (Bashkirian [Westphalian B])

Phylogeny: Eogyrinidae **:** *Diplovertebron* + *.

Characters: ~200 cm; skull roof and palate only weakly attached [C02]; massive stapes [C02]; both pleurocentrum and intercentrum complete cylinders; *anocleithrum* present [C02].

Image: *Pholiderpeton*, (A) skull in dorsal view; (B) in palatal view; and (C) life reconstruction, from [C02], with (C) modified to show elements of internal skeletal features.



Links: Class-Amphibia

References: Clack (2002) [C02]. ATW030414.

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Reptiliomorpha: Chroniosuchia

Abbreviated Dendrogram

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TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Eoherpeton
      |     |--Embolomeri
      |     `--Chroniosuchia
      |        |--Chroniosuchidae
      |        `--Bystrowianidae
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

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2. Chroniosuchia X
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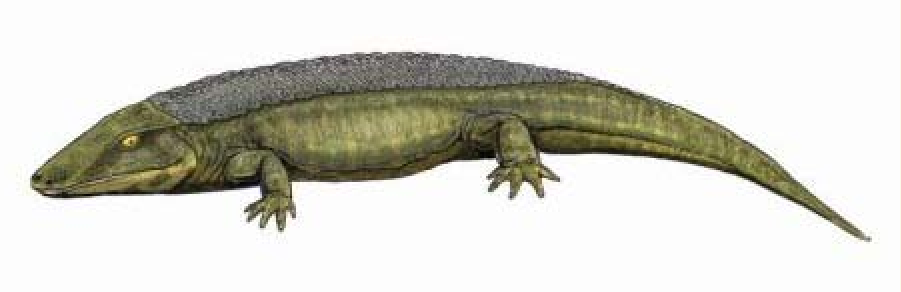
The Chroniosuchia



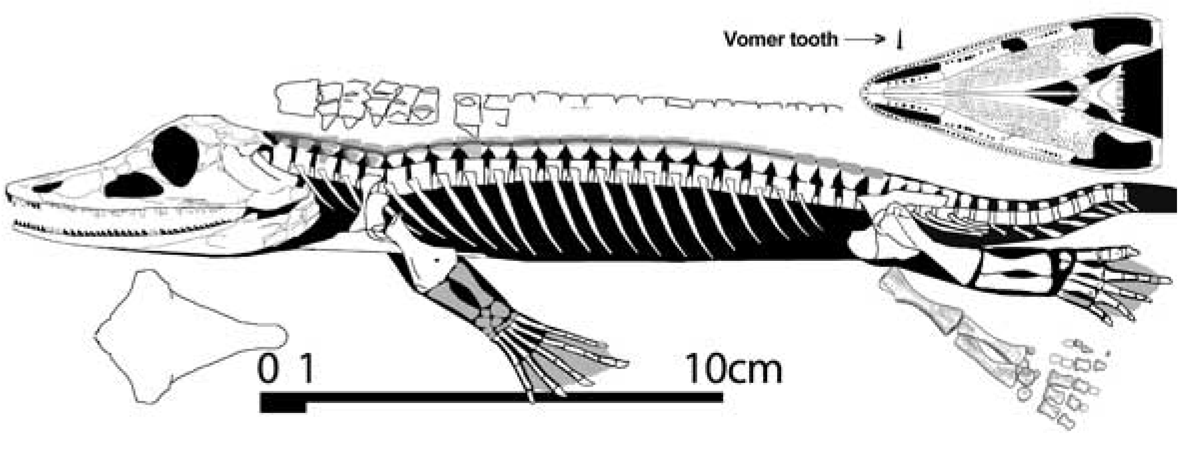
Chroniosuchus paradoxus Vjuschkov, 1957 (family Chroniosuchidae), life reconstruction, by Dmitry Bogdanov, 2007 (Larger image)

From Mark Mancini's blog *The Theatrical Tanystropheus* : Chroniosuchus:

The *Chroniosuchus* species were anthracosaurs which inhabited modern Russia from the latest Permian to the middle Triassic. Anthracosaurs were once considered to have belonged to the obselete “Labyrinthodontia” order. However, recent revisions concerning the cladistic relationships of early amphibians has placed the family Anthracosauridae within the superorder Reptiliomorpha and specifically inside of the order Embolomeri. It’s been suggested that anthracosaurs were closely akin to the order Seymouriamorpha due to several shared anatomcal characteristics, though many authors have questioned this and attributed their similarities to congruent evolution. In “The Age Of Dinosaurs In Russia And Mongolia”, Igor Novikov, Mikhail Shishkin and Valerii Golubev write:

> “Anthracosaurs were crocodile-like piscivorous amphibians with a rather deep elongated skull from 50 to 500 mm long. During their history, they retained a resemblance to the most primitive temnospondyls in such characters as the extent of the lacrimal bone up to the naris(or septomaxilla), presence of an intertemporal (a bar of bone separating the upper and lower temporal fenestrae in reptiles) in most forms, movable basipterygoid articulation (between braincase and upper jaw), narrow interpterygoid vacuities,pterygoids with median [(as in towards the animal's midline)] contact anteriorly, a single concave occipital condoyle, occipital exposure of the opisthotic bone, and, usually, absence of retroarticular process on the lower jaw. Peculiar for anthracosaurs also is the clear demarcation boundary and loose joint between the skull roof and cheek, a condition inherited from rhipidistian fishes.”

Other features sported by anthracosaurs as noted by these authors were a lack of contact between the exoccipital and the skull roof, notably long tabular horns, comparatively narrow vomers, the presence of five digits on the forelimbs (as opposed to four in temnospondyls), and a gastrocentrous (reptile-like) spinal condition in many genera.



Complete specimen (THUg 3308) attributed to *Chroniosaurus dongusensis* by Clack and Klembara (2009), but apparently dissimilar in appearance (judging by the figures) and if so, worthy of its own generic name. ~25 cm in preserved length. - David Peters - Reptile evolution

Chroniosuchus was, not unexpectedly, a member of the Chroniosuchia suborder, which is divided into two families: the Chroniosuchidae and the Bystrowianidae. According to Novikov et al., “They are readily distinguished from older groups by a row of dermal plates over the vertebral column, conspicuously ball-shaped [intercentrum] in most forms, fenestration (presence of holes) of the skull roof (at least in the Chroniosuchidae) and some advanced characters in the skull roof pattern.”

Unlike many earlier and contemporary amphibians, Chroniosuchids lacked a well-developed lateral line system, which indicates that these creatures likely inhabited a largely terrestrial or semiaquatic niche. The teeth of these animals were rather conical and pointed and typically displayed a slight infold at their bases. Chroniosuchids traditionally displayed additional “tusk-like teeth on their vomers, pairs or groups of small tusks on palatines and ectopterygoids.” (Novikov et al.)

However, one of the group’s most striking features was a row of sculptured osteoderm plates which ran down their backs each of which was connected (by a ligament-like structure) to its underlying vertebra via the neural arch. Adding to the intricacies accompanying the spinal cords of these beasts was the fact that their pleurocentra were amphiocoelous (concave on the anterior and posterior ends) and were, in many forms, stutured to the neural arches, and often indistinguishably so.

Biostratigraphy

Period	Regional Stage	Zone	Subzone	Chroniosuchians	Assemblage	Age
Triassic		*Mastodonsaurus*		*Synesuchus muravjevi*		Ladinian
		Eryosuchus				Anisian
		Parotosuchus		*Axitectum georgi*		Olenekian
	Vetlugian	*Benthosuchus-Wetlugasaurus*	*Wetlugasaurus*			
			Benthosuchus	*Dromotectum spinosum*,		
			Tupilakosaurus	*Axitectum vjushkovi*		Induan
Permian	Vyatkian	*Archosaurus rossicus*		*Uralerpeton tverdochlebovae*, *Bystrowiana permira*	Vyazniki	Changhsingian
		Scutosaurus karpinskii	*Chroniosuchus paradoxus*	*C. paradoxus*, *C. licharevi*	Sokolki - Sokolki subassemblage	Wuchiapingian
			Jarilinus mirabilis	*J. mirabilis*		
	Severodvinian	*Proelginia permiana*	*Chroniosaurus levis*	*C. levis*	Sokolki - Ilyinskoye subassemblage	
			Chroniosaurus dongusensis	*C. dongusensis*		
		Deltavjatia vjatkensis		*Suchonica vladimiri*	Kotel'nich	

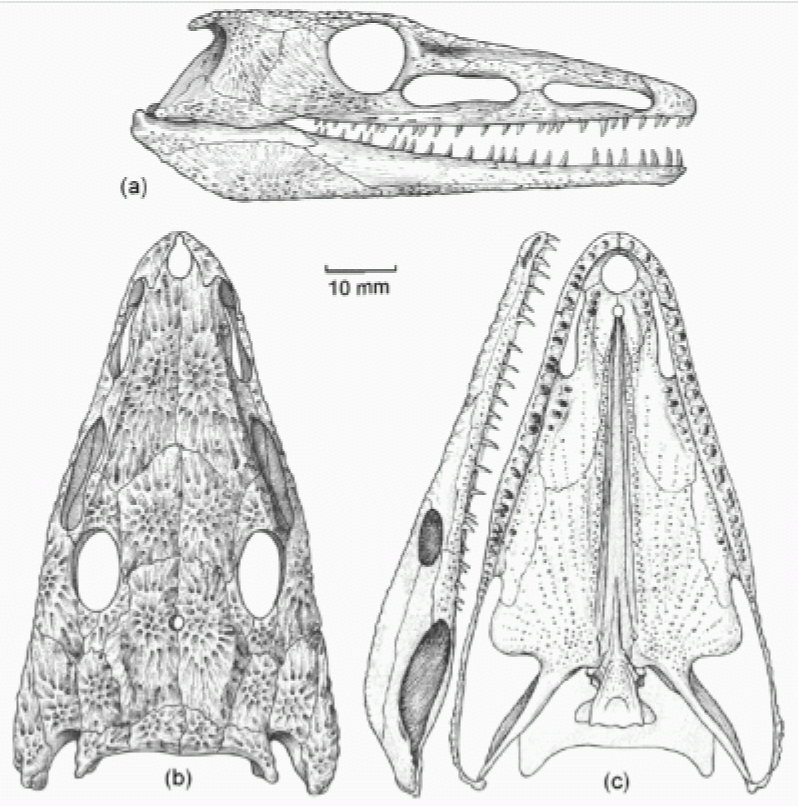
The rapid rate of chroniosuchian evolution, wide distribution and the distinctive characteristics of their armour of their remains makes them useful Eurasian index fossils. The table at the right, shows Russian late Permian biostraigraphy, consisting of four biostratigraphic zones. Three of these are represented by successive parierasaurs. Of these the middle two are subdivided according to chroniosuchid fauna, with the *Proelginia permiana* zone including the *Chroniosaurus dongusensis* and *Chroniosaurus levis* subzones, and the *Scutosaurus karpinskii* zone containing the *Jarilinus mirabilis* and *Chroniosuchus paradoxus* subzones.

During the Triassic, evolution seems to have been a lot slower, with only a few rare Bystrowianids continuing through to the end of the Middle Triassic.

References: Golubev 1998b, Golubev 1999, Shishkin et al 2000

MAK090731

Descriptions



Chroniosaurus dongusensis (Tverdokhlebova, 1972) from the Malokinelskaya Svita (Severodvinian Gorizont, upper Tatarian, Late Permian - Early Wuchiapingian age), Orenburg Region, South Cis-Urals, in lateral (a), dorsal (b), and ventral (c) views, with medial view of the lower jaw (c). From Tverdokhlebov *et al.* 2005 p.49

K. Golubev (*see illustration at right*) has developed a terminology for describing all the aspects of the scutes and the articulations and locks between them; those interested in such minutae are free to consult the accompanying diagram, or even better the original paper which is on line and available in English in pdf format. The articulations with the neighboring scutes are located on the ventral (under) side of the body of the scute, and is different for each of the two familuies (chroniosuchids and bystrowianiids). The dorsal (back) surface is strongly sculptured, while the ventral surface of wings is smooth and contains many small openings, which give rise to grooves and impressions of blood vessels. Golubev 1998a

Size: Skulls of Chroniosuchidae shown in Tverdokhlebov *et al*. (2005) are about seven to ten centimetres long, which would be only a medium-sized

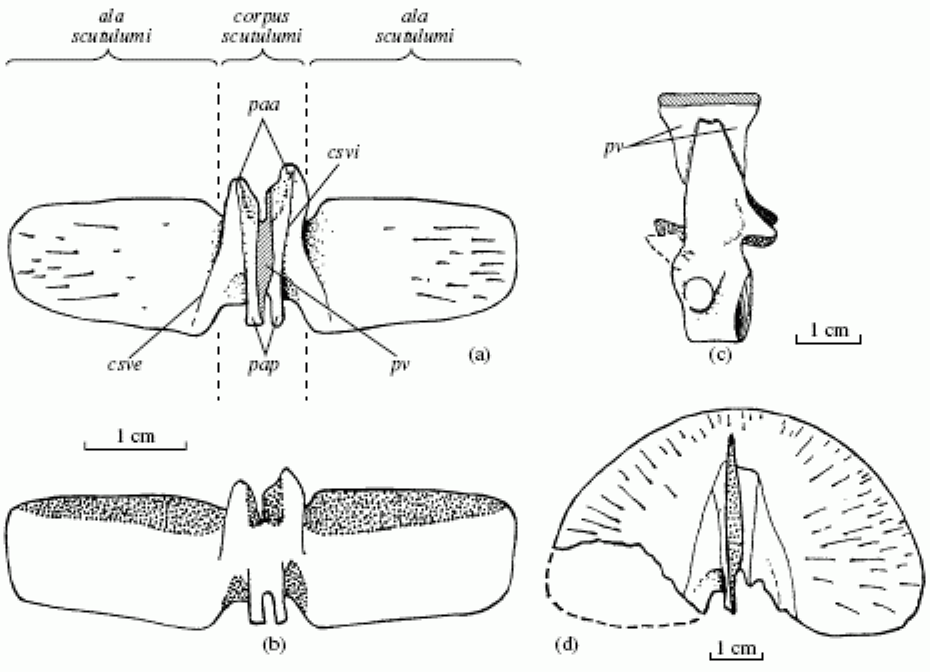
***Chroniosuchia*:**

Range: Tatarian (Capitanian - Middle Permian) to Late Ladinian (middle Triassic); of Eastern Europe, China (Li, 2001), and Germany.

Phylogeny: Anthracosauroidea ::: * : Chroniosuchidae + Bystrowianidae. (In a recent cladistic analysis. chroniosuchids either appear as basal embolomeres, just above *Silvanerpeton*, with specific resemblances to embolomeres in the braincase region, or further crownward, above embolomeres but below seymouriamorphs and other stem amniotes, but here there are no unambiguous synapomorphies. Clack & Klembara 2008)

Characters: Elongated skull, but trunk short with no more than 25 praecaudal vertebrae. Dorsal armor consisting of rows of articulated scutes arranged along the midline of the back, the number of scute numbers matching the vertebrae. Scutes connected to neural spines. Lateral line canals absent. (Golubev 1998a p.283)

Armor: The dorsal osteoderms or armored scutes are roughly rectangular ins hape, except for the anterior (front) one, which is semicircular. One is reminded of Chiton (polyplacophora) molluscs. V.



Details of *Chroniosaurus* armor. (a) *C. dongusensis* trunk scute, ventral view; (b) trunk scute showing overlap areas; (c) *C. boreus* trunk vertebra in left lateral view, (d) the first cervical scute of C. dongusensis ventral view. The heavy main body is the *corpus scutulumi* while the two lateral plates or wings are the *alae scutulumi*. Golubev 1998a describes the articulation and locks of the various scutes, whicha re indicated by the following abbreviations *csve*: crista scutulumi ventralis externa, *csvi*: crista scutulumi ventralis interna, *paa* processus articularis anterior, *pap*: processus articularis posterior, *pv* processus ventralis. From Golubev 1998a

amphibian. However the largest specimens had skull lengths attaining 50 to 55 cm (Golubev 1998a p.283). This would imply an overall length of more than 3 meters, making these animals the dominant semi-aquatic preditors, perhaps replacing the earlier *Melosaurus* (link) temnospondyls (Archegosauroidea), which they would have equalled in size.

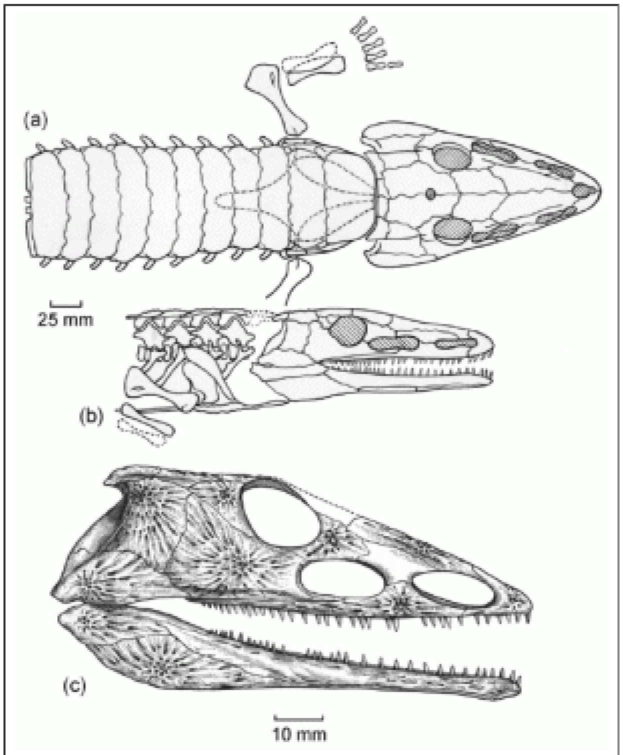
Diet: Piscivores (Tverdokhlebov *et al*., 2005).

Lifestyle: probably semi-terrestrial, although skull specializations that suggest a very different feeding mechanism from that of crocodiles. The interlocking scutes resemble those of some crocodilians and probably allowed a limited amount of flexing of the trunk region. (Clack & Klembara 2008)

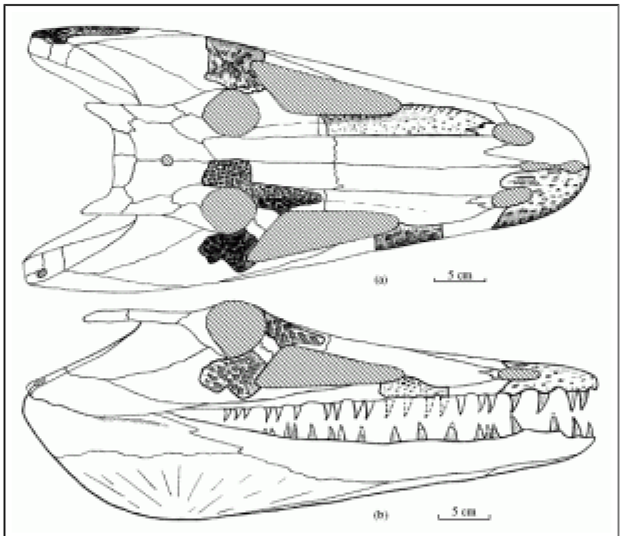
Comments: Chroniosuchia are a group of "anthracosaur"-grade tetrapods best known from the upper Permian, though the family Bystrowianidae survived until the middle Triassic (Novikov & Shishkin, 2000). They seem to have had a superficially crocodile-like appearance with an armor of scutes, and some forms grew to quite respectable size (skull length upto 55 cm). These creatures were most common during the Late Permian, where they have stratigraphic value as index fossils, but survived well into the Triassic.

CKT070522 (Palaeos org - Chroniosuchia), MAK090806

References: Golubev 1998a, Novikov et al. 2000, Tverdokhlebov *et al.* 2005



Chroniosuchus paradoxus V'yushkov, 1957 from the Kulchomovskaya and Kutulukskaya svitas (Vyatkian Gorizont, upper Tatarian, Late Permian - Late Wuchiapingian age). Restorations, based on the holotype (Orenburg Region, South Cis-Urals) and skull remains, showing the anterior part of the animal, and armor plates, in (a) dorsal and (b) lateral views, and (c) lateral view of the skull. From Tverdokhlebov *et al.* 2005 p.50



Uralerpeton tverdochlebovae Golubev , 1998 Upper Tatarian Substage, Vyatkian Regional Stage (Changhsingian Age): (a) and (b) the skull dorsally and laterally, reconstructed from several specimens. This was a large animal (skull lebngth 50-55 cm, one of the last of the Chroniosuchidae. From Golubev 1998a p.282

Chroniosuchidae: *Chroniosuchus Chroniosaurus*, *Uralerpeton*, *Jarilinus*, *Suchonica*

Range: Middle (Capitanian) to Late (Changhsingian) Permian of Eastern Europe and China

Phylogeny: Chroniosuchia **:** + Bystrowianidae + *

Characters: Large, skull length upto 50 to 55 cm. Orbits face dorsolaterally. One pair of pre-oorbital fenestrae between jugal, praefrontal, lacrymal and maxillary. Squamosal contacts postorbital. Armor wide, scute wings overlap each other posteroanteriorly. Intercentra vary from ring-shaped in young individuals to spherical in adults; the neural arch fusing with the centrum during ontogeny; see The Life of

Madygen blog post.

Armor: As represented in *Chroniosuchus*, *Jugosuchus*, and *Chroniosaurus*, the scutes have very wide wings and cover practically the whole upper part of the trunk. The tail scutes are narrower, the last of which lack wings. A long smooth strip extends about a third of the whole wing length along the posterior dorsal edge and represents the overlap area for the next wing of the scute. This is shown in figure (b). The wings of the neighboring scutes overlap each other posteroanteriorly (the reverse to the bystrowianiid condition). The descending ventral process (processus ventralis - *pv* in the same figure) forms the middle part of the lock.

Reference: Golubev 1998a

Links German Wikipedia

MAK090806

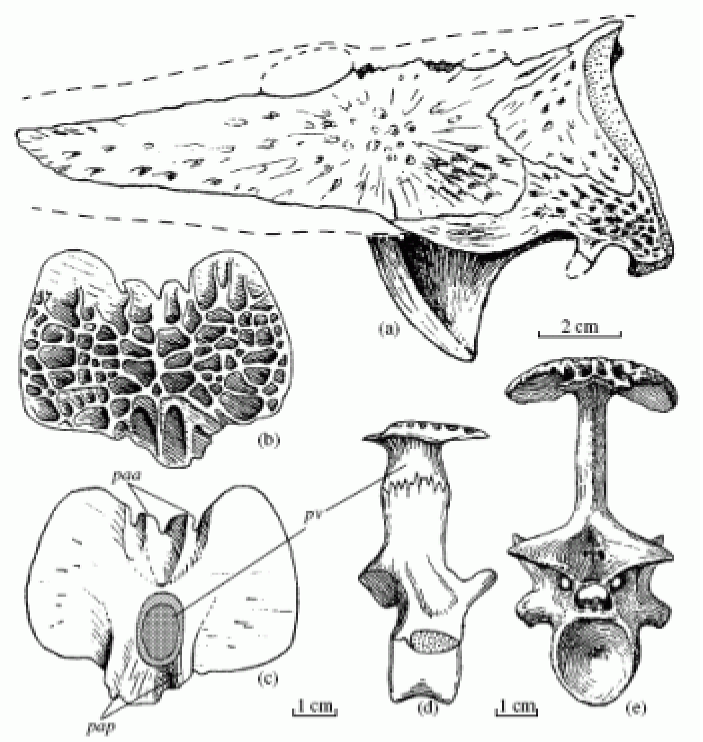
Bystrowianidae: *Bystrowiana*, *Axitectum*, *Bystrowiella*, *Dromotectum*, and *Synesuchus*.

Range: Latest Permian (Changhsingian) to Middle Triassic (Late Ladinian) of Eastern Europe and Germany.

Phylogeny: Chroniosuchia **:** + Chroniosuchidae + *

Characters: Medium sized, skull length not more than 20 cm. Orbits face dorsally. Narrow postorbital fenestra situated between skull roof and cheek. Jugal forms larger part of cheek dorsal margin. Neural arch has numerous deep pits dorsally, which sometimes turn into canals directed anteroposteriorly. Intercentra are ring-shaped or disk-shaped. Armor narrow, overlaps anteroposteriorly.

Armor: This is shown in drawings (b) and (c) (*right*) The osteoderms are narrow and so unlikely to be of protective value. Scute wings, if present, overlap each other anteroposteriorly (the reverse to the chroniosuchid condition), so the smooth overlap area is on the anterior edge of the dorsal surface of each scute wing. In *Bystrowiana* and *Axitectum*, the ventral processes of the neighboring scutes do not meet. Instead there are two massive posterior articulation processes. These usually fuse, forming a single articulation plate.



Bystrowiana permira Vjuschkov; Upper Tatarian Substage, Vyatkian Regional Stage (Changhsingian): (a) part of the skull lateral view (the anterior is to the left); (b) trunk scute dorsal view; (c) the same, ventral view; Note how short these are, in comparaison to the wide wing scutes of *Chroniosaurus*. (d) the trunk vertebra with fused scute from the right laterally; (e) a trunk vertebra with a fused scute posteriorly. From Golubev 1998a p.281

Comments: The only non-amniote reptilomorphs to survive the end Permian extinction event. Not very common; apart from *Bystrowiana*, these animals are known only by their distinctive osteoderms and a few vertebrae. Although for a long time known only from the Permotriassic of Russia, the recent discovery of osteoderms and vertebrae from the Late Ladinian (Keuper) of southern Germany show that these animals were more widespread than previously thought (Witzmann *et al* 2008). *Bystrowiana* is named after the the Russian paleontologist Alexei Petrovich Bystrow.

Reference: Golubev 1998a, Witzmann *et al* 2008

Links Russian Wikipedia

MAK090806

Gephyrostegidae

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

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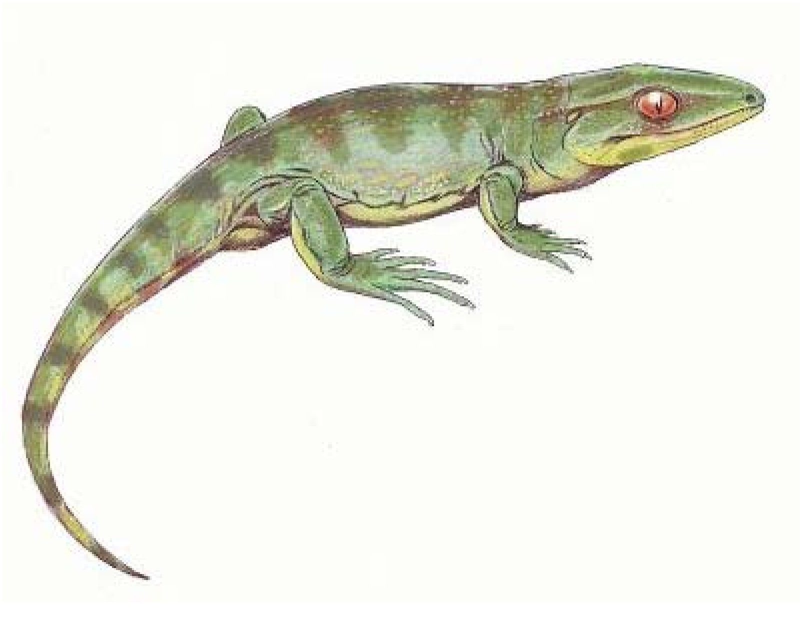
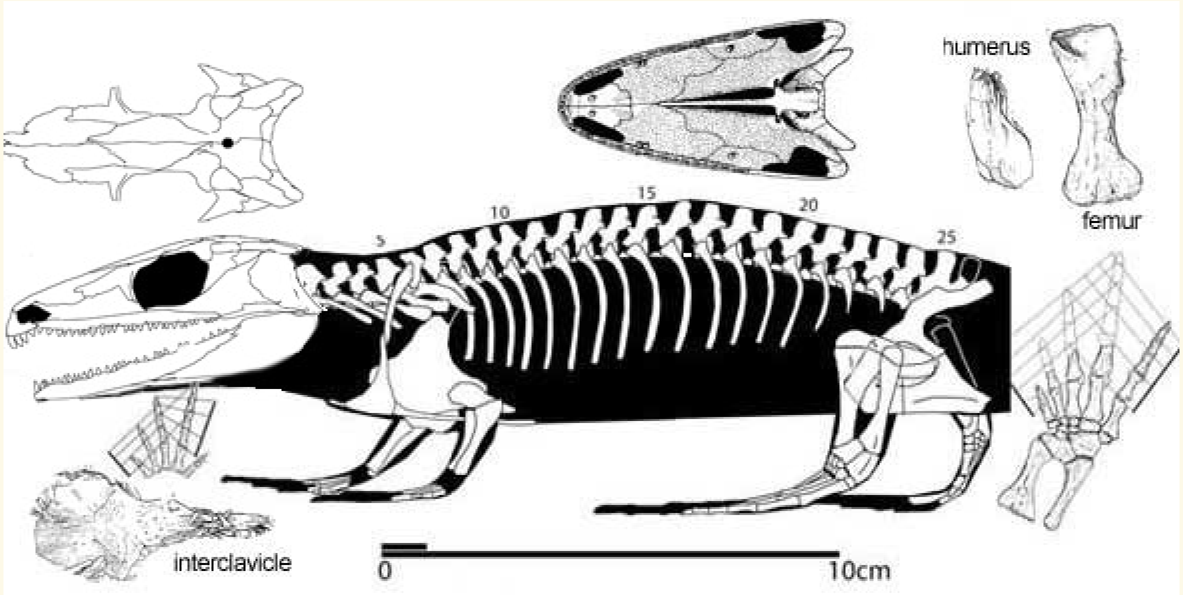


Gephyrostegus bohemicus Jaekel, 1902, a reptile-like amphibian. This animal was moving twoards, but not yet itself the ancestral reptile stage. Life reconstruction, by Dmitry Bogdanov, Wikipedia, GNU Free Documentation/Creative Commons Attribution

Gephyrostegus - almost a reptile

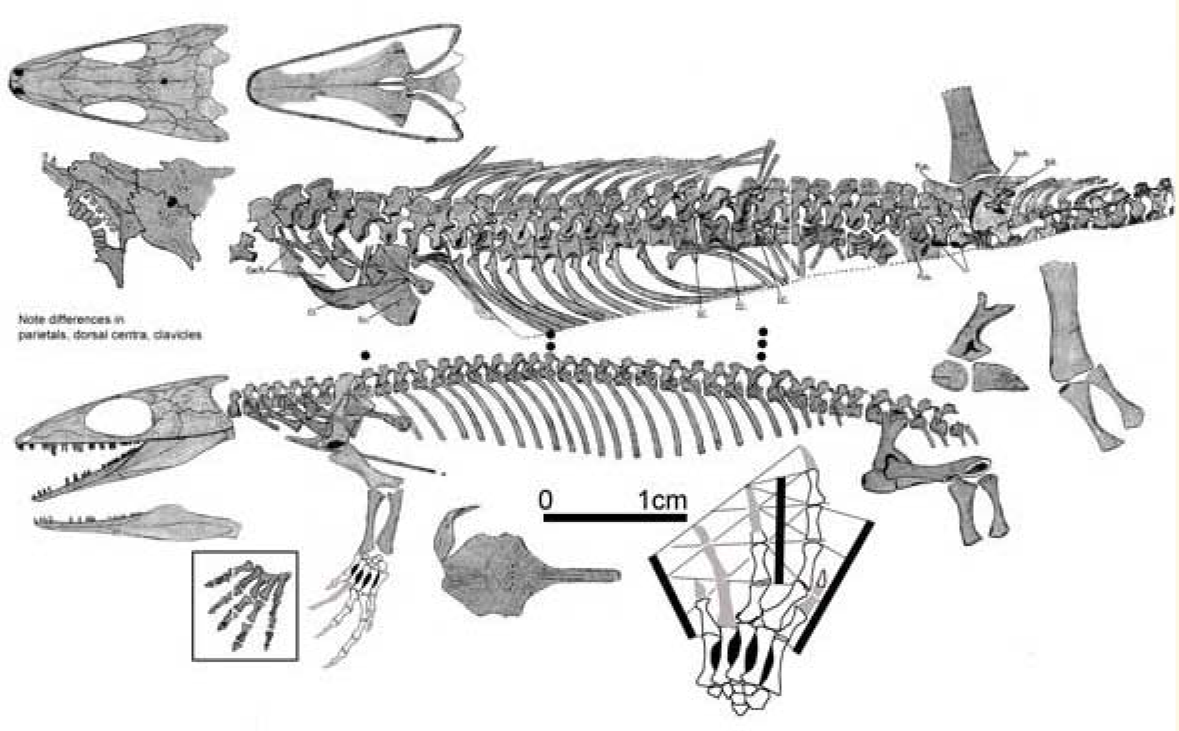


Gephyrostegus is a typical representative of the reptiliomorphs, transitional Permo-Carboniferous forms intermediate between amphibians and reptiles. It was a small animal of generally lizard-like build and presumably habit. It had large eyes and a large number of small, pointed teeth, indicating it was an active insectivorious hunter. The remains have been found in Nyrany, Czech Republic, dating from around 310 million years ago (Moscovian Age - Late Carboniferous) (Jaeckel 1902). It lived millions of years too late to be the actual grand-daddy of the reptiles (and mammals, and birds), but it gives an idea of what such an ancestor (or concestor as Richard Dawkins would say) may have been like. At just 22 cm snout-vent length, *Gephyrostegus* was one of the smallest (if not the smallest) advanced reptiliomorphans found. (Image, right. *Gephyrostegus bohemicus* Jaeckel 1902, by David Peters, Reptile evolution)

Gephyrostegus was originally included among the reptiles as a suborder of Cotylosauria (Colbert 1969). A number of traits unite this genus with the reptiles (Crown Amniota) (as distinct from physiological (or cladistic jargon apomorphic) amniotes:

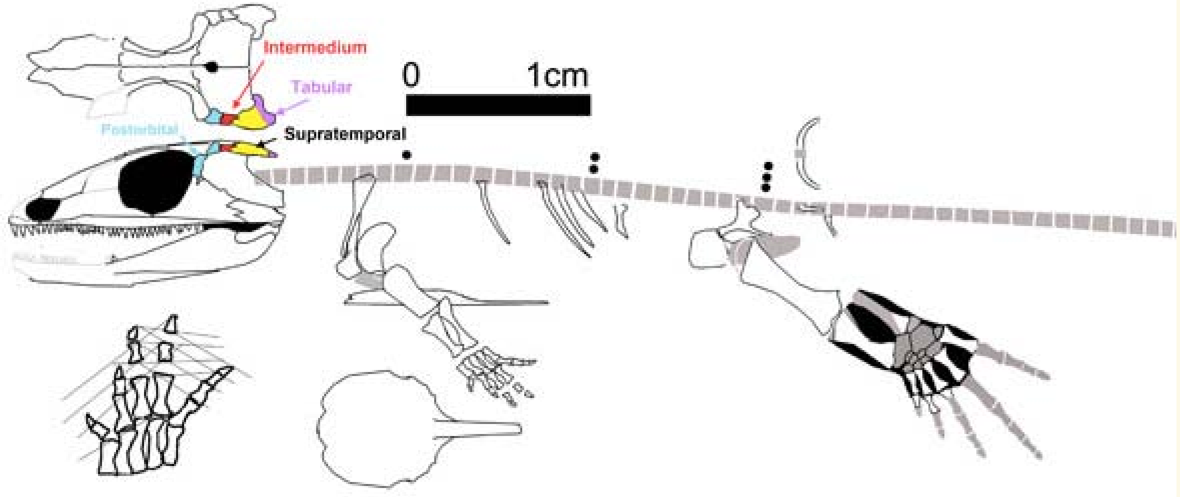
1. Skull width less than twice the height
2. Premaxilla less than a third of the rostral length
3. Prefrontal/postfrontal separated (= frontal contacts orbit)
4. Squamosal descending angle obtuse
5. Jugal shape posterior to maxilla is triangular to expanded
6. Humeral torsion greater than 30º
7. Metacarpals I-III align
8. Astragalus present
9. Distal pedal phalanx 1.1 aligns with distal metatarsals II and III

Later it was transferred to the Anthracosauria Carroll 1988; more recently again cladistic analysis has placed it either as sister taxon to (Laurin & Reisz 1999) or above (Clack 2002b , Ruta et al 2003a, Ruta et al 2003b) the embolomeres, but below the seymouriamorphs,



lepospondyls, and amniotes. Although it would seem then that the reptile-like traits shared with higher reptiliomorphs and early amniotes evolved through convergence, this may not be the case.

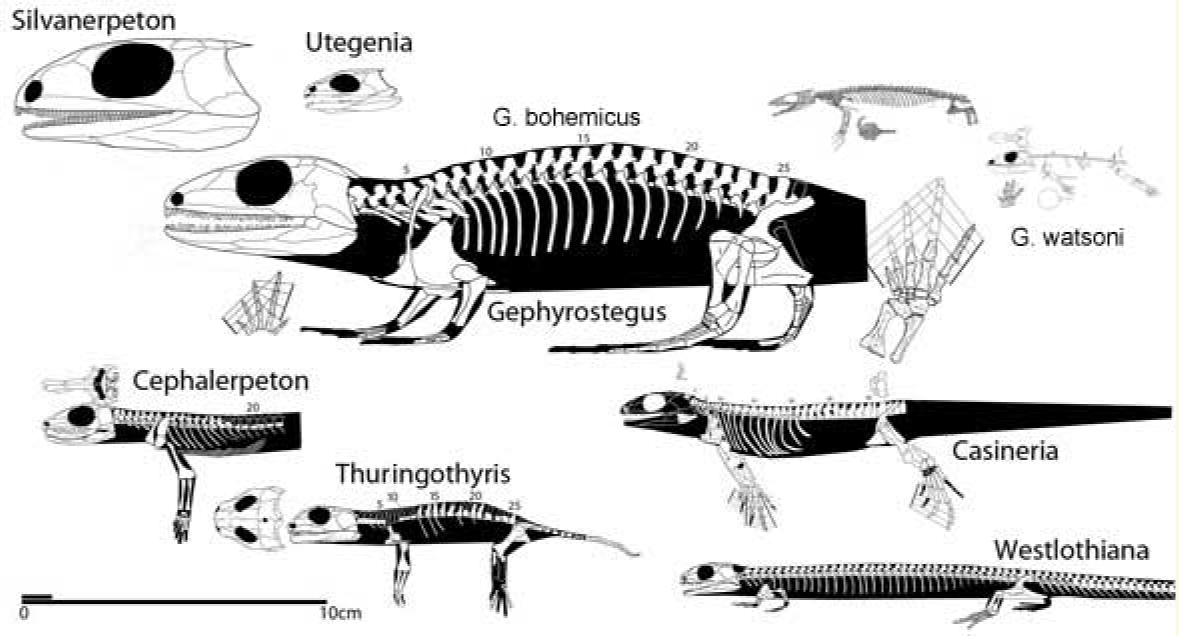
An interesting discovery however were two tiny gephryostegii. *Gephyrostegus watsoni* (Brough & Brough 1967) (*left*) was, erected for two smaller, possibly juvenile individuals, was originally named *Diplovertebron punctatum* (Watson 1926) but was reassigned to *Gephyrostegus* despite the size difference, which may be due to immaturity or not. If indeed this specimen is immature, it does not appear to be a tadpole, but has the appearance of an adult, as in reptiles. If it is an adult, its size would support the hypothesis of Carroll (1970, 1991), that the first amniote (= reptile) would be tiny. Both specimens retain an intertemporal, which no reptile retains. This may simply be an instance of mosaic evolution. Or it may simply be the case that the tadpoles attained an adult form whilst still very small, and then grew normally.



The two tiny *Gephyrostegus* specimens have distinct proportions and element shapes sugggestive of a generic distinction hinting taht even at this very early stage of amniote/reptile evolution a wide grade of organization had developed. The upper one is shown with about 36 presacral vertebrae. The lower one probably had fewer than 30. The large Gephyrostegus (above) had but 24.

One reason it is unlikely that *Gephyrostegus* was a reptile that laid eggs that hatched into minature adults is that the adult *Gephyrostegus* is still too large to qualify as a proto-amniote, as the size comparison below shows. More importantly it is more primitive in every respect than the seymouriamorphs, which are known to have a tadpole stage.

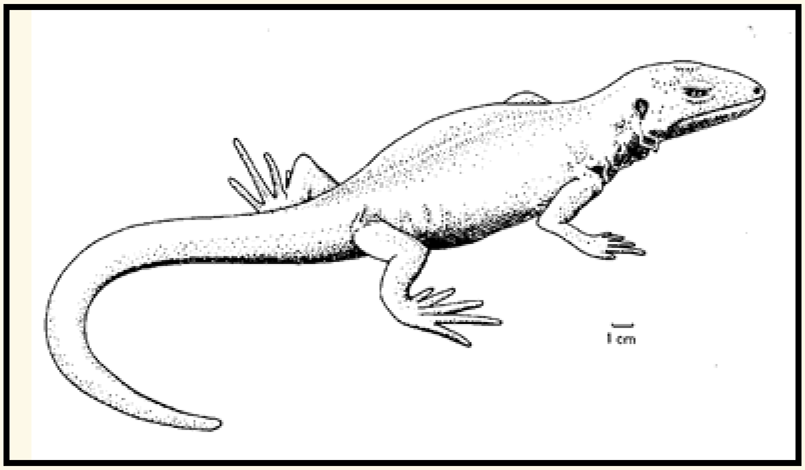
The diagram on the left provides a size comparison of various Stem and crown amniotes. All show a



degree of minaturisation which supports Carroll's hypothesis that the first transitional or proto-, amniotes had to be very small, to avoid problems of carbon dioxide build up that would have occurred prior to the development of a complete amniotic membranes. *Casineria* and *Westlothiana*, both more derived (advanced, reptile-like) forms than *Gephyrostegus*, had snout-vent lengths of 10 cm or less, within the size range predicted by Carroll. The same applies to *Cephalerpeton* and *Thuringothyris*, traditionally basal eureptiles (Crown Amniotes), although given the phylogenetic uncertainty around some of these early forms it is not possible they had a more basal position, although the small size might simply be a later adaptation, like some extant tiny skinks and geckos for example. Interestingly, little *Gephyrostegus* and its similar but more primitive cousin *Silvanerpeton* (an anthracosaur) are giants in comparison, and the baby Gephyrostegii are not much smaller than the adult amniotes and proto-amniotes. So although *Gephyrostegus* was certainly, like the seymouriamorphs, moving towards the reptilian condition, it had not yet itself beco0me a reptile. MAK111109

(Text David Peters 2011 Reptile evolution, Petter Bøckman 110622 Wikipedia, MAK111108. Images David Peters)

Descriptions



Gephyrostegidae: *Bruktererpeton*, *Gephyrostegus*.

Range: Late Carboniferous (Bashkirian to late Moscovian).

Phylogeny: Reptiliomorpha **:** Anthracosauroidea + (Batrachosauria + *)

Characters: Smallish; skull and cheek strongly attached; dermal bones marked by pits and grooves; deep otic notch in quadrate (*flatly contradicted* by [C02] who states that notch is barely present); stapes reduced to narrow rod; 24 vertebrae; pleurocentra large; intercentra small & crescent-shaped; pleurocentrum not fused to neural arches; long limbs; perhaps fully terrestrial. ATW020621 Unlike basal reptiles, the notochord was continuous in Gephyrostegus. An intertemporal bone was present in the skull and a few small palate fangs remained. (David Peters)

Image: *Gephyrostegus* life reconstruction, iirc from an early edition of *Vertebrate Life* by F. Harvey Pough MAK111107

Links: Anthracosauria; Biology 356

References: Clack (2002) [C02] ATW020621.

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checked ATW040109, revised and new page MAK111108

Reptiliomorpha: Seymouriamorpha

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   |
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
              |--Seymouriamorpha
              |  |--Discosauriscus
              |  `--Kotlassiidae
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

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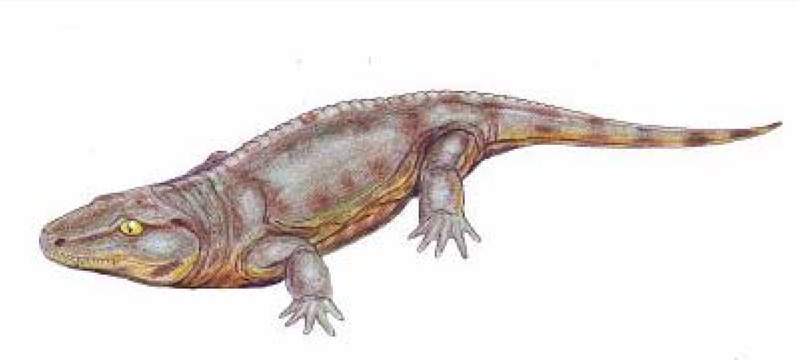


Seymouria baylorensis Broili, 1904, (Seymouriamorpha - Seymouriidae), life reconstruction, by Dmitry Bogdanov (Larger image (*Wikipemia*))

Descriptions

Batrachosauria: *Seymouria* + Jane Seymour

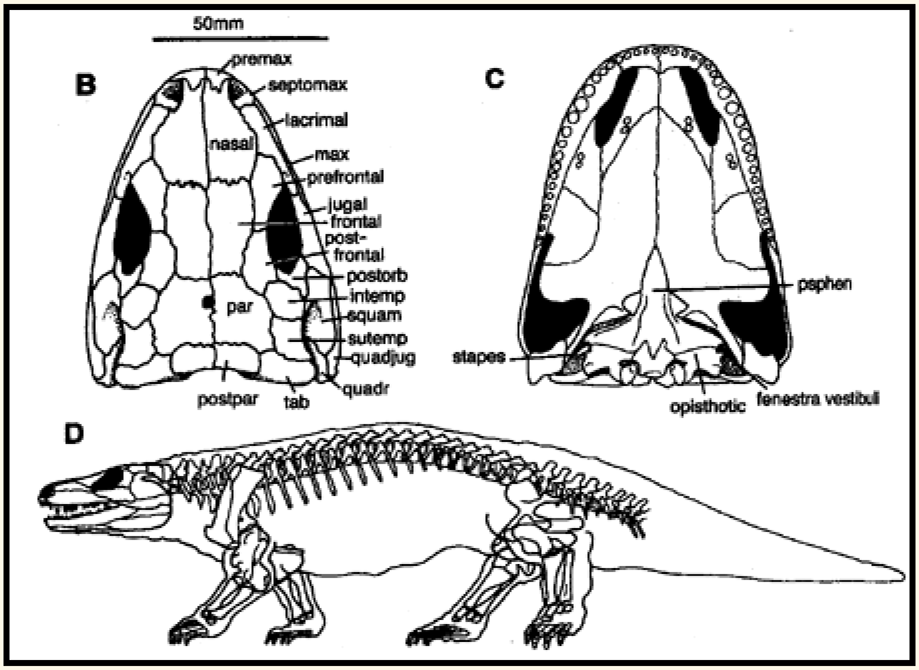
Range: from the Carboniferous

Phylogeny: Reptiliomorpha **:** Anthracosauroidea + (Gephyrostegidae + * **:** Seymouriamorpha + (*Solenodonsaurus* + Cotylosauria)

Characters: Intercentrum reduced, large canine-like maxillary tooth.

Comments: Batrachosauria ("Frog Saurians") is a name given either to very reptile-like amphibians dating from the Carboniferous and Permian periods, or to amniotes and those amphibians very closely related to them. In current cladistic schemes, Batrachosauria is the sister clade to the Anthracosauroidea MAK050702

Links: A Batrachosauroid from the late Cretaceous of France; Untitled Document; Abstracts for PaleoBios 16(4). ATW021125.



Seymouriamorpha: *Ariekanerpeton*, *Seymouria*.

Range: Early Permian to Late Permian of Europe, Russia, Central Asia & North America.

Phylogeny: Batrachosauria **:** (Solenodonsaurus + Cotylosauria) + * **:** *Discosauriscus* + Kotlassiidae.

Characters: long ventrally bent process of tabular?; posttemporal fenestrae small; slender stapes; otic tube composed of opisthotic, prootic, & parasphenoid; palate closed, without interpterygoid vacuities; pterygoid with large, transverse dorsal flange extending to skull roof (= epipterygoid?); trunk short (24-28 presacral vertebrae); vertebrae composed of large, cylindrical pleurocentrum & small, crescentic intercentrum; atlantal vertebra with paired pleurocentra & arches; neural arches "swollen" (strongly convex dorsally, in anterior or posterior view); 1, sometimes 2 sacrals; caudal hemal arches; ribs present from 1st cervical to proximal caudals; pectoral region ribs expanded; limbs stout; pectoral girdle with interclavicle, clavicles and cleithra; robust humerus & femur; phalangeal formula in manus 23443 or 23453, in pes 23453; dermal cranial bones of adults deeply sculptured, with hexagonal pattern of ridges also found in many temnospondyls (suggests skin tightly attached to skull); larvae with external gills known; lateral line present in juvenile specimens, possibly also ampullary electroreceptors.

Image: *Seymouria* adapted from Clack (2002)

Note: Juveniles were aquatic, adults terrestrial.

Links: Seymouriamorpha; Seymouria; First record of *Seymouria* from Early Permian fissure fills at Richards Spur, Oklahoma; Untitled Document; The Journal of Vertebrate Paleontology; The Journal of Vertebrate Paleontology; Seymouriamorpha; Utegenia shpinari; Abstracts for PaleoBios 17(1-4); Amniote origins?; Redescription of Seymouria sanjuanensis (Seymouriamorpha) from ... (abstract); NRC Research Press- Canadian Journal of Earth

Sciences.

References: Clack (2002). ATW031014

Discosauriscus:

Range: Late Permian of Europe & China.

Phylogeny: Seymouriamorpha **:** Kotlassiidae + *.

Characters: skull less ossified than in *Seymouria*; snout shortened, kinetic line absent; rectangular tabular process (= tabular horn?); jugal exposed on ventral margin of skull; suborbital fenestra present; postorbital may contact supratemporal; "Many specimens have subdivided or fused skull roof bones"; quadrate and articular unossified; narrow interpterygoid vacuities in some; transverse flange of pterygoid may project ventrally below margin of skull; small Meckelian fenestrae present on medial face of jaw; 3 coronoids, all with teeth; dentary with up to 43 teeth; labyrinthodont dentition in more mature forms; 1-4 palatal tusks per vomer & 1-5 on palatines; 24 presacral vertebrae; 1 sacral with massive rib; gastralia absent; pectoral girdle with interclavicle bearing long parasternal process; paired clavicles with broad lateral plates; cleithra slender & cylindrical; scapula with stout supraglenoid buttress & large supraglenoid foramen; coracoid with distinct coracoid foramen; phalangeal formula is 2-3-4-5-3 for manus and pes; lateral line well preserved; ampullary electroreceptive organs present; integument of rounded scales with concentric rings.

Image: from Chordata (former site: http://home.t-online.de/home/0403906146-0002/fosswt.htm).

Note: Similar to *Seymouria*, perhaps less terrestrial. It has been repeatedly suggested that *Discosauriscus* is simply a larval form of *Seymouria*. This appears not to be correct, but it is true that many reported "discosauriscids" *are* juvenile forms.

Links: Discosauriscus; Discosauriscus sp.; Synonyms of Discosauriscus austriacus; ?????????? ?????? (Japanese); Paleontology and Geology Glossary: Di; The Journal of Vertebrate Paleontology; Mauro J. Cavalcanti Personal Page - Abstracts; http://www.fossils.ch/img/W(ReAmph)-1.jpg; PERMIANO; Muzeum vychodnich Cech v Hradci Kralove (Czech); Snapshots from the 2002 Show: Ammonoidea 2002 I. ATW020623.

Kotlassiidae: *Buzulukia*, *Bystrowiana*, *Dromotectum*, *Karpinskiosaurus*, *Kotlassia*

Range: Late Permian of Russia.

Phylogeny: Seymouriamorpha **:** *Discosauriscus* + *.

Characters: aquatic seymouriamorph, larger than discosaurs; 1½ sacrals(!), as only one rib of anterior sacral contacts ilium; rhomboidal ventral bony scales.

Links: paleng1_2p72abs; 615921; Seymouriamorpha; Samples2.PDF; PaleoNET | Библиотека (associated fauna). ATW031025.

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Solenodonsaurus

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   |
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
             `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

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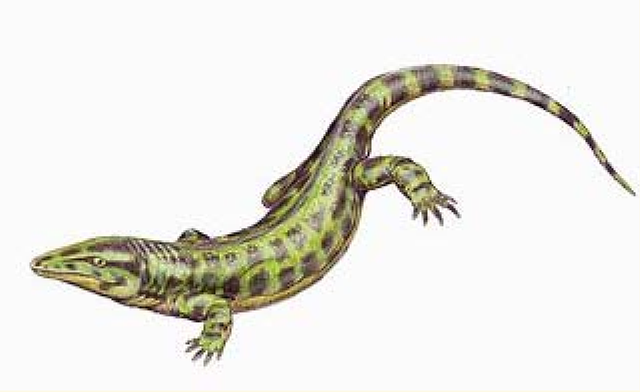
1. *Solenodonsaurus* X

Descriptions



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Solenodonsaurus: *S. janenschi* Broili 1924)

Range: Late Carboniferous (Westphalian D) of Europe.

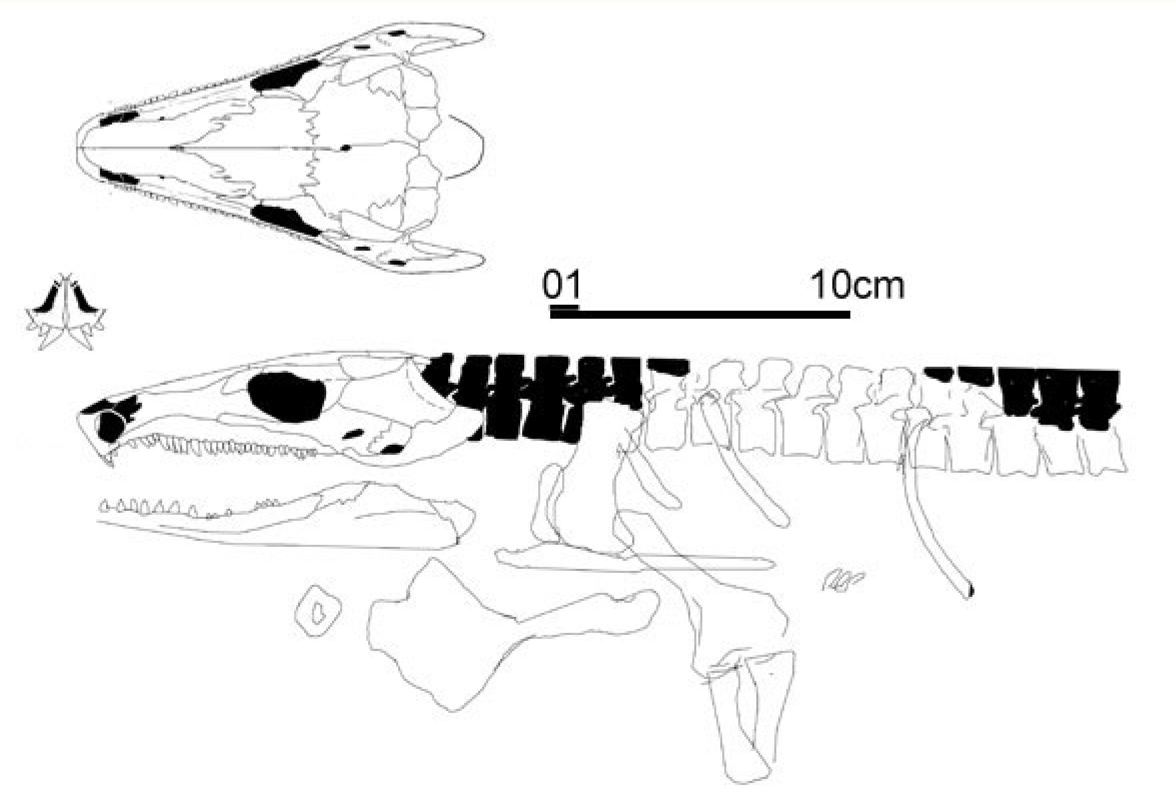
Phylogeny: Stem Amniota : *Casineria* + *Westlothiana* + (Cotylosauria + *)

Size Skull c.13 cm, snout-vent length about 45 cm

Note: The following three fields are copyright Michel Laurin 02 May 2001 (here signed ML010502) adapted from the Tree of Life

Characters: . Shallow temporal emargination (otic notch); humerus fairly robust, with strongly expanded proximal and distal heads. There appears to have been a single sacral rib. Its neural arches were not swollen, unlike those of seymouriamorphs and diadectomorphs. As in many other early stegocephalians, its skin was reinforced by long ventral and circular dorsal, bony scales.. Unfortunately, our knowledge of the skeletal anatomy of this taxon is poor because only a few incomplete skeletons are known. The preserved skulls are also poor. Therefore, the path of some of the sutures on the skull is uncertain. ML010502

Comments: Probably carnivorous or insectivorous, as shown by its sharp, slightly curved teeth. The temporal emargination is shallower than in most other early stegocephalians, and its shape is unsuitable to have supported a tympanum. Thus, *Solenodonsaurus* could probably not hear high-frequency air-borne sounds very well, if at all. ML010502



Relationships to other tetrapods: Solenodonsaurus was erected and described by Broili (1924), who considered that it was a "cotylosaur" (a group that included some early amniotes and their presumed closest known relatives). Its teeth lack the labyrinthine infolding primitively found in stegocephalians, and this is one of the characters (the other being the morphology of the vertebral centrum) that led Broili (1924) to suggest that this animal was an amniote (a "reptile", in his terminology). Its interclavicle has a long posterior stem, and this has long been thought to unite it with other anthracosaurs, but this character has a broader distribution (Laurin & Reisz, 1997). The vertebral centrum of *Solenodonsaurus* resembles that of seymouriamorphs, diadectomorphs, early amniotes and some early amphibians. It consists of a large, cylindrical pleurocentrum and a small, crescentic intercentrum. Other characters that were taken as evidence of amniote affinities of *Solenodonsaurus* are the absence of an intertemporal and the presence of a supraoccipital and of a contact between the tabular and the parietal. However, most of these characters have a broader distribution (Laurin & Reisz, 1997). Subsequent studies confirmed that *Solenodonsaurus* was either an early amniote or a close relative of amniotes (Pearson, 1924; Brough & Brough, 1967; Carroll, 1970). The advent of cladistics clarified somewhat the position *Solenodonsaurus*; this taxon was considered to be definitely outside Amniota, but to be closely related to the clade that includes diadectomorphs and amniotes (Gauthier, Kluge & Rowe, 1988). In a recent analysis that included amphibians (Laurin & Reisz, 1999), *Solenodonsaurus* appears to be the sister-group of all other known anthracosaurs (amniotes and their extinct relatives). ML010502

Image: Life reconstruction by Dmitry Bogdanov - Wikipedia technical illustration by David Peters, Reptile evolution MAK111107

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Diadectomorpha (Cotylosauria)

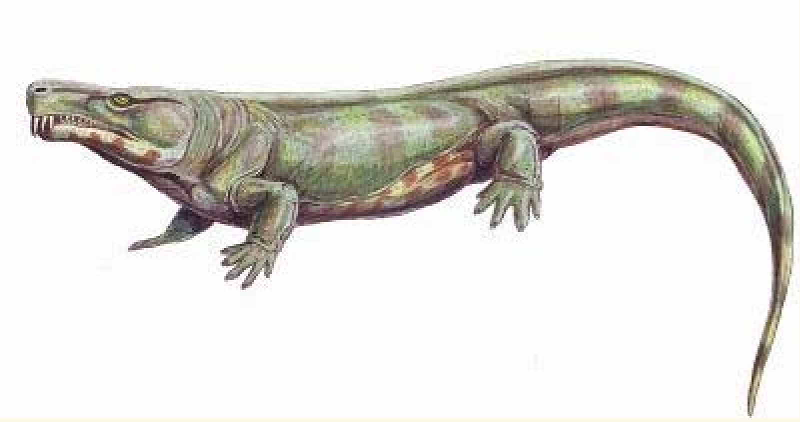
Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   |
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
             `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    |   |--Tseajaia
                    |   `--+--Limnoscelis
                    |      `--Diadectidae
                     `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

Contents

Taxa on This Page

1. Cotylosauria
2. *Tseajaia* X
3. *Limnoscelis* X
4. Diadectidae X
5. Diadectomorpha X



Limnoscelis paludis (Diadectomorpha - Limnosceliidae),

Early Pemian, Texas and New Mexico
an animal very close to the ancestry of amniotes. Length about 1.5 meters
life reconstruction, by Dmitry Bogdanov (Larger image (*Wikimedia*))

Included here are animals so reptile like they might as well be reptiles. In evolutionary systematics books they were considered reptiles, but cladistic analysis places them outside the Crown Group Amniotes, so they are now generally considered anamniotes (non-amniotes, as amphibian is a paraphyletic taxon and hence now depreciated). Although it is possible that they may still be apomorphic amniotes, as egg-laying animals may have evolved long before the evolutionary divergence into Sauropsids and Synapsids, other factors would seme to indicate an amphibian status, such as large size (whereas both proto-amniotes and many early crown amniotes were generally very small, allowing for a transitional stage of less efficient amniote eggs). On the other hand, as far no diadectomorph had lateral-line canal grooves (indicating fish-like aquatic pressure sensing), and no diadectomorph tadpole is known. In contrast seymouriomorphs, an important group of reptile-like amphibians (reptiliomorphs), had tadpole young, and hence were not amniotes. Moreover, diadectomorphs even tend to be placed higher (more amniote-ward, or even (in one supertree analysis) within the amniote crown (Ruta et al 2003b)) than forms like *Westlothiana* and *Casineria*, each considered the first reptile when first discovered, and posessing a number of classic amniote features. For now we have retained the diadectomorphs among the repyile-like amphibians (reptiliomorphs), although they may just as easily be an early group of stem group amniotes or, to use the old classification, primitive reptiles. MAK111108 120321

.

Descriptions

Cotylosauria:

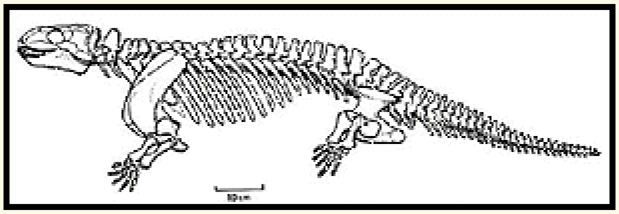
Range: from the Carboniferous.

Phylogeny: Batrachosauria **:** Seymouriamorpha + (*Solenodonsaurus* + * **:** Diadectomorpha + Stem Amniota)

Characters: $ more derived axis-atlas complex; $ sacrum with at least 2 vertebrae, $ robust clawson pes; $ loss of lateral line system.

Links: Phylogeny of Stegocephalians; AMPHIBIA et REPTILIA NGIANA (Chinese); V The four other mass extinctions. ATW020623.

Diadectomorpha: *Limnoscelis, Diadectes, Tseiajaia*.



Range: Late Carboniferous to Early Permian.

Phylogeny: Cotylosauria **:** Stem Amniota + * **:** *Tseajaia* + (*Limnoscelis* + Diadectidae) .

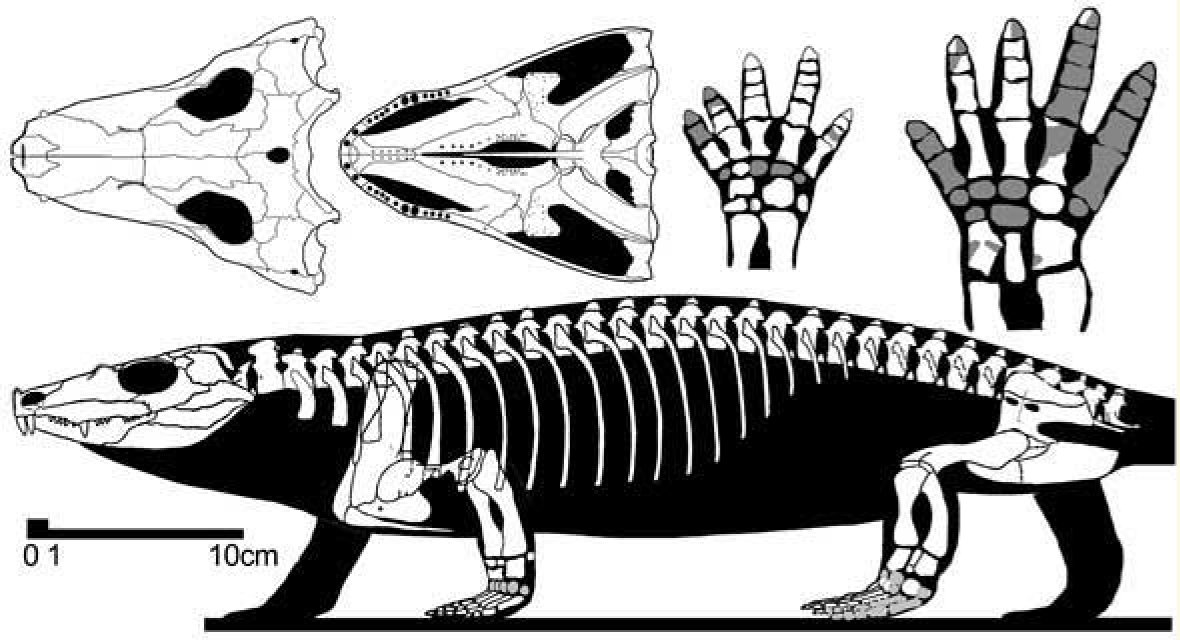
Characters: 1.5-3 m; some fully terrestrial; "swollen" neural arches; some (*Diadectes*) herbivorous.

Links: Diadectomorpha; Phylogeny of stegocephalians (note figures of *Limnoscelis*); Biology 356.

Image: *Diadectes*. ATW030122.

Tseajaia *campi* Vaughn
1964

Range: Early Permian.



Phylogeny: Diadectomorpha: (*Limnoscelis* + Diadectidae) + *. *or* *Limnoscelis* + (Diadectidae + *).

Comments: Traditionally considered the most primitive diadectomorphs, although a recent analysis (Kissel 2010) makes them the sister group to the diadectidae. Limnoscelid-like in appearance, but tending to an omnivorous or herbivorous diet. Only one species is known, a single late surviving form, essentially a "living fossil" co-existing with its more advanced and successful contemporaries. From Wikipedia: *Tseajaia* was described from a single, fairly complete specimen and was given its own family by Robert L. Carroll. It was originally thought to be an seymouriamorph (Moss 1972) Additional finds allowing for a better taxonomic analysis indicate they belong in the Diadectomorpha, as the sister group to the large and more derived Diadectidae. Tseajaia itself being a fairly generalized form, gives a reasonable indication of the build and looks of the closest relatives of the amniotes (Berman et al 1992, Kissel 2010)

Image: David Peters, Reptile evolution MAK111107

Limnoscelidae:

Range: Late Carboniferous to Early Permian.

Phylogeny: Diadectomorpha **:** *Tseajaia* + * **:::** Diadectidae.

Comments: Primitive, small to large, carnivorous diadectomorphs. These animals must have lived a very similar life to ophaicodontid, varanopsid, and sphenacodontid pelycosaurs,which they resembled in overall size and shape; presumably relied on niche partitioning. Teeth retained labyrinthodont infolding of the enamel, and were pointed and slightly recurved at the tip (Carroll 1967, via Wikipedia) Traditionally divided into two genera, *Limnoscelis* and *Limnostygis*, although these may be synonyms

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Diadectidae: *Desmatodon, Diadectes,* , etc

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

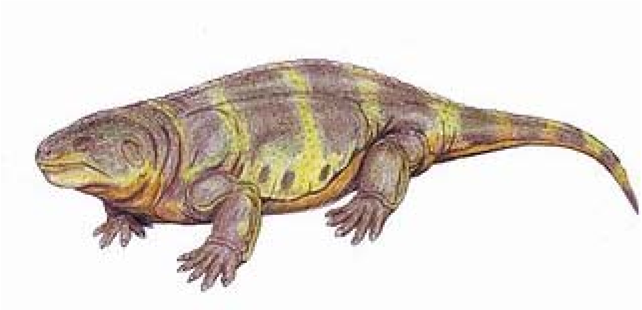
Phylogeny: Diadectomorpha **:::** *.

Comments: Highly successful clade of large herbivores, include the largest animals of their time and teh first exploitation of vegetable matter by tetrapods. Previously tentrapods (amphibians and reptiles() had been carnivores only, feeding on insects, crustacea and other invertebrates, fish, and smaller tetrapods. This means that eco\ystems were inefficent (becaise of long food chains, and tied to water or water margins. While edphosaurs were also herbivores, they never challenged the supremacy of the diadectids. Diadectid extinction at the end of the early

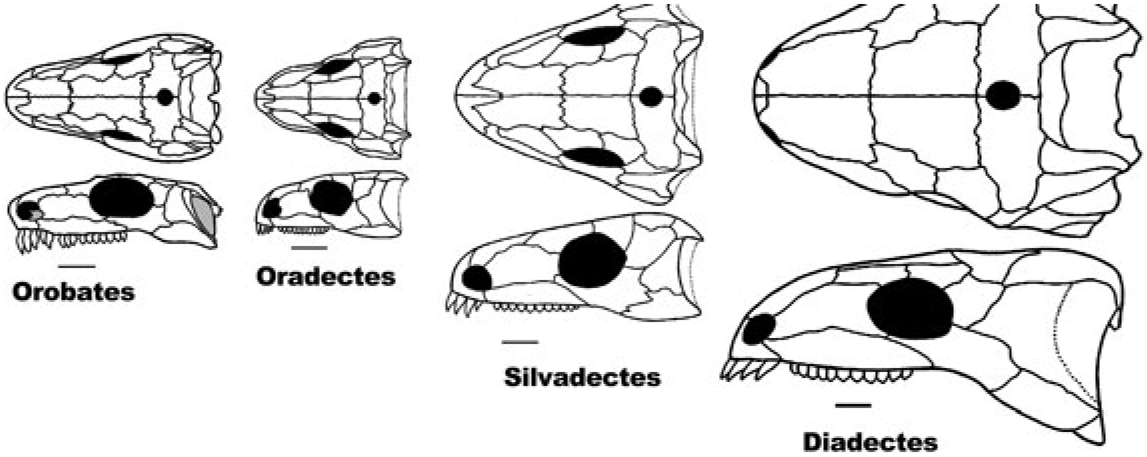
Permian allowed caseid pelycosaurs to replace them as the large herbivores; they were in turn replaced by herbivousrous therapsids (dinocephalia and anomodonts) later in the Permian.

Link Wikipedia

Image: *Diadectes phaseolinus*, American Museum of Natural History, New York, photo by Ghedoghedo,Wikipedia MAK111107



Left: Life reconstruction of *Diasparactus zenos*, by Dmitry Bogdanov . Length 1.35 metres. Wikipedia, GNU Free Documentation/Creative Commons Attribution
Below Left: the skulls of Orobates, Oradectes, Silvadectes and Diadectes from Kissel 2010, via David Peters, Reptile evolution. Scale bar = 2 cm.
Below Right: Cladogram from Kissel 2010 via Wikipedia:



```
Diadectomorpha:
--+--Limnoscelidae
   `--+--Tseajaiidae
      `--+--Ambedus
pusillus
Diadectidae
         `--+-
-Oradectes
sanmiguelensis
            `--+-
-Orobates pabsti
               `--+-
-Desmatodon
hesperis
                  `-
-+--Silvadectes
absitus
`--+--Diadectes
tenuitectes
               |--Diadectes sideropelicus
               `--Diasparactus zenos
```

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Reptiliomorpha: Dendrogram

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

Contents

```
TETRAPODA MH, ToL
|--TEMNOSPONDYLI X MH, ToL
`--+--LEPOSPONDYLI MH
   `--REPTILIOMORPHA MH
      |--Anthracosauroidea X
      |  `--+--Eoherpeton •X
      |     |--Embolomeri X MH
      |     |   |--+--Proterogyrinus  •X
      |     |   |  `--Pholidogaster •X
      |     |   `--Eogyrinidae X
      |     |      |--Diplovertebron  •X
      |     |      `--Pholiderpeton •X
      |     `--Chroniosuchia •X
      |        |--Chroniosuchidae •X
      |        `--Bystrowianidae •X
      `--+--Gephyrostegidae •X
          `---Batrachosauria
              |--Seymouriamorpha X ToL, MH
              |  |--Discosauriscus •X ToL
              |  `--Kotlassiidae •X
             `--+--Solenodonsaurus  •X
                 `--Cotylosauria
                     |--Diadectomorpha •X MH
                     |   |--Tseajaia  •X
                     |   `--+--Limnoscelis   •X
                     |      `--Diadectidae   •X
                       `--AMNIOTA (Stem and crown groups) MH, ToL
```

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Reptiliomorpha: References

Abbreviated Dendrogram

```
TETRAPODA
|--TEMNOSPONDYLI
`--+--LEPOSPONDYLI
   `--REPTILIOMORPHA
      |--Anthracosauroidea
      |  `--+--Embolomeri
      |     `--Chroniosuchia
      `--+--Gephyrostegidae
          `--Batrachosauria
             |--Seymouriamorpha
              `--+--Solenodonsaurus
                 `--Cotylosauria
                    |--Diadectomorpha
                    `--AMNIOTA
```

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Anapsida: Overview

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

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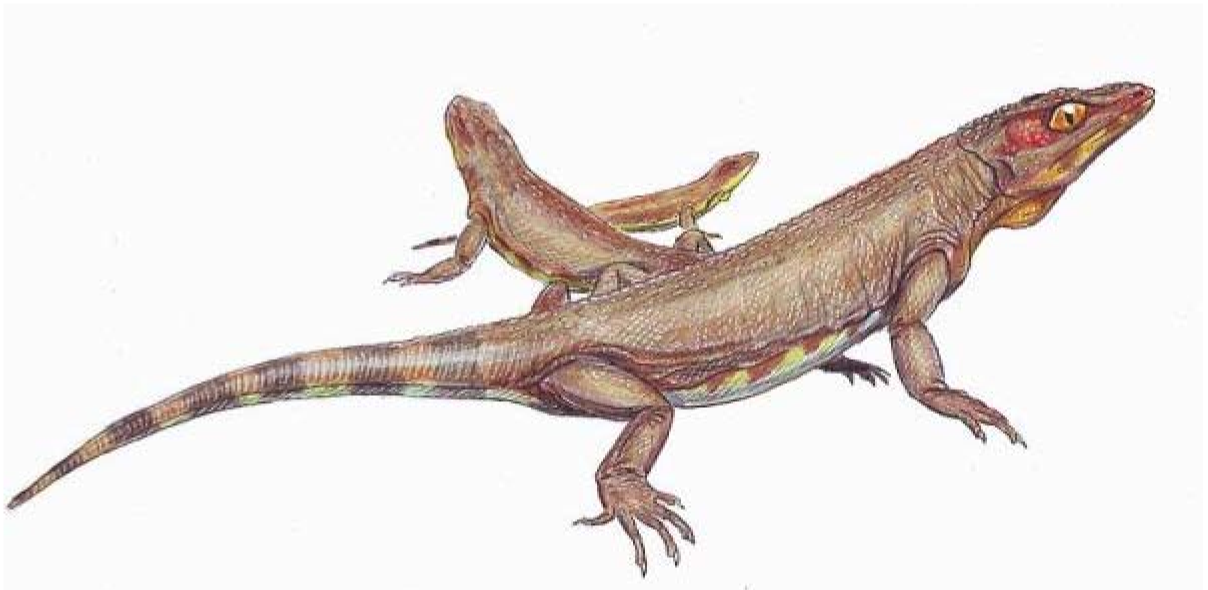
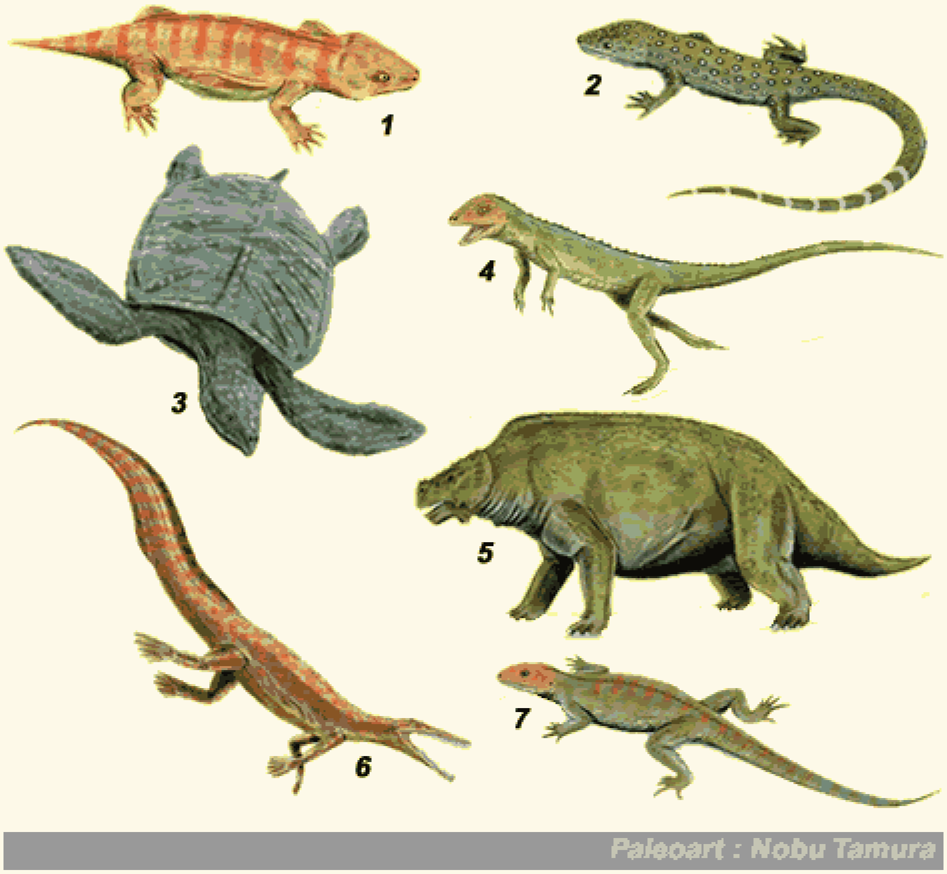


The stem-procolophonian *Nyctiphruretus acudens*, Middle Permian (Roadian/Wordian) of Russia
Artwork by Dmitry Bogdanov, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Introduction



Paleoart : Nobu Tamura

The term Anapsida ("no arch") originally referred to all those reptile groups that lack skull openings behind the eyes. Originally most of the primitive ancestral reptiles were included here, as well as the turtles. It is now known that this is a rather artificial group. The lizard-like Permo-Carboniferous captorhinids - originally placed here (see no.7 in the illustration at the right), have bene shown to represent a seperate group. There is also some controversy about whether the Turtles, for a long time included among the anapsids, belong here (in these dendragrams we have gone with the rather unimaginative option that turtles evolved from procolophonian anapsids);. That still leaves a diverse selection of Permo-Triassic reptiles, from small insectivorous species superficially similar to living lizards to great cumbersome armoured herbivores (such as the *Scutosaurus* no.5 at the right). The alternative term "Parareptilia" ("alongside reptiles") is sometimes used to describe eitehr the group as a whole (Tsuji & Müller 2009) or the majority subgroup (Modesto & Anderson 2004). This would be fine if the premise was that this was a totally extinct group, but this term is often used even when including turtles. Because this is as confusing (even if technically correct) as calling crocodiles pseudosuchia ("false crocodiles") (Gauthier 1986), we have chosen to retain the more traditional name.

In terms of their known evolutionary history, the Anapsids appeared suddenly during the later part of the early Permian; in the evolutionary stratigraphic paradigm they evolving from captorhinomorphs (Carroll 1988), whereas in the cladistic paradigm both anapsids and captorhinids evolved from an unknown common ancestor (Laurin and Reisz 1995). Regardless of their origin, anapsids diversified quickly, supplanting the captorhinids as a lizard-like ecomorph.

During the Middle Permian, some anapsids evolved into huge, heavily armored herbivores, the pareiasaurs like the afore-mentioned *Scutosaurus*. These early ankylosaur or glyptodont analogues often had widely-flared skulls, ornamented with irregular blobs of bone, looking like half-melted wax. The overall appearance is so bizarre that MSY Lee has aptly named the pareiasaur - lanthanosuchid taxon the Hallucicrania. Lee (1997) has argued forcefully that turtles evolved from a dwarf lineage of pareiasaurs. Apart from the question of turtle relationships, it seems only a single lineage of anapsids the procolophonids - survived into the Triassic. There they flourished and diversified, before dying out at the end of the period to be replaced by lepidosaurian sphenodonts (Rhynchocephalia).

(ATW & MAK, revised MAK120401)

Image: A selection of anapsids and reptiles that have previously been considered anapsids. (1) (1) *Procolophon*, a specialised herbivorous anapsid that ranged widely across Gondwana during the early Triassic; (2) *Millereta*, A small Late Permian anapsid from South Africa superficially very similar to extant lizards; (3) *Archelon* a gigantic Cretaceous protostegid turtle from the Western inland sea (the anapsid affinities of turtles (4) *Eudibamus*, an Early Permian bolosaur from Western Europe, a facilatively bipedal lizard-like form; (5) *Scutosaurus*, a giant armored

herbivore of the late Permian of Eastern Europe (Laurasia); (6) *Mesosaurus* a highly specialised aquatic reptile from the early Permain of Gondwana, (7) *Hylonomus* a middle Carboniferous captorhinomorph eureptile (not an anapsid, but previously classified as one).
Artwork by Norbu Tamura, Creative Commons Attribution Share Alike, via Reptiles org; MAK120401

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Anapsida or Parareptilia?

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   Anapsida/Parareptilia
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |?--TESTUDINES
               `--Procolophonidae
```

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1. Anapsida

Anapsida or Parareptilia?

Parareptilia ("at the side of reptiles") is an alternative term for a clade of early amniotes which are variously defined as an extinct group of primitive "reptiles", or a more cladistically correct alternative to Anapsida. Whether the term is valid or even useful depends a lot on the phylogenetic position of turtles, the relationships of which to other reptilian groups are still uncertain, as well as on ever shifting trends in popularity of terms.

A bit of history. The name Parareptilia was coined by Olson 1947 to refer to an extinct group of Paleozoic reptiles, as opposed to the rest of the reptiles or Eureptilia ("true reptiles"). The name soon fell into disuse, until it was revived by cladistic studies, to refer to anapsida that were thought unrelated to turtles. Gauthier et al. 1988 provided the first phylogenetic definitions for the names of many amniote taxa, including Sauropsida as the parent clade for Reptilia, and argued cladistically that captorhinids and turtles (or "Testudines" to give the technical scientific term) were sister groups, constituting the clade Anapsida (in a much more limited context than the definition given by Romer 1966). A name had to be found for various Permian and Triassic reptiles no longer included in the Anapsids, and "Parareptiles" was chosen. However, they did not feel confident enough to erect Parareptilia as a formal taxon. Their cladogram was as follows:

```
--o Amniota
  |-- Synapsida
  `--o Sauropsida
     |--o "Parareptiles"
     |  |-- Mesosauridae
     |  `--+-- Procolophonidae
     |     `--+-- Millerettidae
     |         `-- Pareiasauria
     `--o Reptilia
        |---o Anapsida
        |   |-- Captorhinidae
        |   `-- Testudines
        `--o Romeriida
           |-- Protorothyrididae
           `-- Diapsida
```

Laurin and Reisz 1995 presented a different cladogram, in which the Reptilia are divided into Parareptilia (now a formal taxon) and Eureptilia. The Captorhinidae are transferred to the Eureptilia, and the Parareptilia includes both early Anapsid reptiles and turtles, but not the Captorhinidae and Protorothyrididae. The mesosaurs are placed outside both groups, as the sister taxon to the reptiles (but still sauropsids). The traditional taxon of Anapsida is rejected as paraphyletic. This gives the following:

```
--o Amniota
  |-- Synapsida
  `--o Sauropsida
     |-- Mesosauridae
     `--o Reptilia
        |--o Parareptilia
        |  |-- Millerettidae
        |  `--+-- Pareiasauria
        |     `--+-- Procolophonidae
        |         `-- Testudines
        `--o Eureptilia
           |-- Captorhinidae
           `--o Romeriida
              |-- Protorothyrididae
              `-- Diapsida
```

The term Parareptilia has also been adopted by Russian workers, who have discovered a number of interesting lineages of early anapsid reptiles from the Middle Permian. They also follow a fairly standard classification of turtles.

In contrast, Rieppel, 1994, 1995; Rieppel & deBraga, 1996; and deBraga & Rieppel, 1997 have argued that turtles are actually related to sauropterygia, and hence are diapsids. They give this cladogram (the following is from deBraga & Rieppel, 1997, care of dinosaur mailing list archives):

```
--+--Seymouriadae
  `--+--Diadectomorpha
     `-o Amniota
        |--o Synapsida
        |   `--+--+--Caseidae
        |      `--+--Ophiacodontidae
        |         `--+--Edaphosauridae
        |            `--+--Gorgonopsia
        |               `--Cynodontia
        `--o Sauropsida
           |--+--Millerettidae
           |  `--+--+--Lanthanosuchidae
           |     |  `--Acleistorhinus
           |     `--+--Macroleter
           |        `--+--+--Procolophonidae
           |           | `--Owenettidae
           |           `--+--Bradysaurus
           |              `--+--Scutosaurus
           |                 `--Anthodon
           `--+--Captorhinidae
              `--+--Paleothyris
                 `--+--Araeoscelidia
                    `--+--Claudiosaurus
                       `--+--Younginiformes
```

```
`--+--+--Choristodera
   |  `--+--Prolacertiformes
   |     |--Archisauriformes
   |     `--+--Rhynchosauria
   |        `--Trilophosaurus
   `--+--+--Kuehneosauridae
      |  `--+--Sphenodontia
      |     `--Squamata
      `--+--Testudines
         `--+--Eosauropterygia (=Sauropterygia)
            `--Placodus
```

The diapsid affinities of turtles is unanimously supported by molecular phylogeny (e.g. Zardoya and Meyer 1998). This makes the Parareptilia a wholly extinct clade. I (MAK) have adopted this arrangement for now and followed the molecular concensous that turtles are diapsids and probably archosaurs. However this hypothesis is not very widely accepted among vertebrate paleontologists, and Benton 2000, 2004, retains the traditional class Anapsida for the "parareptiles" and turtles. (see Chelonian origins for more)

Regardless of whether one says "anapsid" or "parareptile", these animals formed an important element of Middle Permain terrestrial ecosystems, and these small to occasionally medium-sized lizard-like insectivorous and herbivorous forms were doubtless more numerous and diverse than their few scattered fossil remains indicate. It seems that most of these little animals did not survive the end-Gaudapadian mass extinction, their place taken by Owenettids and a few relict Millerettids in the late Permian, while a single lineage, the Pareiasaurids, grew to huge size during the later Middle Permian and survived till the end of the period. In the Triassic period, in the wake of another mass extinction, the end Permian extimnction, a single anapsid lineage, the Procolophonids, became enormously successful and diverse as small terrestrial herbivores. MAK09xxxx

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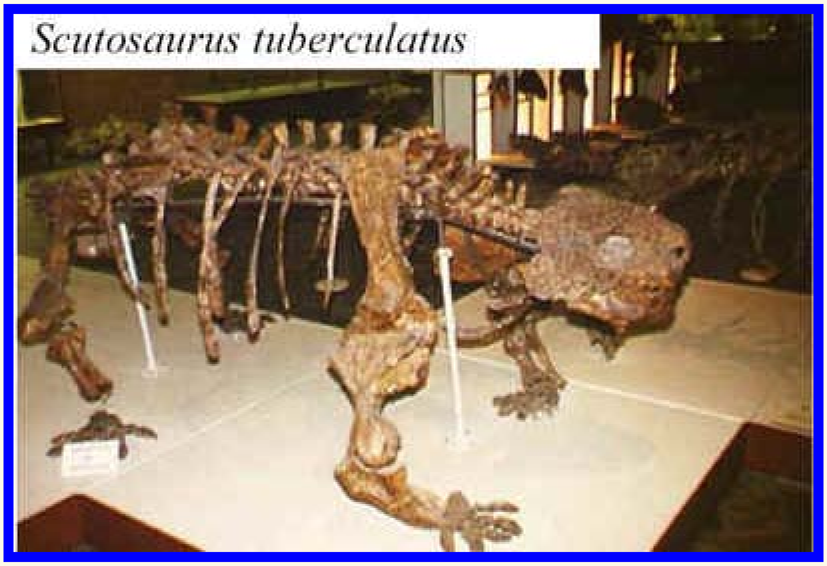
Descriptions



Anapsida (= Parareptilia):

Range: from the Permian

Phylogeny: Sauropsida : Eureptilia + * : Mesosauridae + (Millerettidae + *Eunotosaurus*) + Procolophonomorpha MAK120323

Characters: Caniniform teeth absent; posterior emargination of skull; dorsal expansion of quadratojugal; expanded iliac blade. Classically, no posttemporal fenestra; but this could be derived from the diapsid condition. ATW030912

Comments: The term *Anapsida* has also been used for Mesosauridae + all other anapsids; with this latter clade, the sister taxon of Mesoauridae,is called *Parareptilia* (see dendogram *right*).

```
Anapsida
|--Mesosauridae
`--Parareptilia
   |--Millerettidae
   `--Procolophonia
```

(Reisz & Scott 2002; also see Modesto & Anderson 2004 for general discussion of clade names). For reasons explained elsewhere, we have chosen not to incorporate that phylogeny. Throughout these pages then, anapsida and parareptilia are used synonymnously and interchangeably MAK120323

Links: Introduction to the Anapsids; Phylogeny & Classification of Amniotes; Parareptiles; Reptiles - Subclass Anapsida; Anapsida -- The Dinosauricon; ANAPSIDA; Basal Anapsida after Berman et al., 2000, Lee, 1993, 1996 and ...; Literature - Anapsida; F el ning 5; Nathis Fauna Reptilelen. ATW030912.

Image: from F el ning 5 (Lecture notes of Prof. John Peel & Prof. Lars Holmer, **Uppsala Universitet, Department of Earth Sciences**). *Scutosaurus* is a well-known pareiasaur. ATW030912

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Millerettidae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |?--TESTUDINES
               `--Procolophonidae
```

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1. Millerettidae X

The Millerettids are one of several types of anapsid reptiles known from the Middle and Late Permian of Southern Africa. Like other early anapsids, they were superficially very similar to modern lizards in appearance, and probably lived a similar, insectivorous lifestyle. Yet they did have some intriguing adaptations. In contrast to the classic anapsidan model, in which the cheeks are solid, some millerettids have temporal openings (fenestra) of the synapsid sort behind the orbits (eye sockets), but these wese acquired independently.

The presence of a concave area at the back of the skull called a quadrate emargination implies that millerettids had an ear drum (tympanum) and could hear high-frequency airborne sounds. However, the stapes (the sound-conducting bone in the middle ear) are still more solid than those of later anapsids such as the procolophonoids, suggesting that their hearing was not as good (ref: UCMP).

Despite their primitive nature, Millerettids appear quite late in the fossil record, some 30 million or so years after the first appearance of the bolosaurids, who represneta more specialised group. Many anapsids seem to have only appeared after a period of cryptic evolution, although whether this can account for their appearance so much later than the first and much more derived protorothyridids in the mid Carboniferous is another matter. As yet, no stratocladistic analyses have been performed to test against this, nor does there seme to be much or nay interest in such methodologies in the morphology-only dominated field of of early amniote evolution

Whenever they first evolved, Millerettids were common by the Capitanian age, and continued to flourish until the end of the Permian, co-existing alongside similar but more advanced anapsids such as nycteroleterids, owenettids, and procolophonids, as well as basal neodiapsids, captorhinids and younginiformes. What all this shows is that middle and late Permian terrestrial ecosystems were populated by a diverse range of generalised and basically lizard-like, anapsid and diapsid reptiles, constituting an ecosystem that may have been just as rich and diverse as today's environments. MAK120323

Descriptions

Millerettidae Romer, 1956 **:** Most primitive anapsid group? (*Broomia*, *Heleophilus*, *Milleretoides*, *Milleretta*, *Millerettops*, *Milleropsis*, *Millerosaurus*, *Nanomilleretta* (clearly oversplit and in need of revision!))

Range: Middle (Capitanian) to Late Permian of South Africa.

Phylogenetic definition: all taxa more related to *Milleretta rubidgei* Broom, 1938, than to *Macroleter poezicus* Tverdokhlebova & Ivakhnenko, 1984. (Cisneros et al 2008)

Phylogeny: Anapsida **:** Mesosauridae + (Bolosauridae + Procolophonia) + *.

Length about 60 cm

Characters: Simple, conical teeth; retention of tabular, large supratemporal and postparietals; some forms with lateral temporal fenestra, but independently derived; lower temporal bar incomplete; stapes relatively small(?), light; impedance-matching ear likely; squamosal and quadratojugal embayed to support tympanum likediapsids (?) but unlike Testudines, which use quadrate; lizard-like?

Links: Introduction to Millerettidae; Nathis Fauna Reptilelen (Dutch -- brief discussion); reptiles (basic data); Kardong K (summary of phylogenetic placement); PANGEA (Italian -- quick summary and picture). ATW030304. Milleretta - All About Reptiles Paleofieldguide - *Milleretta rubidgei*, Millerosaurus - Wikipedia

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Anapsida: *Eunotosaurus*

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosauridae
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |?--TESTUDINES
               `--Procolophonidae
```

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Taxa on This Page

- *Eunotosaurus* X

Life restoration of *Eunotosaurus africanus*. illustration by Smokeybjb (Wikipedia)

Descriptions

Eunotosaurus africanus Seeley, 1892

Phylogeny: Anapsida **:** Mesosauridae + (Bolosauridae + Procolophonia) + Millerettidae + *.

Range: Late Middle Permian (Capitanian) of Southern Africa .

Comments: A Tapincopehalus Assemblage Zone index fossil (Rubidgeetal99). Once considered the ancestor of the Chelonia, it is now known that this small animal independently evolved turtle like characteristics. The semi-rigid, turtle-like ribcage implies a tortoise-like fashion of walking (Sumida & Modesto) . Beyond being a member of the anapsida, evolutionary relationships were for a long time uncertain, which is not surprsiing for a highly derived taxon (the same thing is the case with *Mesosaurus*). But recent cladistic studies (Müller & Tsuji 2007, Cisneros et al 2008) show *Eunotosaurus* to be be a Millerettid. More unexpected (and unlikely?) is the study by Lyson et al 2010 that even restores the chelonian ancestor hypothesis. One problem here is that *Eunotosaurus* is too early to be a good ancestor, some 45 million years separate it from *Odontochelys*, the oldest known turtle (there's a similar problem with the time difference between "Protoavis" and *Archaeopteryx*; a major adaptive radiation such as birds, turtles, or placental mammals would be expected to be immediately evident in the fossil record) MAK120324

Links: Eunotosaurus And Turtle Evolution - All About Reptiles Eunotosaurus - Wikipedia

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Anapsida: Mesosauridae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosauridae
   |---Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |?--TESTUDINES
               `--Procolophonidae
```

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- Mesosauridae X

The Amazing Mesosaurs

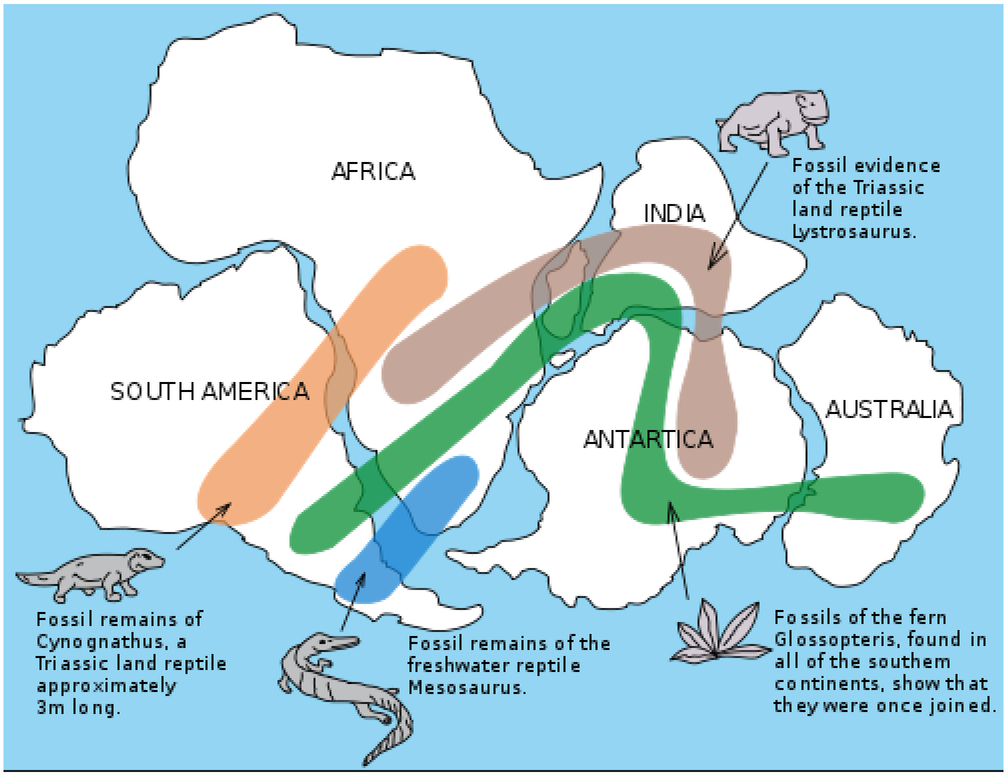
Among the most distinctive of Permian reptiles are the Mesosaurs ("middle lizards"), a highly specialised group of small aquatic (or semi-aquatic) reptiles known only from the early Permian (perhaps Artinskian?) of South Africa (Namibia) and South America (Brazil, Paraguay, and Uruguay). The presence of such an endemic and stratigraphically restricted animal at opposite sides of the Atlantic ocean was a powerful argument in favour of continental drift, formulated by Alfred Wegner in the early part of the 20th century

The instantly recognisable, if unlikely coloured for an aquatic animal, tiger-striped Mesosaurus, by classic paleo artist Zdenek Burian. This was one of the iconic reconstructions of prehistoric life that shaped several generations of budding paleo enthusiasts (including yours truly) MAK120322

(see map at the right). Du Toit 1937

Resembling a large lizard or miniature crocodile, Mesosaurus was remarkable for its long needle like teeth, which were probably used to feed on small crustacea (they are too delicate to have been of any use for catching larger prey, such as small fish). There presence so far south during the early permian is also unusual, as much of Gondwana was still covered by glaciers. The creatures probably fed during the warm summer months, and hibernated through the winter. Their extinction would have been due to changing conditions, we could speculate that the slowly warming climate would have eventually resulted in the extinction of the specialised crustacea on which they fed

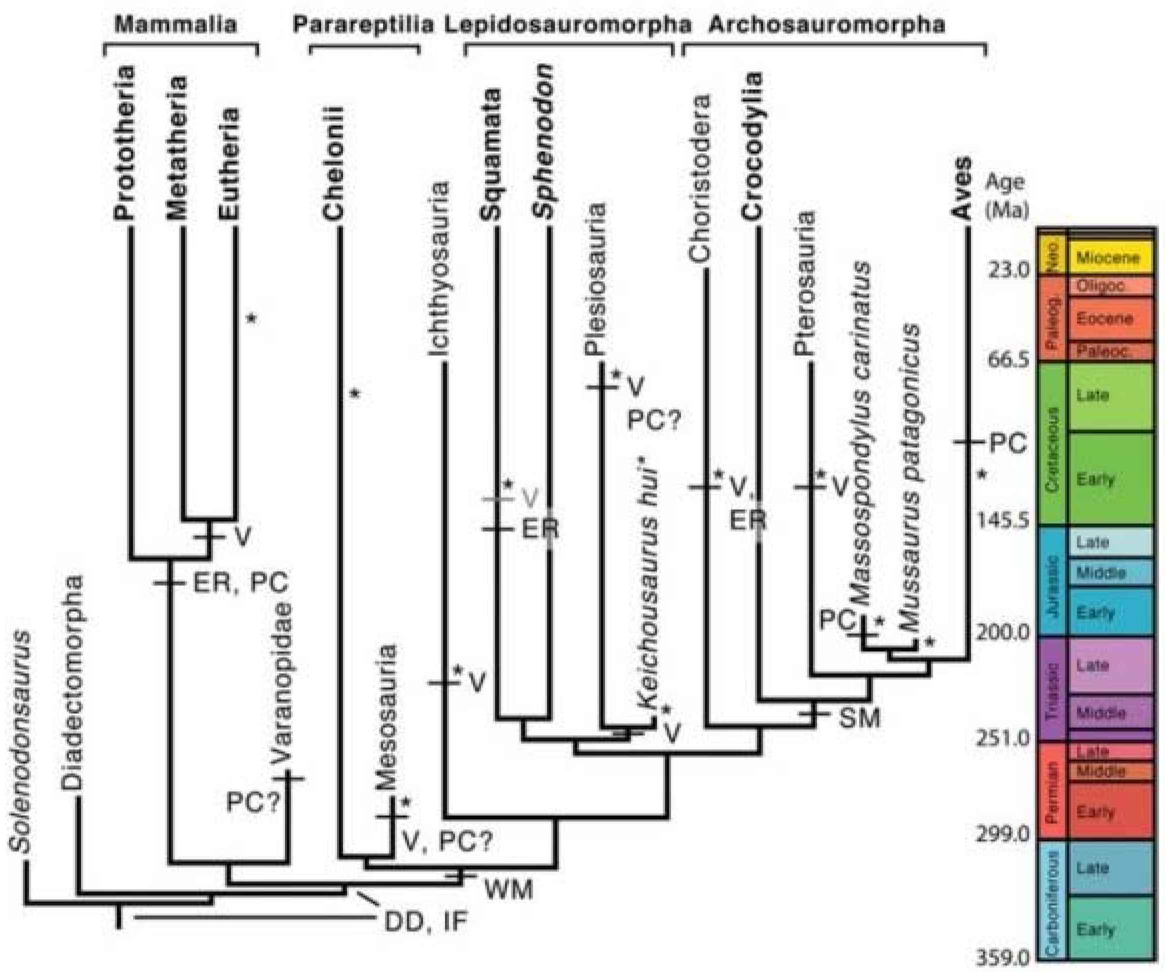
Although three genera have been named (in keeping with the tendency towards monotypal genera in vertebrate paleontology) they may be similar enough to be considered three species of the same genus; in cladistic analysis they form a closely linked monophyletic assemblage (Tsuji & Müller 2009) MAK120322

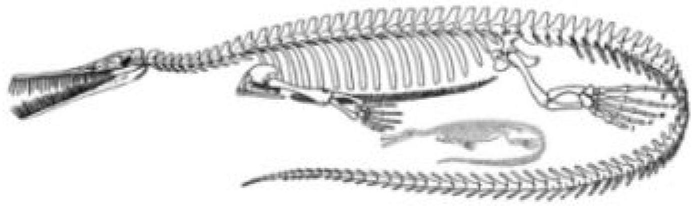


The Snider-Pellegrini Wegener fossil map, showing fossils distributed across the ancient supercontinent of Gondwana. *Mesosaurus* is shown at the bottom center, represented by the blue patch. This version by Osvaldocangaspadilla, Wikipedia, public domain

Viviparity in mesosaurs

Recently, exceptionally well preserved mesosaur embryos have been found within an adult individual, presumably a pregnant female. Several specimens also show associations between an adult and a possibly neonate. All of which suggests that mesosaurs were likely viviparous and practiced parental care (K-selection strategies). This is the earliest known case of viviparity (Pi&ntildeeiro et al 2012). Such reproductive strategies have emerged independently a number of times among amniotes, as the following dendrogram shows MAK120323

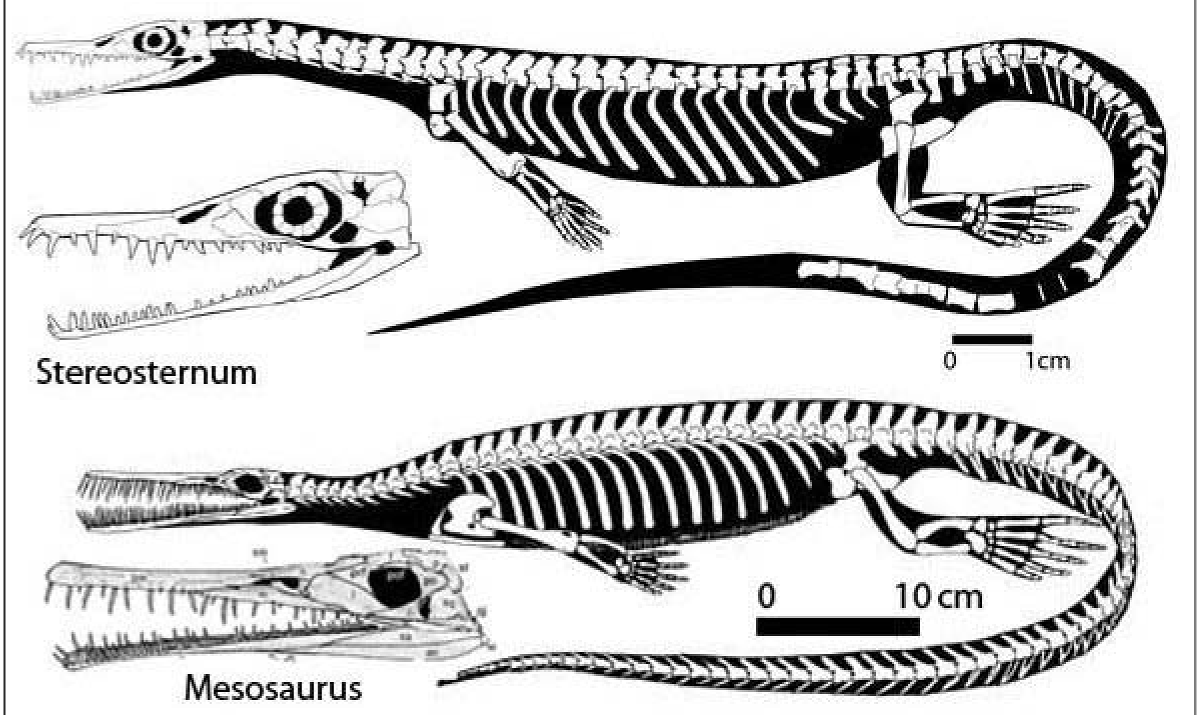




Above: Amniote phylogeny showing the evolution of relevant developmental characters. Extant taxa in bold. Coloured timescale on right. Characters that occur only in some taxa are in grey. DD, direct development; ER, embryo retention; IF, internal fertilisation; PC, parental care; SM, strongly mineralised eggshell; V, viviparity; WM, weakly mineralised eggshell; *earliest fossilised embryos along each branch of the tree. *Right*, reconstruction of an adult and a posthatched *Mesosaurus tenuidens*, showing putative average-sized adult/neonate relation Both diagrams from Pi&ntildeeiro et al 2012

Mesosaurs as diapsids? Or what?

The exact phylogenetic affinities of the mesosaurs have varied over the years. Originally they were simply included under the evolutionary linnaean Subclass Anapsida (Romer 1966, Colbert 1969, Carroll 1988), a wastebasket taxon for all reptiles that lacked



Skeletal reconstructions of the mesosaurs Stereosternum and *Mesosaurus*, Early Permian of Gondwana. Artwork by David Peters, used with permission

temporal openings. Initial cladistic analysis showed them to be basal parareptiles (Gauthier et al 1988). Later they were reinterpreted as basal Sauropsida (as sister taxon to Reptilia) (Laurin & Reisz 1995). They are now almost universally as the most basal Anapsida/Parareptilia clade and sister taxon to all other anapsids/parareptiles (Modesto 1999b, Modesto & Anderson 2004, Tsuji & Müller 2009, Lyson et al 2010, , Tsuji et al 2012), which is basically where Gauthier et al placed them in the first place; although Hill (2005)'s total evidence tree places them even stemward of synapsids.

A basal-most taxon could mean at least one of several things:

1. It really could be the most primitive or ancestral member of a group known; this doesn't seem to be the case with an animal as highly specialised as *Mesosaurus*.
2. The basal position would be the result of a highly specialised form lack of shared apomorphies (rendering cladistic synapomorphy-based methods ineffectual. The present author (MAK) believes this is the case with placodonts in the Sauropterygia, there is also the same problem as with trying to understand Hupehsuchians), rather than a long period of cryptic evolution.
3. The taxon may not belong in the group in question at all and its placement there may simply be the result of shared primitive characteristics or convergences. For example, golden moles (Superfamily Chrysochloroidea) are placed as the most basal insectivora on morphological grounds (even stemward of fossil species) but have been shown on molecular grounds to belong to a totally different group, the afrotheria.

The discovery of transitional forms would help resolve this problem. According to maverick paleo geek and artist David Peters [1], *Stereosternum* is less derived than *Mesosaurus*, and might therefore constitute such a transitional species. In email correspondence David suggests that the reason for the anomolous results in cladistic analyses would be because most researchers code *Mesosaurus* rather than *Stereosternum*, and in illustrations (*right*) shows the difference between the two genera., although Tsuji & Müller 2009 show all three mesosaur genera as forming a close-knit basal clade. Peters' own cladistic analysis locates the mesosaurs within the Diapsida. In view of the fact that at least one type of aeroscelid, *Spinoaequalis*, had become aquatic even before the Permian began, a diapsids ancestry for mesosaurids may not be unreasonable. The same result was recovered by Maisch 2010 who, like Peters, found *Mesosaurus* to be a sister taxon to the Ichthyosauria.However he felt this was the result of homoplasies, when he reran his analysis using a different way of coding character states, *Mesosaurus* was recovered in the more traditional placement of basal anapsid.

Considering mesosaurs and ichthyosaurs, two groups that are never considered together in current phylogenies, The present author is reminded of one of his childhood books on prehistoric life, it would have been circa early or mid 1960s, which had a simple evolution tree in which *Seymouria* was an ancestral reptile, *Mesosaurus* an ancestral ichthyosaur, and so on. The idea goes back to the early to mid 20th century German paleontologist Friedrich von Huene, who believed that *Mesosaurus* shared a common ancestry with the ichthyosaurs, deriving both from

Carboniferous embolomerous amphibians, or even loxommids. Still on this subject, Huene's older American contemporary Samuel Wendell Williston placed mesosaurs, ichthyosaurs, squamates, and protorosaurs (including aeroscelids) in a separate subclass, Parapsida, based on a shared upper temporal opening (Callaway 1997 p.5). Although the Parapsida in one form or another was still a respectable taxon in the 1950s, none of these theories are now considered to have any validity.

Although we can safely discard Huene's mesosaur-ichthyosaur association, given the huge morphological disparity and long period of time between the two groups, and the highly endemic and stratigraphically restricted range of the Mesosauridae (although Peters attempts to bridge this with several other taxa [2]), that does not mean the consensus paradigm is automatically the correct one. Given the curious topologies that regularly result through molecular phylogeny (according to which morphology is not reliable, this is a controversial subject) it is not impossible that mesosaurs may be diapsids or proto-diapsids that converged on anapsids. Of the three alternatives listed above, the present author considers the first the most unlikely, which leaves option 2 or 3. For now we have opted to follow option 2 (retained mesosaurs among the anapsids, although not as the most basal taxon), as option 3 means we have aboslutely no idea where the mesosaurs should go. MAK120323

Notes:

[1] Despite his obvious artistic talent, hard work, and dedication to unbiased research, David Peters is poorly regarded by other workers in the field. This is perhaps not so much because of his unique photo-interpretation technique, which uses Photoshop as a camera lucida, as his resulting eccentric pterosaur interpretations; see e.g. discussion on Tetrapod Zoology. In personal correspondence with the present writer (MAK) he comes across as a humble and dedicated researcher, albeit one obviously outside the mainstream. The huge cladogram on his website *Reptile Evolution*, shows a very deep amniota split which puts captorhinids, anapsids, diadectomorphs, turtles, and lepidosaurs in one branch, and all other diapsids, *Casineria, Westlothiana*, microsaurs, protorothyrids, mesosaurs, and synapsids in the other. Although parts of his tree differ from other published phylogenetic hypotheses, Peters argues that his topology is recovered when a sufficient number of taxa are included. To date no other study has attempted an analysis of the size or scope of the Peters study.

[2] Peter's results here are *Stereosternum* + (*Wumengosaurus* + (Thalattosauria + (*Hupehsuchus* + *Utatsusaurus*))). Apart from *Stereosternum* and the basal sauropterygian *Wumengosaurus*, this is a pretty uncontroversial phylogeny. Hupehsuchids are often linked with ichthyosaurs but that may be convergence. *Wumengosaurus* is a particularily interesting form as its long rostrum gives it an ichthyosaur or polycotylid like appareance,

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Descriptions

Mesosauridae: *Brazilosaurus, Mesosaurus, Stereosternum*

Range: Early Permian of South America & Africa.

Phylogeny: Sauropsida: Reptilia + *.

Characters: secondarily aquatic; elongated snout & neck (~10 vertebrae); nares posterior, near orbits; postorbital contacts the supratemporal; quadratojugal does not extend dorsally and is narrowly exposed on the cheek (primitive); supraoccipital lacks anterior parasagittal flanges (primitive); supraoccipital plate broad & extends farther laterally than postparietal (primitive);.jaw articulation at level of occiput (primitive); ossified dorsal process of stapes (primitive); pterygoid palatal ramus extends anteriorly medial to choanae; teeth thecodont; long teeth (strained plankton?); pachostosed trunk ribs and wide neural arches, long, broad tail; well-developed anterior limbs; iliac blade with long, low posterodorsal process, lacking anterior expansion; large paddle-foot pes.

Image: *Stereosternum* from **Permian Tetrapods.** We recommend a visit to this site which has some excellent images in which some of the listed characters can be seen.

Links: Phylogeny and Classification of Amniotes; MESOSAURIA; Nathis Fauna Reptilelen (Dutch). ATW060129.

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checked ATW040118, revised MAK120323

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Anapsida: Lanthanosuchoidea

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |  `--Eunotosauridae
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      |   |---Acleistorhinidae
      |   |   |---Acleistorhinus
      |   |   `---Colobomycter
      |   `-Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |  `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |  `?--TESTUDINES
               `--Procolophonidae
```

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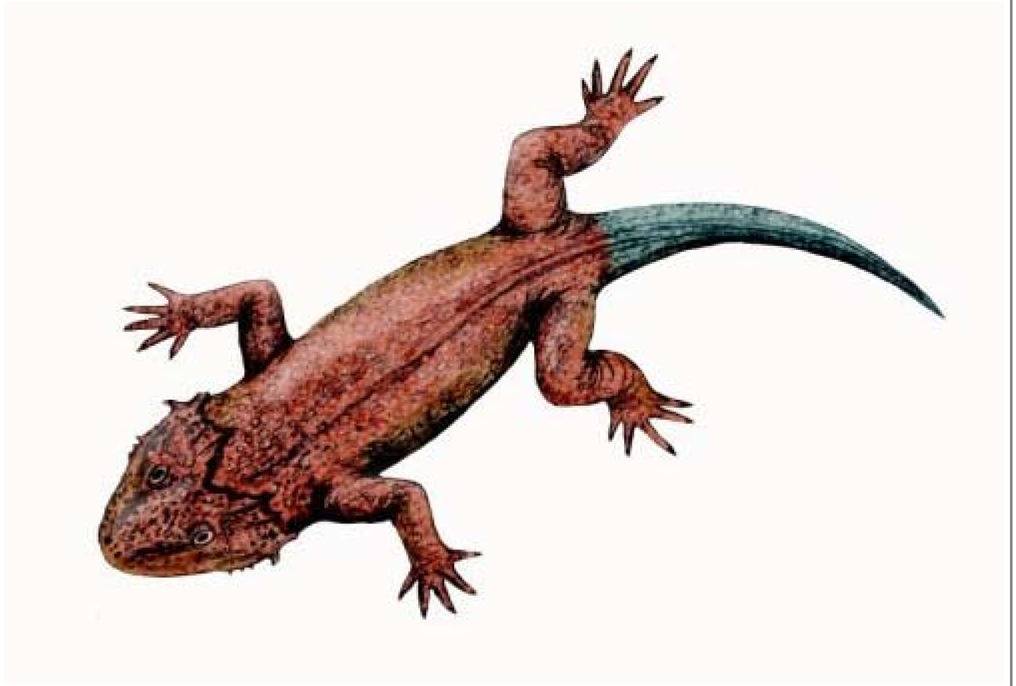
- *Acleistorhinus* X
- *Colobomycter* X
- Lanthanosuchidae X
- Lanthanosuchoidea X
- Procolophonomorpha

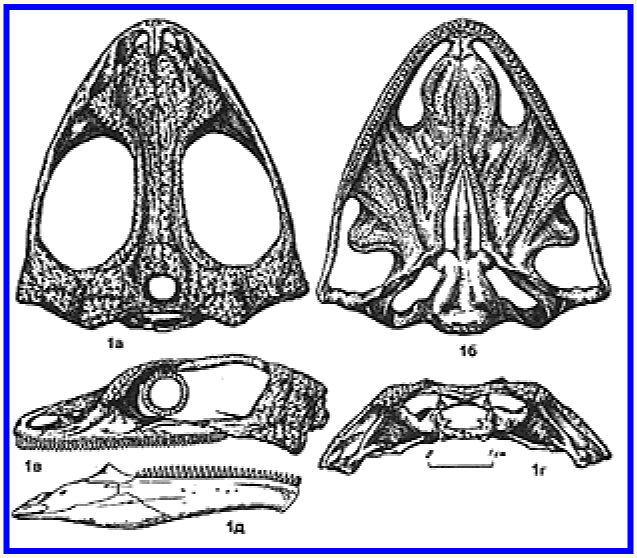
Lanthanosuchoidea



Life reconstruction of *Lanthanosuchus watsoni*, known from the Isheevo locality (Early Capitanian of Russia). At over a meter in length, this is the largest known representative of the clade
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

The Lanthanosuchoidea were one of several lines of Permian anapsids, which included several diverse and superficially very disimilar forms. While early forms, known from the Kungurian (latest Early Perman) of Oklahoma, were small or tiny, the very specialised flat-headed Lanthanosuchidae, illustrated above, reached over a meter in length. Like their cousins the Bolosaurs and Nycteroleterids, none of these animals are known to have survived the End-Gaudalupian mass-extinction.

Descriptions



Procolophonomorpha (= Ankyramorpha *sensu* deBraga & Rieppel (1997)?)

Range: Mid Permian to recent

Phylogeny: Anapsida : Mesosauridae + (Millerettidae + *Eunotosaurus*) + * : Lanthanosuchoidea + (Bolosauridae + Procolophonia)

Comments: The Procolophonomorpha are an order or clade of early reptiles that appeared during the Middle Permian. They constitute a diverse assemblage that includes a number of lizard-like forms, such as the Procolophonia and several related groups like the Acleistorhinidae, Lanthanosuchidae, paraphyletic "Nycteroleteridae", and Rhipaeosauridae, as well as the Pareiasaurs. It may or may not also include the Turtles. However Lee 1995, 1996, 1997 argues that turtles evolved from Pareiasaurs but this view is by no means held unanimously. Rieppel & deBraga, 1996 and deBraga & Rieppel, 1997 argue that turtles evolved from Sauropterygians. The traditional view that turtles evolved from unspecified Procolophonids seems to be no longer current. MAK091119

Links: More Nyctiphruretus acudens; Phylogeny and Classification of Amniotes; Introduction to Procolophonoidea

Image: *Nyctiphruretus acudens* from Mathematics. ATW010213.

Lanthanosuchoidea:

Range: Early to Middle Permian of Nth Am and Russia

Phylogeny: Anapsida **:** Millerettidae + (Procolophonia + (* **:** Acleistorhinidae + Lanthanosuchidae))

Characters: **$** reduction in size of the postparietal, **$** long basicranial articulation (ref UCMP)

Links: Paleobiology Data Base - Lanthanosuchoidea

References: deBraga & Reisz 1996

MAK091128

Acleistorhinidae: *Acleistorhinus*, *Colobomycter*

Range: Early Permian of Nth Am (Kungurian of Oklahoma)

Phylogeny: Lanthanosuchoidea : Lanthanosuchidae + * (Reisz & Scott 2002)

Characters: **$** the largest tooth is located far anteriorly on the maxilla; **$** cranial ornamentation consists of sparse and shallow circular dimples. (Wikipedia). Superficailly synapsid-like temporal fenestration. Temporal fenestrata (openings in the cheek area for muscles to strengthen the bite, and perhaps also lighten the skull) are a common feature found in a number of other early anapsids (parareptiles) (Cisneros et al 2004 p.1544)

Comments: With Bolosaurudae the oldest-known anapsid clade.

Links: Wikipedia

References: Cisneros et al 2004 p.1544, Reisz & Scott 2002

MAK091128

Acleistorhinus: *A. pteroticus* Daly 1969.

Range: Early Permian of Nth Am (Kungurian (Mitchelcreekian LVF of Lucas 2006) of Oklahoma)

Phylogeny: Acleistorhinidae **:** *Acleistorhinus*, *Colobomycter* + *

Size: skull about 3 cm in length

Characters: Synapsid-like lower temporal fenestra

Comments: A tiny but already specialised and probably superfically-lizard-like animal.

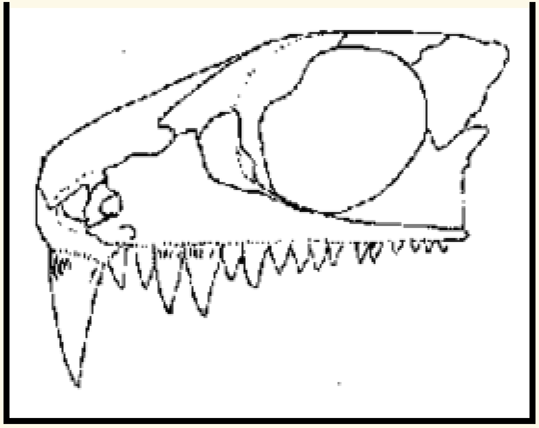
Links: Acleistorhinus - UCMP (Best on the Web), Wikipedia, Paleobiology Data Base - Acleistorhinus

References: Daly, 1969.

MAK091128

Colobomycter: *C. pholeter* Vaughn, 1958

Range: Early Permian of Nth Am (Kungurian of Oklahoma)



Phylogeny: Acleistorhinidae **:** *Acleistorhinus* + *

Size: skull 7-8 cm in length

Characters: remarkabble for its greatly enlarged, serrated, caniniform teeth, the length of each being greater than half the height of the skull.

Comments: Originally believed to be a pelycosaur. the smallest predatory amniote from its locality (Richard's Spur). The function of the enormous and obviously specilaised canines are unclear.

Links: Wikipedia (Best on the Web), Colobomycter Pholeter - Permian Tetrapods, Paleobiology Data Base - Colobomycter

References: Modesto 1999. Modesto & Reisz 2008, User:Greygirlbeast (Wikipedia)

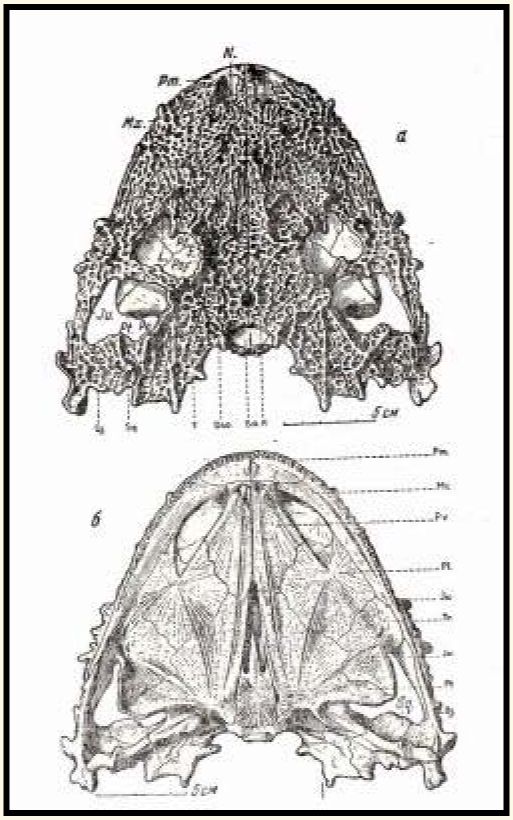
Graphic: Modesto & Reisz 2008. via Wikipedia

MAK091128

Lanthanosuchidae: *Chalcosaurus, Lanthaniscus, Lanthanosuchus*

Range: Middle Permian (Wordian to Capitanian) of Russia

Phylogeny: *either* Lanthanosuchoidea : Acleistorhinidae + * (Reisz & Scott 2002).; *or*, Hallucicrania **:** Pareiasauroidea + *. (Lee 1995, Lee, 1997).



Size: *Lanthanosuchus watsoni* (illustrated) skull about 20 cm long and wide

Characters: wide, flat skull; lateral temporal fenestra present; dermal sculturing strongly marked

Comments: These strange creatures had extremely flat skulls. So flat in fact that even the jaw muscles could not fit inside, and had to go outside through special openings behind the eyes. The bony tubercles and ridges (a common charcateristic among early anapsids and seymouriamorphs) probably served to strengthened the skull roof. It used to be thought, because of their flat heads, that Lanthanosuchids were aquatic, like temnospondyls, but recent studies have questioned this. Perhaps they subsisted on insects and grubs in forest litter, using the strange head to push under leaves, debris etc. MAK000415.

Links: Introduction to the Lanthanosuchidae; Lanthanosuchus watsoni (Mathematical com); The Journal of Vertebrate Paleontology (abstract: sister clade of *Acleistorhinus*). ATW030322. Lanthanosuchus - All About Reptiles - makes an intersting hypothesis regarding *Lanthanosuchus* as a flattened bottom-dweller like a flounder or ray. Also similarity of form with *Pelorocephalus*. So maybe the Lanthanosuchids were aquatics after all. J. A. Efremov. On the subclass Batrachosauria -- an intermediary group between Amphibians and Reptiles - in Russian, includes detailed drawings of skull. Note: *Lanthanosuchus* is no longer considered a batrachosaur; Lanthanosuchidae - Wikipedia (in German) MAK091129

Graphic: life reconstruction Mathematical com, drawing of skull from Efremov. (see above link) via Russian Wikipedia link small link large

MAK091129

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checked ATW040118

Bolosauridae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         |  |--Belebey
         |  |--Bolosaurus
         |  `--Eudibamus
         `--Procolophonia
            |--Nyctiphruretus
            `--+--+--Nycteroleteridae
               |   `--Pareiasauridae
               `--Procolophonoidea
                  |?--TESTUDINES
                  |--Owenettidae
                  `--Procolophonidae
```

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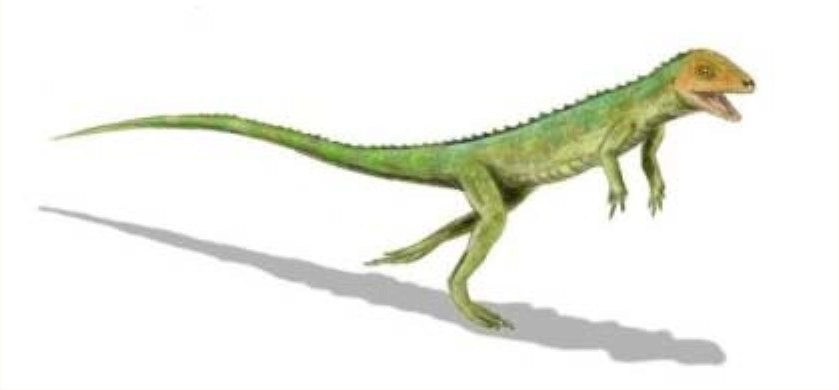
1. *Belebey* X
2. Bolosauridae X
3. *Bolosaurus* X
4. *Eudibamus* X

Bolosauridae

The Bolosauridae were one of several lines of distinctive small, lizard-like Permian anapsids. They are also the earliest known anapsids, as far as the current fossil record goes. were widely distributed across Laurasia (low and middle latitude Northern Pangea) during the early and middle Permian but do not seem to have survived the End-

Gaudalupian mass-extinction, or extended to the high latitudes. As well as being herbivorous with specialised bulbous teeth, they seem to have been capable of short bursts of bipedal running, although for the most part they would have moved in a sprawling posture. The two illustrations above show the two postures. MAK

Two representations of bolosaurids:



As a biped. Life reconstruction of *Eudibamus cursoris* by Arthur Weasley - Wikipedia, based on Berman *et al.* (2000).

As a quadraped. Life reconstruction of *Belebey vegrandis*, illustration by Dmitry Bogdanov - Wikipedia.

There is no reason why both of these explanations may not be correct, nor why eiethr species shown here could not be both faculative bipeds as well as quadrapeds

---

Descriptions

Bolosauridae: *Eudibamus* & co.

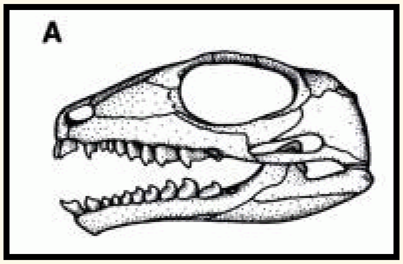
Range: Early to Middle Permian of Nth Am, Germany, Russia, and China.

Phylogeny: Procolophonomorpha : Lanthanosuchoidea + (Procolophonia) + * : *Belebey* + *Bolosaurus* + *Eudibamus*).

Characters: Palate without teeth; transverse flange of pterygoid in same plane as palate; dentary and surangular form tall coronoid process; proximal portion of dentary covered by anterior process of prearticular; bulbous, occluding teeth; temporal fenestra long and low, between jugal and squamosal dorsally and quadratojugal ventrally; herbivorous. ATW

Links: Basal Anapsida after Berman et al., 2000, Lee, 1993, 1996 and Modesto 1999, 2000 (dendrogram); Bolosaurus - All About Reptiles (Best on the Web)

References: Berman *et al.* (2000).



Belebey *B. vegrandis* Ivachnenko, 1973 (type); *B. maximi* Tverdochlebova, 1987; *B. chengi* Müller 2008. Horizon, locality, and size for *B. vegrandis* (illustrated right)

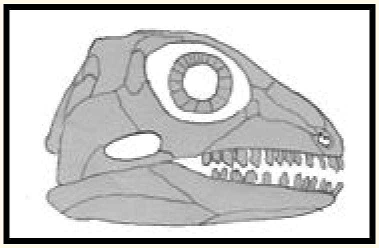
Range: Middle Permian of Russia (several species) and China *B. chengi*

Phylogeny: Bolosauridae ::: *

Horizon: Belebey Svita, Upper Kazanian

Locality: Krymskii, Orenberg region, South Cis-Urals, European Russia
Length (skull): about 6.5 cm
Age: Roadian to Early Wordian
Comments: *Belebey* (known from several species, although some of these may be synonymous) and *Davletkulia gigantea* (known from a single large tooth) were small terrestrial lizard-like animals that seem to have been reasonably common in the Kazanian. It is not known wherther they were faculatively bipedal like *Eudibamus*. *Belebey vegrandis* is the best known bolosaur from Eastern Europe. As the name indicates, it is named after the Belebey Svita (formation) where its fossil remains have been found. Similar material has been found in China, indicating the wide distribution of the group.
References: Modesto and Rybczynski 2000, V.P. Tverdokhlebov *et. al.* 2005
Links: Permian Triassic localities (spreadsheet)

Graphic skull from Modesto and Rybczynski 2000 p.22



Bolosaurus: B. striatus Cope, 1878 (Type); *B. grandis* Reisz, Barkas & Scott, 2002,

Range: Early Permian (Artinskian and Kungurian) of Nth Am

Phylogeny: Bolosauridae ::: *

Comments: A long-ranging herbivore with bulbous teeth and synapsid-like temporal openings. The Kungurian (Mitchelcreekian LVF) *B. grandis* is larger and more derived than the Sakmarian/Artinskian to earliest Kungurian (Coyotean-Seymouran LVF) *B. striatus* and may represent an ancestor-descendent lineage (Lucas 2006 p.78)

Links: Bolosaurus grandis - Permian Tetrapods

References: Watson, 1954 Lucas 2006

Graphic: Derawing of skull by Ghedoghedo - Wikipedia

MAK091129

Eudibamus: *E. cursoris* Berman, Reisz, Scott, Henrici, Sumida & Martens 2000

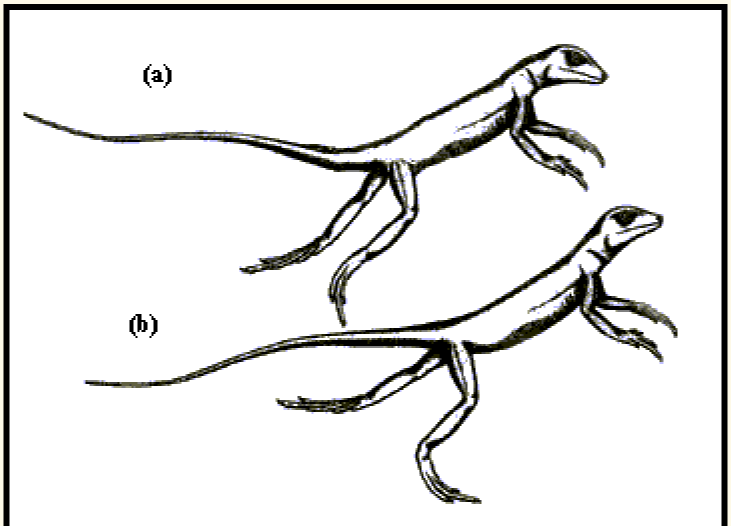
Range: Early Permian (Artinskian) of WEur (Tambach Formation, Upper Rotliegend, in the Bromacker quarry locality of the middle part of the Thuringian Forest

Phylogeny: Bolosauridae ::: *

Length (overall): about 25 cm

Comments: along with *Bolosaurus*, this is the oldest known representative of the Anapsida. Both animals appear at about the same time.

Links: Dinosaur News: Eudibamus - ZoomDinosaurs.com; Early Permian Bipedal Reptile article in Science 11-3-00; PALEONTOLOGIA Correndo veloci nel passato (Italian); Reisz Lab: Bromacker Locality.



Eudibamus cursoris reconstructed as (a) saltorial or (b) cursorial. Modified from Berman et al. (2000).

References: Berman *et al.* (2000).

Image and Note: *Eudibamus cursoris* from the Eary Permian of Germany, is the earliest known biped. Berman et al. reconstruct *Eudibamus* as a cursorial form. The image (a) shows a possible alternate reconstruction as saltorial.

Berman et al. reject an arborial clinging & jumping habit because the penultimate phalanges are not elongated as in other organisms with this locomotor style. However, no other cursor *or* jumper has the primitive tarsal structure of *Eudibamus*. Accordingly, it may not be entirely safe to rely on such comparisons. *Eudibamus* has the short neck of a jumping form, although the pelvis is so slight as to make either running or jumping questionable. ATW010416.

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Anapsida: Procolophonia

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |    `--Eunotosaurus
   |--Mesosauridae
   `--+--+--Acleistorhinidae
      |  `--Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--Nyctiphruretus
            |--+--Nycteroleteridae
            |  `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |    `?--TESTUDINES
               `--Procolophonidae
```

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1. *Nyctiphruretus* X
2. Procolophonia

Nyctiphruretus acudens

Nyctiphruretus acudens, a parareptile from the Middle Permian of Russia (Subtropical Pangea) illustration by ArthurWeasley - Wikipedia

Introduction

The Procolophonia are a group of primitively insectivorous, and then early herbivorous reptiles that flourished during the Permian to Triassic periods, and, while rarely exciting or glamorous (although the big lumbering pareaisaurs do have an ideosyncratic appeal, even appearing in a sci fi television series) were among the most successful animals of their time.

Phylogeny

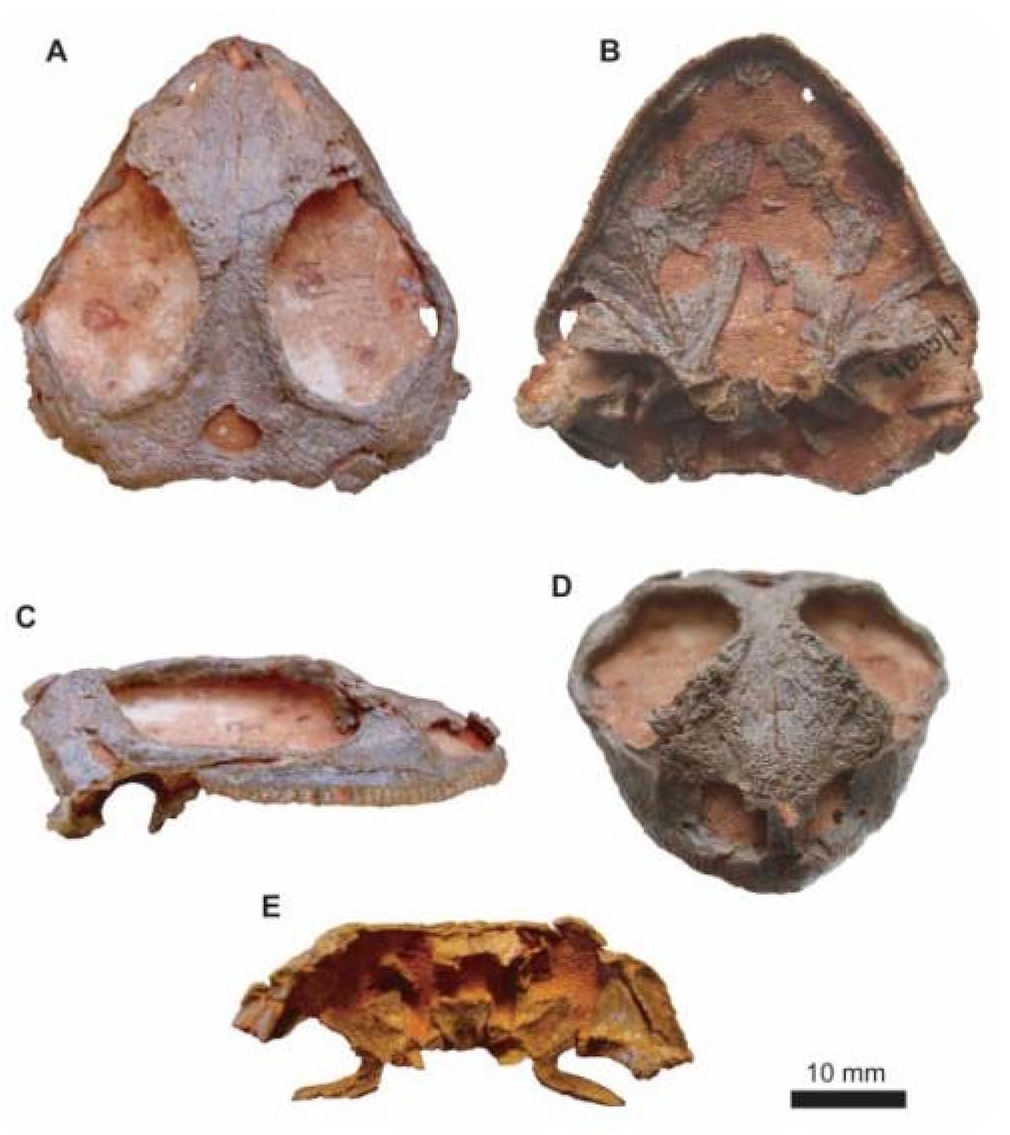
The Procolophonia were originally included as a suborder of the Order Cotylosauria or "stem reptiles". Other groups often included among the cotylosaurs were Diadectids, Captorhinids, and millerosaurs, although these were placed in different suborders. Pareiasaurs were placed with, and then separate from, the procolophonids. (Romer, 1966 Colbert, 1969, Kuhn, 1969, Carroll, 1988).

It is clear that all these and other small unspecialised Permian reptiles were similar in many ways, and that they constitute an evolutionary grade, based on shared features found in early reptile-like amphibians and primitive reptiles. In the 1980s and 90s, the introduction of cladistic methodology and emphasis on shared specialised features (Gauthier et al. 1988, Laurin and Reisz 1995, Lee 1995) demolished the Cotylosauria (and its short-lived synonym Captorhinida (Carroll 1988)) and replaced it with a number of distinct clades (evolutionary lineages), some of which are not even very closely related to each other (the diadectids for example are now consideredreptiliomorph amphibians [1]).

Evolutionary history

The Procolophonia appeared suddenly in the middle Permian, as the *nyctiphruretid* and nycteroleterids, evolving from basic millerettid or bolosaur like ancestors. From this primitive stock, both small Procolophonoids and giant pareiasaurs flourished during the Mid to Late Permian. Only the highly specialised procolophonids and the persistanly primitive owenettids survived to the Triassic, the former group being astonshingly successful for much of the period. They also are good candidates for turtle ancestors. One hypothesis is that turtles evolved from miniature pareiasaurs (Lee 1995), another that are related to owenettids (Reisz & Laurin 1991). However, the pareiasaur origin is now looking much less likely following the discovery of the aquatic turtle-ancestor *Odontochelys*). MAK, updated 120322.

Nyctiphruretus



A remarkably well preserved skull of *Nyctiphruretus acudens*, specimen number PIN 4659/1. A, dorsal; B, palatal; C, right lateral; D, anterior, and E, occipital views. Until 2010, no actual specimens of this species were illustrated or described in detail; hence they have the potential to offer much phylogenetic information. Photo from Säilä 2010b fig.1

Nyctiphruretus ("gardian of the night") is a small lizard-like animal from the middle Permian of Russia, at the time a warm equatorial region. Originally considered a primitive procolophonoid, it was interpreted cladistically as not a member of the Procolophonia, but of the Procolophonomorpha, the clade that includes all Procolophonia plus their immediate sister and stem taxa (Lee, 1995, Tsuji et al 2012). A recent monograph by Säilä (2010b) was the first to illustrate and briefly describe some of the best-preserved cranial specimens (the postcrania were not considered in that paper), the new information incorporated into two published data matrixes, The results confirmed that Nyctiphruretus is closely related to procolophonoids, pareiasaurs and Nycteroleterids, but interrelationships within this group remain unresolved. In that study *Nyctiphruretus* was recovered either as the sister taxon of all other procolophonia, or as the sister taxon of procolophonoids only, the first time the *Nyctiphruretus*-Procolophonoidea clade received support in a phylogenetic analysis. (Säilä 2010b). Although the former would seem to be the more popular cladistic option (Müller & Tsuji 2007, Tsuji et al 2012), making *Nyctiphruretus* a persistantly primitive "living fossil" continuing alongside its descendents, a *Nyctiphruretus*-Procolophonoidea clade makes more sense evolutionarily, as it would bridge the stratigraphic and morphological gap between Procolophonoidea and basal parareptiles, and allows two lines of very similar ancestral procolophonia, one evolving towards stocky spiny lizard like herbivores, the other to bulky megaherbivores. The close similarities between *Nyctiphruretus* and the nycteroleterids - (which together constitute the Nyctiphruretia - are simply due to the fact that neither taxon has diverged much from its common ancestor (this applies to either hypothesis in any case). The Nyctiphruretia would then, like other groups such as the rhyniacea, halkeriids, *Dendreperton*, podokesaurs, iguanodonts, and hyracotheres, represent an assemblage of morphologically very similar species. In each case, they constitute an ancestral (in cladistic jargon, a paraphyletic) evolutionary grade. As their descendents evolve, they branch out in different directions, each of the very similar species in each grade standing at the base of a different evolutionary lineage (monophyletic clade). More insights may be waiting to be revealed through the use of these additional methodologies; as yet no one for example has performed a stratocladistic analysis on these parareptiles for example. Given in any case the ambiguity regarding the exact placement of *Nyctiphruretus*, and the fact that interrelationships between other Parareptilian groups also remain poorly resolved (Säilä (2010b)), we have retained *Nyctiphruretus* as an unresolved basal procolophonian, representing along with the Nycteroleterids, a basal assemblage within the Procolophonia, transitional between Millerettids and Bolosaurs on the one hand, and more advanced procolophonioidea and pareiasaurs on the other, representing the evolutionary grade that gave rise equally to pareiasaurs and procolophonids. MAK120326

Notes:

[1] cladists of course do not recognise the term Amphibia

Descriptions

Procolophonia. Seeley 1888: defined as LCA Pareiasaurs + Procolophonoids or Pareiasaurs + turtles. A stem group definition (say, closer to *Procolophon* than *Bolosaurus*) would also include *Nyctiphruretus*

Range: fr Middle Permian.

Phylogeny: Procolophonomorpha **:** + Lanthanosuchoidea + (Bolosauridae + * **:** *Nyctiphruretus* + (Nycteroleteridae + Pareiasauridae) + Procolophonoidea.

Comment: In the most recent cladistic analysis (at the time of writing) of Tsuji et al 2012, if the node-based (or crown-group so to speak) using the LCA-based definition is used, then *Nyctiphruretus* is not a procolophonian. If a stem based definition is used, say, Procolophon > Bolosaurus, then it almost certainly is. We have followed the latter interpretation MAK120325

Nyctiphruretus acudens

illustration from Dinosauria A to Z

Nyctiphruretus acudens Efremov, 1938 (monotypal Nyctiphruretidae)

Range: Middle Permian of Russia;

Phylogeny: Procolophonia **:** (Nycteroleteridae + Pareiasauridae) + Procolophonoidea + *.

Horizon: Belebei-Mezen Cotylosaur Complex, Lower Tatarian (Roadian/Wordian)

Locality: Mezen River, Arkhangelsk Region, northern European Russia

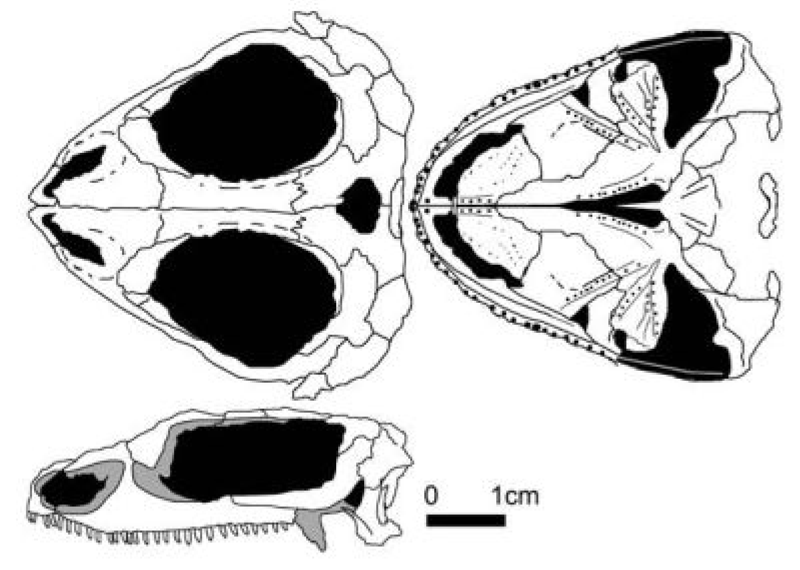
Length skull 4.4 cm; total length 36 cm

Characters: thickened, finely-sculptured prefrontal; pineal foramen at the posterior edge of the skull table (also found either convergently or as a synapomorphy that is later lost (a reversal) in bolosaurs). (Lee, 1997 p.203)

Comments: [1] *Nyctiphruretus* is a small insectivorous Procolophonomorph that has been found preserved in lake sediments. The name means "Guardian of the Night" (indicating perhaps that it is thought that these animals were nocturnal). These animals probably lived among the undergrowth in pond and lake margins, and filled the terrestrial small lizard niche. The diet consisted of invertebrates, and possibly also water plants. This is the most common animal known from the Mezen locality, amounting to over two-thirds of total number of specimens MAK

[2] Differs from the more related but more primitive *Lanthanosuchus* in having larger naris, orbit and pineal openings, less ornamentation and probably no lateral temporal fenestra on a greatly reduced postorbital area (David Peters)

[3] Originally considered an ancestral procolophonoidean and/or included with *Barasaurus* and *Owenetta* (Colbert, 1946; Romer, 1966, Ivachnenko et al 1979; Carroll, 1988), *Nyctiphruretus* shares no synapomorphies with the procolophonoids, and those similarities it does have are primitive



for Procolophonomorpha as a whole (Lee, 1995). Cladistic analysis by Lee 1995 and 1997 places *Nyctiphruretus* with the Nycteroleterids in the somewhat tentative new clade Nyctiphruretia, defined by three unambiguous traits (long external naris; maxilla broadly entering orbital margin; pineal foramen near or on parietal-postparietal suture) and four doubtful ones. More recent studies however show the Nyctiphruretia to be a paraphyletic or polyphyletic assemblage of basal procolophonia (Müller & Tsuji 2007, Säilä 2010b, Tsuji et al 2012). Or to be more precise, the Nyctiphruretia (*Nyctiphruretus* + nycteroleterids) appear, the ceratosauria to be a monophyletic clade when only few obvious synapomorphies are used, but more recent computaionally intensive statistical analysis shows both to be pseudomonophyletic ancestral taxon. For now, *Nyctiphruretus* resides as the only species in a monotypal family, although of course that could always change with new discoveries and analyses. MAK120326

Graphics image above left from Nyctiphruretus (in German); Drawing of skull © David Peters, used with permission, compare with photo

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Nycteroleteridae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--Nyctiphruretus
            |--+--Nycteroleteridae
            |   |--Macroleter
            |   |--+--Nycteroleter
            |   |   `--Emeroleter
            |   `--+--Rhipaeosaurus
            |      `--Pareiasauridae
            `--Procolophonoidea
               |?--TESTUDINES
               |--Owenettidae
               `--Procolophonidae
```

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4. Nycteroleteridae X
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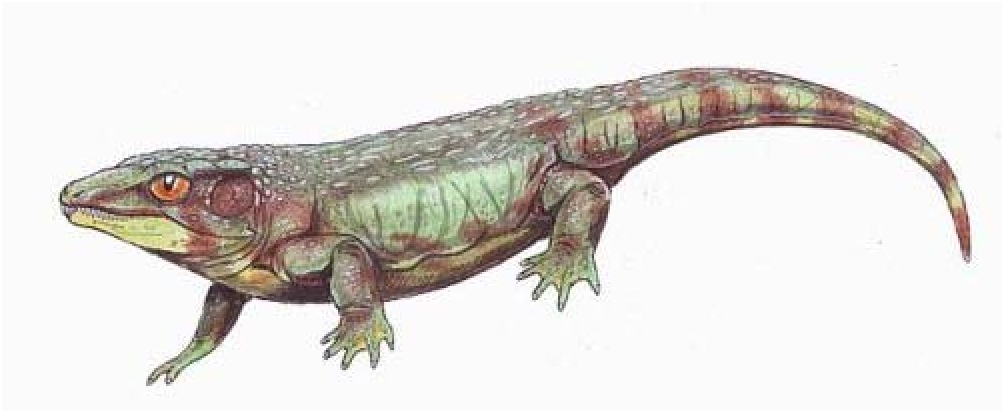

The stem-procolophonian *Macroleter poezicus* (= *Tokosaurus perforatus*), Middle Permian (Roadian/Wordian) of Russia. Like the contemporary *Nyctiphruretus*, this animal was of the type that was close to the common ancestor of procolophids and parieasaurs, although a little closer to the pareiasaur side of the family
Artwork by Dmitry Bogdanov, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

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Descriptions

Nycteroleteridae Romer, 1956 **:** *Bashkyroleter Emeroleter, Macroleter, Nycteroleter, Rhipaeosaurus*, and unnamed newly discovered specimen NM QR3061. (Cisneros & Tsuji 2009)

Range: Middle Permian of Oklahoma (Reisz and Laurin 2001), Russian Cis-Urals (Ivakhnenko et al. 1997, Tverdokhlebov et al 2005), and South Africa (Cisneros & Tsuji 2009)

Phylogeny:
Conventional (cladist): Procolophonia **:** *Nyctiphruretus* + Procolophonoidea + (Pareiasauridae + * **:** *Macroleter* + *Rhipaeosaurus* + (*Nycteroleter* + *Emeroleter*)
Gradist: Procolophonia **:** (*Nyctiphruretus* **:::** Procolophonoidea) + * **:** *Macroleter* + (*Nycteroleter* + *Emeroleter*) + (*Rhipaeosaurus* **:::** Pareiasauridae)

Characters: deeply-incised otic notch, the postparietals entering the pineal foramen, the skull ornamentation composed of regular circular pits, and the row of palatal teeth extending from the interpterygoid vacuity to the lateral margin of the choana. (Lee, 1997 p.203)

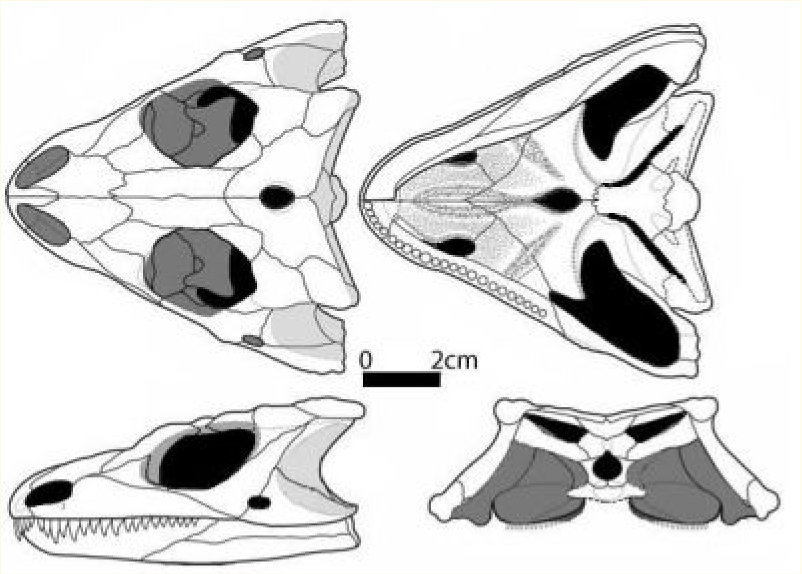
Comments: [1] Small-to medium sized parareptiles, combining procolophonoid and pareiasaurid features (Cisneros & Tsuji 2009). Using modern amniotes as analogues, Muller and Tsuji 2007 have argued that Nycteroleterids possessed efficient impedance-matching hearing, suggesting ecological adaptations to dim-light environments. These animals were particularly common and diverse in subtropical CisUral Russia.

[2] Recently a nycteroleter has been found in the Middle Permian *Tapinocephalus* Assemblage Zone of South Africa, the first record of the family from Gondwana (Cisneros & Tsuji 2009)

[3] Nycteroleterids have variously been described as procolonophoidean reptiles Colbert, 1946; Romer, 1966, Holmes, 1984 and seymouriamorph amphibians (e.g. Heaton, 1980; Milner, 1993). Lee 1995 suggests the amphibians interpretation is due to these animals being reconstructed with an intertemporal, posteriorly-located jaw articulation, and a slit-like, dorsally-located (i.e. ‘amphibian’) otic notch when they lack these features, and in any case the otic notch, often considered a phylogenetically important feature, has appeared and disappeared repeatedly in tetrapods. Cladistic analysis by Lee 1995 and 1997 instead placed Nycteroleterids with *Nyctiphruretus* in the new taxon Nyctiphruretia as the sister clade to the both pareiasaurs and procolophonids. More recent studies do not support a monophyletic Nyctiphruretia (Müller & Tsuji 2007, Säilä 2010b). Reisz & Scott 2002 place the basal Nycteroleterid *Macroleter* as sister taxon of pareiasauridae + procolophonoidea. Muller and Tsuji 2007 found that, apart from *Nyctiphruretus*, all non-pareiasaurian parareptiles from the Mezen River Basin formed a monophyletic group, which they informally termed the 'nycteroleters,' that was either sister group to the Procolophonia or else sister group to the Pareiasauridae within the Procolophonoidea. Tsuji & Müller 2009, Lyson et al 2010 put the nycteroleterids closer to pareiasaurs. Tsuji et al 2012 using both parsimony and Bayesian inference recovered a monophyletic nycteroleter clade using parsimony, whereas they found the group to be paraphyletic with Bayesian inference). It's interesting to consider that tree toplogy and the relationship of *Archaeopteryx* to deinonychosaurs on the one hand and birds on the other likewise various according to methodology used. MAK120324

Links Vyatka Palaeontological Museum MAK120322

Macroleter poezicus **Tverdokhlebova and Ivakhnenko 1984 =** ***Tokosaurus perforatus*** Tverdochlebova & Ivachnenko, 1984



Range: Middle Permian of Russia;

Phylogeny: Nycteroleteridae **:** *Rhipaeosaurus* + (*Nycteroleter* + *Emeroleter*) + *

Horizon: Belebey Svita, Upper Kazanian (Roadian/Wordian)

Size: ~8 cm skull length, ~75 cm overall length

Comments: *Tokosaurus* was a small common, insectivorous amphibious animal. As with *Nycteroleter*, to which it might be related, there is disagreement over whether this lizard-like animal was a reptile-like amphibian or a primitive reptile. It was also placed in its own family, the Tokosauridae. Recently, Tsuji et al 2012 have shown that *Tokosaurus perforatus* say that it is a junior synonym of *Macroleter poezicus*, and the most basal member of the Nycteroleteridae. MAK

References: V.P. Tverdokhlebov *et. al.* 2005

Graphics Skull of *Macroleter poezicus* (= *Tokosaurus perforatus*) © David Peters, used with permission

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Nycteroleter ineptus Efremov, 1938

Range: Middle Permian of Russia;

Phylogeny: Nycteroleteridae **:** *Macroleter* + *Rhipaeosaurus* + (*Emeroleter* + *)

Horizon: Belebei-Mezen Cotylosaur Complex, Lower Tatarian (Roadian/Wordian)

Locality: Mezen River, Arkhangelsk Region, northern European Russia

Comments: *Nycteroleter* was a small insectivorous, lizard-like animal, found at the same locality as *Nyctiphruretus*, and traditionally included in the same family. Although similar in form and, perhaps, environment and lifestyle, it differs regarding details of the rear of the skull. For example, *Nycteroleter* has a deep otic notch and tabulars extending back, these being primitive amphibian features. For this reason it has been suggested that *Nycteroleter* is actually a reptile-like amphibian, perhaps, like *Seymouria*, indistinguishable from a true reptile in life. Most authorities however still consider *Nycteroleter* a primitive reptile (anapsid/parareptile). For some time there was no consensus regarding the status of *Nycteroleter* and related members of its family, so this question must remain unresolved until further fossils come to light that might clarify the issue. Recent cladistic analyses however revealed it to be a primitive procolophonian, related to parieasaurs Tsuji & Müller 2009,

References: Olson, 1962

Graphics image above right from Nyctiphruretus (in German); Drawing of skull © David Peters, used with permission

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Emeroleter levis

Ivachnenko 1997

Range: Severondvinskian Gorizont, Upper Capitanian, (Latest Middle Permian) Kotel'nich locality in central Russia

Phylogeny: Anapsida : Millerettidae + Mesosauridae + (Bolosauridae + (Procolophonia + *).

Horizon: Late Kazanian to Early Tatarian) Mezen River Basin, Central Russia.

Characters long quadratojugal with posterior portion curving dorsally into a pointed projection. (Tsuji et al 2012)

Comments: this long-legged and slender cousin of *Nycteroleter* lived later in the middle Permian and was a contemporary of the pareiasaur *Deltavjatia vjatkensis*. Previously known only from isolated crania, recent excavations have recovered well-preserved postcrania, allowing a complete redescription. The skull of Emeroleter is typified by dermal sculpturing of evenly spaced small, round pits and supratemporals that extend posterolaterally into broad horns. The limbs are very gracile with a long, sigmoid femur, and slender carpal and tarsal elements (Tsuji et al 2012) The tail, although incomplete, appears to be short and gracile. The manual and pedal proportions were close to those found in *Owenetta*. The short terminal phalanges indicate a terrestrial, rather than an arboreal niche was selected, despite the extremely long limbs (David Peters). Quite likely this was a fast sprinting form

Known at first from an incomplete skull (there are few finds of isolated upper jaw bones), a fragment of a skull, and then two complete skeletons, found by the collaborators of Kotelnich Palaeontological Museum in 1998. Both skeletons were found in a bent position. One of them belonged to a small animal, probably a juvenile; the second specimen being larger. They were found together, about 10 cm apart. Both were curled up with the skull directed towards the tail and hind limbs, possibly indicating they lived in burrows; the close proximitity indicates they perished together. (Vyatka Palaeontological Museum)

Graphics Photograph of *Emeroleter levis* © Albert Khlyupin and Vyatka Palaeontological Museum - original page (Parareptilia), used with permission.

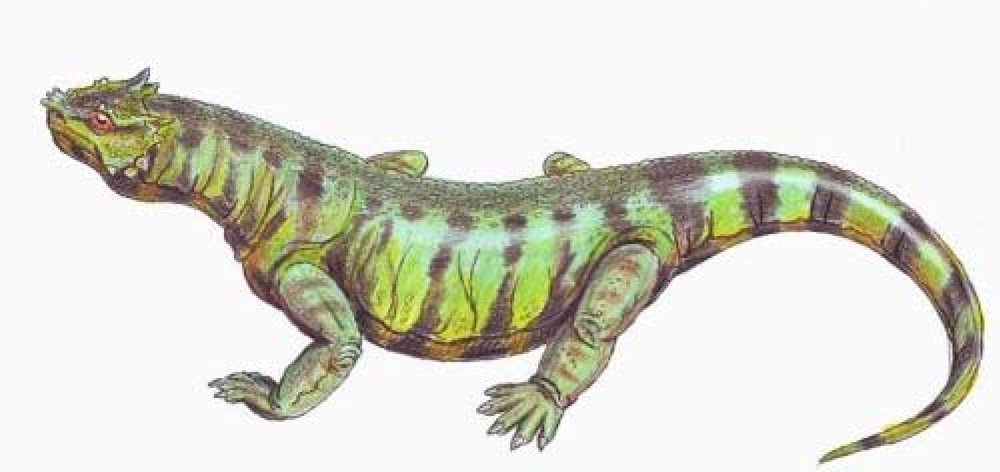
Link Palaeocritti, Vyatka Palaeontological Museum,

Graphic Skeletal reconstruction © David Peters (skeletal reconstruction)

Rhipaeosaurus tricuspidens Efremov, 1940 (monotypal Rhipaeosauridae)

Range: Middle Permian of Russia;

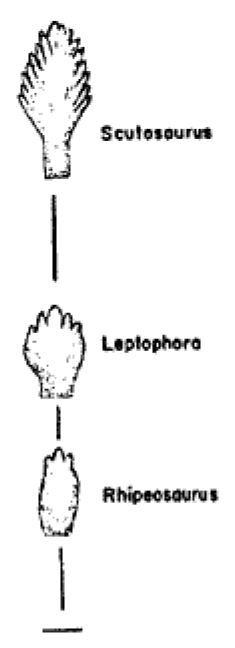
Phylogeny: Conventional (cladist):



Nycteroleteridae : *Macroleter* + (*Nycteroleter* + *Emeroleter*) + *
Gradist: Nycteroleteridae : *Macroleter* + (*Nycteroleter* + *Emeroleter*) + (Pareiasauridae + *)

Horizon: Belebey, Bashkortostan, Russia (latest Kazanian)

Comments: known from an articulated skeleton, *Rhipaeosaurus* is intermediate in size between small lizard-like procolonomorphs and pareiasaurs, as well as preceeding the latter and stratigraphically. It was considered a pareiasaur relative by Chudinov 1955, and 1957, who referred to the weakly tricuspid teeth as ancestral to the leaflike multicuspid teeth of pareiasaurs. (right, from Olson 1962 (I think, needs confirmation))



Rhipaeosaurus tricuspidens became the type species of the family Rhipaeosauridae, to which a number of Middle Permian forms were assigned, although these were mostly on the basis of very fragmentary remains. Rhipaeosauridae was then placed with the Pareiasauridae in the Superfamily Pareiasauroidea (Chudinov, 1957; Kuhn, 1969) or Suborder Pareiasauria (Ivachnenko, 1987 or Pareiasauroidea Carroll, 1988). (Pareiasauroidea is used in a totally different context by Lee 1995)

As it turned out, all the Rhipaeosaurids, except for *Rhipaeosaurus*, were not Rhipaeosaurids. *Parabradysaurus* is now known to be a dinocephalian therapsid (specifically an estemmenosuchid, albeit the earliest known member of the group), and *Rhipaeosaurus talonophorus* and *Leptoropha novojilovi* have since been identified as a Seymouriamorph amphibian. With only *Rhipaeosaurus tricuspidens* remaining, Rhipaeosauridae is now a monotypal taxon, and a member of the Nycteroleteridae (Lee, 1995).

Although cladistic analysis places *Rhipaeosaurus* in a fairly basal or even more derived (Tsuji et al 2012) position in a monophyletic Nycteroleteridae, it is also very likely that Nycteroleterids are a paraphyletic assemblage that include the ancestors of pareiasaurs. MAK120325

Graphic *Rhipaeosaurus tricuspidens*, life reconstruction by Dmitry Bogdanov - Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Link Palaeocritti

Pareiasauridae (Hallucicrania)

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--Millerettidae
   |--Mesosauridae
   `--+--Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |  `--Pareiasauridae (=
Hallucicrania)
            |       |--Bradysaurs
            |       `--Velosauria
            `--Procolophonoidea
               |--Owenettidae
               |    `?--TESTUDINES
               `--Procolophonidae
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The Pareiasaurs

Editor's note: much of the following has been copied as is from kheper net and needs to be integrated more with the Paleos com format. There may also be some overlap in the following text, some of which has been incorporated and doubtless improved by ATW. A small amount of new material has been added. MAK120323

Scutosaurus portrait from Russian Dinosaur Exposition

The Pareiasaurs were large late Permian herbivores. They were heavy ungainly animals, frequently the size of an ox, with capacious bodies, strong limbs, broad feet, and thick solid skulls ornamented with bizarre knobs and ridges. They were armoured with bony scutes or osteoderms set in the skin, The largest types were 3 metres long and about 1 1/2 meters tall, with weights exceeding a tonne.

The leaf-shaped multi-cusped teeth (left) resembled those of iguanas, caesids, and other reptilian herbivores. This dentition, together with the deep capacious body (which obviously housed an extensive digestive tract) are proof that these fearsome-looking animals were in reality inoffensive herbivores.

Pareiasaurs appear very suddenly in the fossil record. It is clear that these animals evolved from Nycteroleterids, perhaps a Rhipaeosaur-like form to fill the large herbivore niche (or guild) that had been occupied early in the Permian period by the Caesid pelycosaurs and before then the Diadectid amphibians and Edaphosaur reptiles. They are much larger than the diadectids, more similar to the giant caseid pelycosaur *Cotylorhynchus* (Colbert 1965 p.52). In fact it may well have been the extinction of the Caesids created an ecological vacuum that enabled the Pareiasaurs to appear and suddenly diversify as rapidly as they did (within the span of only two million years). Although the last Pareiasaurs were no larger than the first types (indeed, many of the last ones became smaller), there was a definite tendency towards increase of armour as the group developed.

It has been often suggested that these animals were semi-aquatic. Skeletons have been found in a standing position, indicating that the animals became mired in the mud and swamps while feeding on vegetation. Their remains are also consistently found in channel stream deposits (riverbeds). Of course, this does no mean that they were semi-aquatic; and actually the fact that the animals became stuck argues *against* aquatic adaptations (a semi-aquatic animal would not likely become stuck, whereas a terrestrial animal would; e.g. the remains of sauropod dinosaurs, which were as terrestrial as elephants, are sometimes found in this position). A more plausible explanation is that these were fully terrestrial animals that frequented watercourses in order to get at the succulent aquatic vegetation.

It has been argued that Pareiasaurs may have evolved into turtles. They had turtle-like skull features, and several genera had bony plates in the skin, possibly the first signs of a turtle shell. However, the case for turtle ancestry is not proven.

Recent reports of a slender stapes (a sound-conducting middle ear ossicle) indicate that pareiasaurs had an efficient ear drum (tympanum) and were able to hear high frequency airborne sounds. MAK000124

References: Benton 2000, 2005, Carroll, 1988 p.205; Colbert19651965 pp.52-3; Fenton & Fenton 1958 p.306; Kuhn, 1969, Laurin, 1996 , Zittel & Eastman 1932 , pp.241-243

Number of Species and Genera

Remains of Pareiasaurs are quite common in the Lower Beaufort Series of South Africa, and a great many generic and specific names were originally proposed. It would be very unlikely that such a large number of similar species would co-exist in the same time and space, and it is now recognised that many of these different types are actually the result of individual variation, growth stages, geological deformation of fossils, etc. Now no more than five genera are recognised from South Africa, four from Russia, two from Europe and one from China. MAK000124 Because of the influence of current cladistic nomenclature there is a tendency now toawards monotypal genera (i.e. allowing each genus only a single species); we have resisted this in favour of consistency with non-paleoherpetological and non-vertebrate paleontological taxonomy MAK120329

Descriptions

Pareiasauridae Lydekker 1889 = Pareiasauridae Cope, 1896 (= Pareiasauria, Hallucicrania) **:** Herbivorous anapsids, some very large (up to 3m).

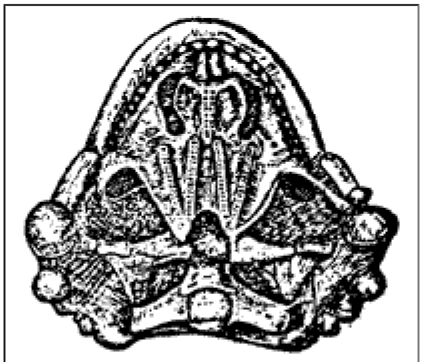
Range: Middle to Late Permian of Africa, Europe, Russia, Sth Am, & China.

Phylogeny: Procolophonia **:** *Nyctiphruretus* + (Procolophonoidea + (Nycteroleteridae + * **:** *Bradysaurus* + Velosauria.))

The beautifully preserved complete remains of the intermediate-grade Russian pareiasaur *Deltavjatia vjatkensis*. In life this animal would have had a posture very similar to the closely related South African genus *Bradysaurus* (see mounted skeleton, below). And as with the *Bradysaurus*, a large number of complete skeletons of these animals have been found in association; the exact causes of for these mass-mortality asemblages is still not clear. Image © Albert Khlyupin and the Vyatka Palaeontological Museum, used with permission.

Characters: Short, laterally expanded skull, short, foliate teeth; probably herbivorous; palate strongly integrated with braincase; **$** palate raised above level of tooth row; transverse process of pterygoid bears marginal teeth; **$** the transverse process is at 45 deg. to the midline (rather than 90) and curved ventrally; interpterygoid vacuities closed; choanae not parallel with maxilla; jaw articulation well anterior to occipital condyle; **$** lacrimal excluded from narial margin (unclear if this is correct, much less synapomorphic); **$** frontal excluded from orbit & in contact with post-frontal; tendency to form flat dorsal surface to head, with orbits on sides & some fusion of dorsal dermal bones; post-parietals fused; supratemporal with large boss; strange, "melted" rugose dorsal cranial surface with projections downward from lower jaw and laterally projecting quadratojugal; **$** < 21 presacral vertebrae; caudal vertebrae not posteriorly bent; gastralia absent; deep body with strong ribs; extremely long scapula with long, blade-like acromion process; stocky limbs, with epipodials relatively vertical and facing forward; metapodials wider than long(!); pelvis mammal-like, with ilium dorsoventrally elongated, and short, retroverted pubis & ischium; dorsal buttress over acetabulum; extensive body osteoderms (dermal scutes) in some species.

Further Systematic Description: The skull is short, broad (laterally expanded), massive, and strongly sculptured and knobby. The sutures are not clearly distinguishable. The quadratojugals (cheekbones) project laterally downwards (almost like the hanging "jowls" on a cartoon bulldog-type character). The orbits (eye sockets) are relatively small, and laterally (side of the head) placed. There is an opening for the pineal body ("third eye", use to regulate metabolism in the case of seasonal extremes). the brain-case is long and low, the ear-cavity separated by bone from the brain cavity. The tabular and post-parietal bones of the skull are on the dorsal (upper) surface only. The jaw articulation is well forward of the occipital condyle (the connection between the skull and vertebra), increasing the mechanical efficiency of the jaw musculature while decreasing the gape.



Pareiasaurus palate from Kuhn 1969

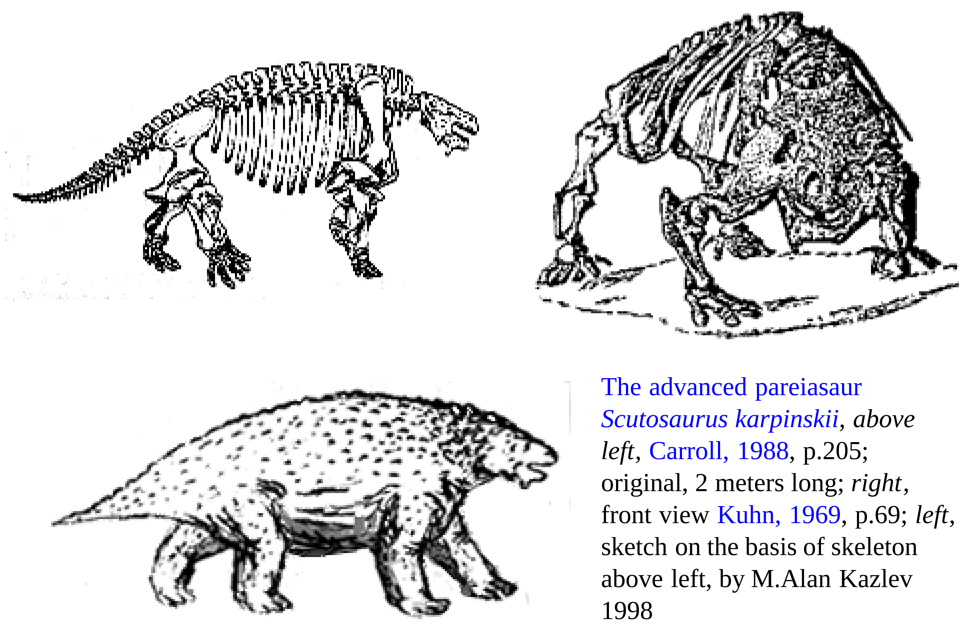
The palate (*left*) strongly integrated with the base of the braincase and the skull margins. The bones of the palate are fused, and bear several series of small teeth. The teeth are conical with leaf-shaped crowns. Those on the margins of the jaws area arranged in a close regular series.

There are about eighteen presacral (neck and trunk) vertebrae, each with deep articulation for the ribs, and generally four sacral vertebrae. The sacral vertebrae are unfused (an inefficient arrangement). There are thirty caudal (tail) vertebrae with the anterior ones bearing short ribs. Generally the tail is quite short.

The pelvic bones are massive and ossified. The scapula is much longer than in other primitive tetrapods, and the pelvis has an almost mammalian configuration. This may have helped accommodate muscles that moved the rear limb in a manner similar to the fore and aft gait of mammals.

The humerus is short, massive, and expanded at the ends; the ulna very stout. The hind limbs are slightly shorter than the fore-limbs. The stocky limbs are held close to the body to support the weight. Both fore and hind feet have five digits, which are equipped with broad claws. MAK000124

Discussion: It is easy to lose track of the main points in the wealth of detail about pareiasaurs poured out in recent years. Whether or not Permian pareiasaurs gave rise to turtles, were a sister group of turtles, or would sooner shoot their sister than be related to a turtle, they were not turtles. Neither were they simply aberrant lizards or Paleozoic proto-bovines or terrestrial placodonts. They were, from all appearances, rather unique products of the late Paleozoic radiation of amniotes. In common with other lost branches of early radiations, they show a mosaic of characteristics and show some similarity to all of the above.



The advanced pareiasaur *Scutosaurus karpinskii*, *above left*, Carroll, 1988, p.205; original, 2 meters long; *right*, front view Kuhn, 1969, p.69; *left*, sketch on the basis of skeleton above left, by M.Alan Kazlev 1998

Let us, for a moment, forget both Cenozoic models and cladistics and look at them for what they were as animals. They had a short, blunt jaw. The skull was generally boxy, particularly by Paleozoic standards. Likely this was a function of jaw specializations. These herbivores needed big mouths, since vegetation is relatively nutrient poor. They had also developed a short jaw and deep skull in order both lengthen the jaw muscles and to get a more vertical angle on the lower jaw with bigger muscle mass. The pareiasaurs also developed some dental specializations: nothing fancy, just flattened, foliate teeth along the jaw while retaining palatal teeth. The pterygoid had to assume a new and more complex shape as a result of the other changes. The palate as a whole became more tightly integrated with the skull, and this consolidation and buttressing is even reflected in a tendency to fuse some of the dermal skull elements, particularly near the midline and at the "new" breakline where the top of the skull curved down to form the sides.

In life, the skull might not have reflected these changes on casual inspection because the posterior dorsal elements are flared out and ornamented with lumps, horns, bosses, and a remarkable variety of other motifs for protection, display, solar panels or something completely unknown. It also seems rational to suppose that, like many herbivores, they possessed cheeks and, given the large flare, potentially *enormous* cheeks. As a result, the possible functions of the laterally expanded skull might relate to volume as well as just dorsal area. By way of speculative example, one might consider: fat storage, an elaborate salivary digestive system, mechanisms for hearing or sound production, or the oral equivalent of a gizzard. By way of analogy, pelecaniforms also use large gular pouches for feeding young and in cooling behaviors, both entirely plausible behaviors for pareiasaurs. None of these are, of course, supported by a shred of evidence. They are listed solely to suggest that conventional models based on living creatures may be inadequate.

The primitive pareiasaur *Bradysaurus baini* - reconstructed skeleton, from the Museum of Natural History in Berlin (Museum für Naturkunde) Photo by Masur, Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

The limb structure of pareiasaurs is also a peculiar mosaic. The limb girdles have been elongated. Undoubtedly one reason for this was simply to allow the enormous gut to clear the ground. However, most extant animals solve this problem by lengthening the limbs themselves. Pareiasurs had elongated limb girdles, but relatively short, squat limbs. Much has been made of the mammal-like shape of the pelvis, but the comparison may be over-played. An organism with this general shape *cannot* move effectively using only lateral undulations like a lizard or a salamander. It follows that the limbs, however locomotion is accomplished, have to translate their force along the central axis. Thus, selection will necessarily favor a rigid body and limb girdles that act, as much as possible, by exerting force on the vertebral column. Hence, the scapula is very long and think, the ribs are stout, the vertebral number is reduced, the pelvis is slanted forward and the iliac crest lies parallel with the vertebral column, the tail (no longer much connected with locomotion) is short and wide. The limbs themselves are still perhaps closer to *Ichthyostega* than to mammals or dinosaurs. The epipodialia are not as short as some illustrations make out, but the metapodia certainly are. Perhaps the length of the girdle elements was designed precisely to prevent and dampen torsion while making the most of the relatively small vertical motions possible with a lizard-like leg structure. By contrast, the feet are surprising. The astragalus has overgrown the calcaneum to such an extent that there is essentially only one tarsal, and the digits have a strangely dinosaurian look to them. These are not exactly long-distance runners, but not just outdoor furniture, either.

In short, Pareiasaurs make sense, but on their own terms. We might imagine a specimen of medium-large size, under 2m long and perhaps 200kg, as a moderately selective low browser. It moves slowly about in rolling, fairly open country, working steadily away at a huge mouthfuls of leaves, occasionally shaking its head in an odd fashion to redistribute the load and clear away insects. Its head looks far larger than its skull would suggest, inflated by pendulous cheeks. It bears an irregular, patchy pattern of scutes on its broad back and sides, with smaller elements on its limbs. Skin and scutes are of contrasting earth tones, breaking up its outline in the brush and tall ferns.

Had they survived the end-Permian extinction better, they might have competed well with Ornithiscian dinosaurs or even mammals. Perhaps they did survive -- as turtles. Whatever the case, pareiasaurs are best understood as a group unto themselves, rather than an early model of anything that walks today.

Note: This taxon has been one of the battlegrounds of one of the more interesting taxonomic battles of recent years, with the respective forces led by (among others) MSY Lee (turtles are Pareiasaur sisters) and Olivier Rieppel (turtles are part of a third major diapsid lineage) These Notes follow the more orthodox path, with some serious doubts expressed elsewhere. ATW030308

Links: Introduction to Pareiasauria, Pareiasauria: More on Morphology; dinosaurs- scutosaurus karpinski; Phylogeny and Classification of Amniotes; Turtle Origins; South African Museum - Fossil Reptiles of the South African Karoo; PANGEA (Italian); pareiasaur; Provelosaurus; Provelosaurus reconstruction; animals. ATW030308

Some associated clades:

Hallucicrania Lee 1995. The clade Hallucicrania was coined by MSY Lee, for Lanthanosuchidae + (Pareiasauridae + Testudines) (see links: Tree of Life Phylogeny and Classification of Amniotes and Hallucicrania [Pareiasauriformes] after Lee, 1993, 1996 and 1997 ...). Lee's pareiasaur hypothesis is looking rather less likely following the discovery of *Odontochelys*, a transitional aquatic turtle with very non-pareiasaur-like teeth and whose half shell matches embryonic development in modern testudines (an intriguing case of Haeckel's ontogeny recapitulates phylogeny). From another angle, recent cladistic analyses reveal Lanthanosuchids to have a much more basal position in the Procolophonomorpha , and that the nearest sister taxon to the pareiasaurs are the rather unexceptional and conventional looking Nycteroleterids (Müller & Tsuji 2007, Lyson et al 2010) the two being united in the clade Pareiasauromorpha (Tsuji et al 2012). The weird dermal sculpturing in both pareiasaurs and lanthanosuchids, that inspired Lee to coin such a wonderful name, is therefore the result of convergence. It would be a real shame though to discard such a wonderful name as Hallucicrania. For now at least we're keeping it as a synonym for Pareiasauria. ATW030402 updated and expanded MAK120323.

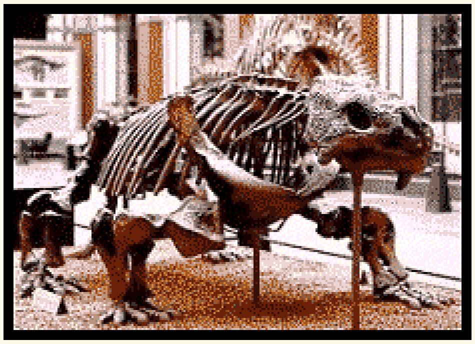
Pareiasauroidea Nopsca, 1928. The clade Pareiasauroidea (as opposed to the superfamily or suborder Pareiasauroidea) was used by Lee 1995 for Pareiasauridae + *Sclerosaurus*. More recent cladistic studies place *Sclerosaurus* in the procolophonid family Leptopleuroninae (Cisneros 2006, Sues & Reisz 2008) which means the similarities with pareiasaurs are the result of convergences

Pareiasauria Seeley, 1988. If neither Lanthanosuchids or Testudines are included in the clade, the Pareiasauria only contains the monophyletic family Pareiasauridae. There seems little reason to use Seeley's ordinal-style name. For this reason we have reverted to the traditional linnaean term. MAK120323.

References: deBraga & Rieppel (1997); Lee (1997).

Links: Introduction to Pareiasauria; South African Museum - Fossil Reptiles of the South African Karoo final run.PM6; E V (Dutch -- excellent materials); cordados répteis primitivos (Spanish); Turtle Origins; PANGEA (Italian). ATW030308. Palaeocritti - Pareiasauria (brief but useful coverage of every species) MAK120401

Bradysaurs: Watson 1914 (monotypal Subfamily Bradysaurinae Huene 1948)



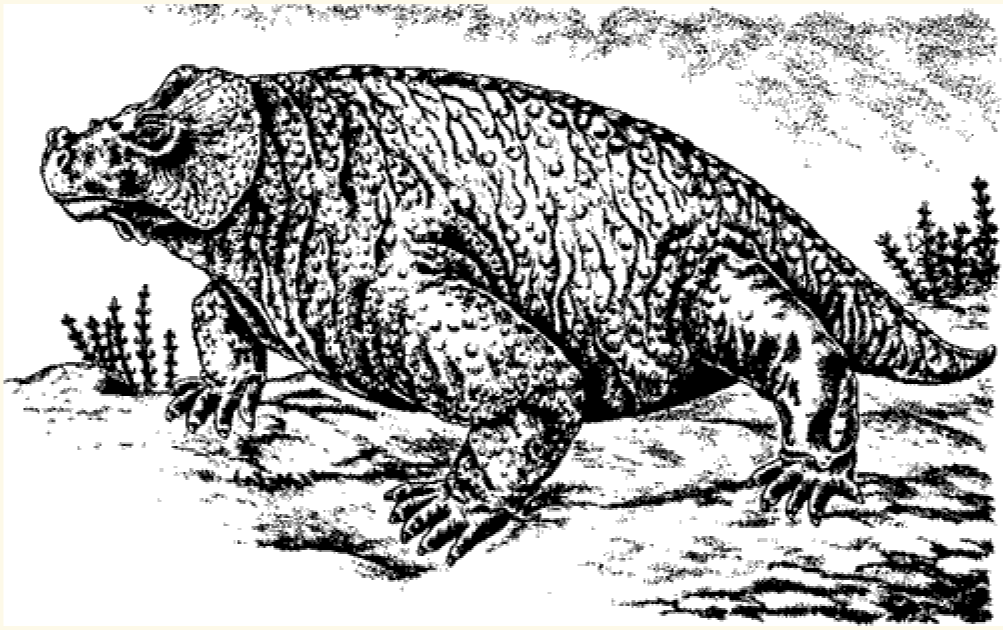
Synonyms: *Brachypareia*, *Bradysuchus*, *Koalemasaurus*, *Platyoropha*

Stratigraphic range: Lower to Upper Tapinocephalus zone, Lower Beaufort Beds, of the Karoo basin, South Africa; most common in the Lower Tapinocephalus zone (Lower to Middle Tapinocephalus zone in Boonstra, 1969 pp26, 32,; Lower Tapinocephalus to Pristerognathus (= old Upper Tapinocephalus) zone in Ward et al 2005, supplem. info, range data; both = Capitanian age)

Phylogeny: Pareiasauridae **:** Velosauria + *.

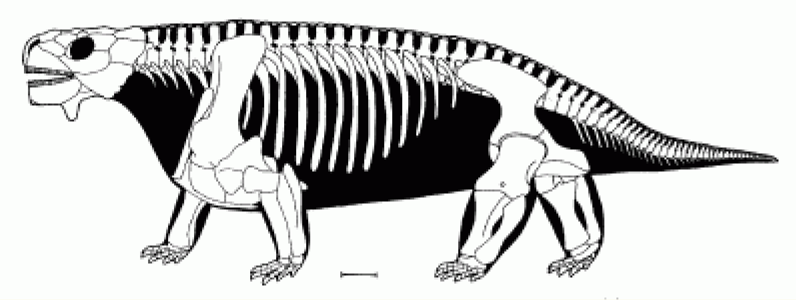
Characters: single row of vertebral scutes

Size length about 2.5 meters long, weight about half a tonne to a tonne (Fenton & Fenton 1958 p.306; Colbert 1965 p.52).



Comments: Despite its large size, *Bradysaurus* is actually the most primitive known genus of Pareiasaur. The Bradysaurs can be considered the ancestral type from which the others developed, even if it lived at the same time as one or two other genera. It can be assumed that *Bradysaurus* evolved somewhat earlier in time, during the Wordian epoch (Eodicynodon zone). Fossils are rare in the Eodicynodon zone, which may explain its absence.

The skull is large, broad, flattened, and rounded at the front. The skull-bones are coarsely sculptured and knobby, the sutures between them not clearly visible. The marginal teeth are high-crowned with only a few cusps, this being a primitive characteristic. The cusps consist of a terminal group of three cusps, the anterior with one to three and the posterior two to three cusps.



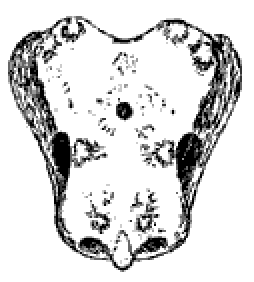
The phalangeal count is 2,3,3,3,2 on the fore-foot and 2,3,3,4,3 on the hind. The whole body is covered in thin dermal scutes, which are quite smooth over the back. The armour is not as heavily developed as in later forms.

The top of the ilium is vaulted. There are 5 cervical, 15 dorsal, 4 sacral, and about 39 tail vertebrae.

Kuhn lists no less than nine species for this genus, but this is certainly an excessive number. Boonstra distinguishes only four species on the basis of tooth structure, two of which Kuhn places in the genus *Embrithosaurus.* I have decided to take the more cautious position and only have two species in this genus. MAK000124

With the genus *Bradysaurus*, this clade contains only *B. seelyi*. Lee (1997) argues that the only available material from other putative species of this genus, *B. baini*, lacks any distinguishing autapomorphies. However, *B. seelyi* is closely related to *Nochelesaurus* and *Embrithosaurus* and they are treated here as a paraphyletic stem group of all primitive pareiasaurs except *Deltavjatia*. ATW

Graphics Skeletal reconstruction from Lee 1997, life reconstruction from Fenton & Fenton 1958 p.306



Bradysaurus baini (Seeley 1892)

Synonyms: Pareiasaurus baini Seeley, 1892, Platyoropha broomi Haughton & Boonstra, 1929, Bradysaurus broomi (Haughton & Boonstra, 1929)

Stratigraphic range: Tapinocephalus zone (Capitanian), Lower Beaufort Beds, Karoo basin, South Africa

Comments: This is the type species for the genus. The quadrajugal region (cheek-bones) are only moderately developed. The snout is broad and rounded. There are 15 or 16 pairs of overlapping teeth in each jaw. The genera *Brachypareia*, *Bradysuchus*, *Koalemasaurus*, *Platyoropha* would also seem to belong here. *Platyoropha* and *Brachypareia* are indistinguishable from *Bradysaurus*, and *Brachypareia* based on apparently immature specimens (Boonstra, 1969 p.30), although *Brachypareia watsoni* is now considered a synonym of *Embrithosaurus angustus*, *Bradysuchus*, is based on a pathological feature. The skull illustrated is 42 cm long MAK000124

Tsuji & Müller 2009 in their unpublished analysis make this the most basal species of pareiasaur MAK120325

Graphics illustration of skull from Kuhn 1969

Bradysaurus seeleyi Haughton and Boonstra 1929

Synonyms: *Bradysaurus vanderbyli* Haughton & Boonstra, 1929

Stratigraphic range: Tapinocephalus zone, Lower Beaufort Beds, South Africa

Characters: - Lee 1997

Comments: Boonstra considered this a valid species of *Bradysaurus*. The cheekbones are greatly enlarged and heavy. There are 19 or 20 pairs of strongly overlapping teeth on each jaw. This species clearly was not as common as *B. baini*. Length of specimen at left 44 cm MAK000124

According to Lee 1997 this is a "metaspecies" and lacks unique characteristics that can be used in phylogenetic analysis. Tsuji & Müller 2009 in their unpublished analysis place it between *B. baini* and as the most basal species of pareiasaur MAK120325

Links: Introduction to Pareiasauria; The first Karoo Reptiles and their origin; Victoria west; Paleontology and Geology Glossary- Br; Bradysaurus (German); Bradysaurus (skull photos); museum für naturkunde berlin-bradysaurus baini; UCMP Mystery Fossil Number 13; South African Museum - Fossil Reptiles of the South African Karoo; South African Museum - Trace Fossils of the Ancient Karoo; ALBANY MUSEUM - KAROO FOSSILS (view the *Tapinocephalus* Zone landscape); Bradysaurus. ATW031009.

Graphics illustration of skull from Kuhn 1969

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Anapsida: Pareiasauridae (2)

Velosauria

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--Millerettidae
   |--Mesosauridae
   `--+--Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            |      |==Bradysaurus
            |      `--Velosauria
            |          |--Embrithosaurus 
alexanderi
            |          `--+--Embrithosaurus 
schwarzi
            |             `--+--Deltavjatia
            |                `---+==Pareiasaurus
            |                    `--+-
-Scutosaurus
            |                        `--+-
-Elginia
            |                            `-
-Pumiliopareiasauria
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

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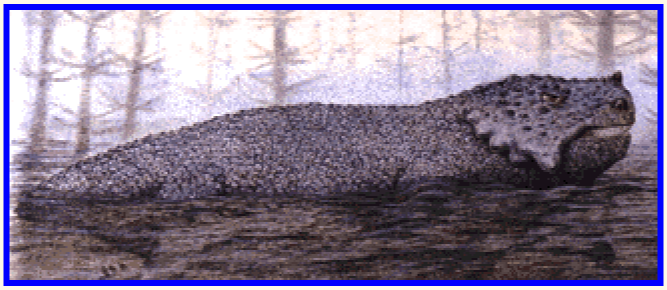
2. *Embrithosaurus* X
3. *Embrithosaurus alexanderi* (= *Nochelesaurus*) X
4. *Embrithosaurus schwarzi* X
5. Velosauria X

Descriptions



Velosauria : *Anthodon, Deltavjatia, Pareiasuchus, Scutosaurus*. Typical pareiasaurs.

Range: Middle to Late Permian

Phylogeny: Pareiasauridae **:** *Bradysaurus* + * **:** *Embrithosaurus* + (*Deltavjatia* + ((*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + Pumiliopareiasauria))))

Characters: **$** 12 or more cusps on teeth of lower jaw; **$** parallel, closely spaced rows of palatal teeth; **$** parasphenoid greatly shortened; large, U-shaped interpterygoid vacuity; **$** <20 caudal vertebrae; cleithrum absent; **$** greater trochanter present and deflected (?) from femoral head; **$** bony dermal armor, with large osteoderms; **$** armor covers entire dorsal surface, united over shoulder and pelvis; **$** conical studs over appendages.

References: deBraga & Rieppel (1997); Lee (1997). ATW020924

Links: Introduction to Pareiasauria; Parareptilia; Scutosaurus karpinski.

Images: *Scutosaurus karpinskii* © mathematical.com, used with permission. ATW020924. revised MAK120331

Comments: **(1)** Includes the Subfamily Pareiasaurinae Nopcsa 1923. Oskar Kuhn (*Cotylosauria,* p.75) includes the following genera here: Pareiasaurus, Pareiasuchus (Dr Carroll includes this genus under *Pareiasaurus*), *Embrithosaurus*, *Anthodon*, *Scutosaurus*, *Shihtienfenia*, and *Nanoparia*. Von Huene however places *Scutosaurus*, *Shihtienfenia*, and *Nanoparia* each in their own subfamilies. Cladistics substituted taxonomy with phylogeny, but this didn't help because hypotheses keep changing. Lee (1997) argues that this group (his clade 'D') is paraphyletic and should include Testudines (or Chelonia). The current consensus is that the pareiasaur origin is no longer valid, the two most popular turtle origin hypotheses now being thequite morphologically implausible crown archosauria of molecular phylogeny, and sauropterygian lepidosauromorpha, although we have gone for a more conservative prtocolophonoid origin

(2) includes the "typical" Pareiasaurs. The heads decorated by knobs and ridges. The teeth each have nine cusps. The upper margin of the ilium is flat, never vaulted. The surface of the back is armoured to varying degrees with bony scutes. Some forms like the ancestral genus *Embrithosaurus* had only weak armour; while later forms like *Pareiasaurus*, *Scutosaurus*, and *Anthodon* were well protected. The limb posture is advanced and upright to support the weight of the body (graviportal).

(3) In view of the paraphyletic status of *Bradysaurus* (Tsuji & Müller 2009) there doesn't seem to be a clear point where node Velosauria should be placed. Mikko Haraama offers two alternatives, Velosauria Lee, 1994 sensu Lee, 1997, which is an apomorphy-based definition, everything more derived than *Bradysaurus*, and Velosauria Lee, 1994 sensu Jalil & Janvier, 2005, which is a node-based definition (Therischia + Pumiliopareiasauria) for everything more derived than *Deltavjatia*. Given that there is no unanimity regarding the Therischia - Tsuji & Müller 2009's unpublished analysis (see cladogram in that paper) did not recover it - we have gone for the former option. MAK120323

Embrithosaurus Watson 1914

Range: Mid Permian of Sth Afr

Phylogeny: Velosauria **:** *Embrithosaurus (Nochelesaurus) alexanderi* + (*Embrithosaurus schwarzi* + (*Deltavjatia* + (*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + Pumiliopareiasauria)))))

synonyms: *Dolichopareia*, *Nochelosaurus*

Stratigraphic range: Lower to Upper Tapinocephalus zone, Lower Beaufort Beds, of the Karoo basin, South Africa; most common in the Lower Tapinocephalus zone (Lower to Middle Tapinocephalus zone in Boonstra, 1969 pp26, 32,; Lower Tapinocephalus to Pristerognathus (= old Upper Tapinocephalus) zone in Ward et al 2005, supplem. info, range data; both = Capitanian age)

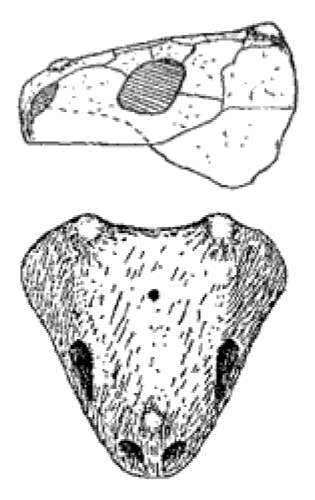
length: about 2.5 meters long

weight: about 600 kg

Comments: [1] *Embrithosaurus* is another huge early Pareiasaur, a contemporary of *Bradysaurus*. The skull is relatively deep and narrow. The body is lightly armoured with thin, smooth dermal scutes. This genus would seem to be ancestral to *Pareiasaurus*. MAK000124.

[2] Lee 1995 and Jalil & Janvier 2005 have three species, and Tsuji & Müller 2009 four as a scalloped paraphyletic series. Four pareiasaur taxa (*Bradysaurus baini*, *Bradysaurus seeleyi*, *Embrithosaurus (Nochelesaurus) alexanderi* and *Embrithosaurus schwarzi* co-existing in the same environment seem excessive, so either this was intraspecies variation, gender difference, a stratigraphic and anagenetic (chronospecies) series, or niche partitioning MAK120326

[3] Cladistic analysis makes *Embrithosaurus* as originally described paraphyletic, or in other words, an evolutionarily intermediate form between *Bradysaurus* and higher pareiasaurs, and to avoid paraphyletic taxa the synonym *Nochelosaurus* is restored. The present writer (MAK) is opposed to the prohibition against representing transitional and ancestral species in accounts of Earth History, as he feels that this is a too literal application of cladistic formalism, which is concerned with hypothesis testing, not with describing the actual evolutionary history of species in deep time. Also, although phylogenetic nomenclature tends towards monospecific genera (hence preference here of *Nochelesaurus* over *Embrithosaurus*, this creates an incongruency with taxonomy of plants, invertebrates, and quaternary and recent vertebrates, all of which ares based multi-species genera. For this reason, *Embrithosaurus* is retained for all species in these evolutionary series (ditto for *Bradysaurus* and *Pareiasaurus*); in any case there is no restriction on paraphyletic genera in linnaean (binomial) taxonomy. MAK120329



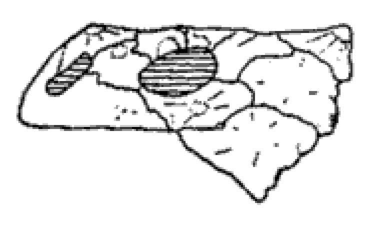
Embrithosaurus strubeni (Broom, 1924)

Synonyms: *Bradysaurus strubeni* in Boonstra, 1969 p.30

Stratigraphic range: Lower to Upper Tapinocephalus zone, Lower Beaufort Beds, South Africa

Comments: The skull is large and deep, pointed at the front, and elevated in the jugal region. This species was originally made the type species of *Nochelosaurus* by Haughton and Boonstra. Boonstra later (1969) moved it into the genus *Bradysaurus*, on the basis of the primitive tooth structure. Kuhn however considers it belongs under *Embrithosaurus*

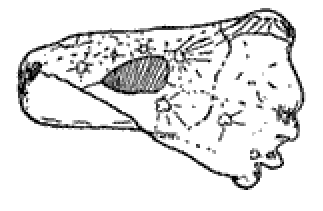
The specimen shown in lateral view (top) is 48 cm long, the other 35 cm long MAK000124



Embrithosaurus alexanderi (Haughton and Boonstra 1929)

Synonyms: *Nochelesaurus angustus* Haughton and Boonstra, 1929, *Embrithosaurus angustus* (Haughton and Boonstra, 1929), *Dolichopareia angusta* Haughton and Boonstra, 1929, *Brachypareia watsoni* Haughton and Boonstra, 1929, *Pareiasaurus bombidens* Seeley, 1888, *Bradysaurus watsoni* (Haughton & Boonstra, 1929)

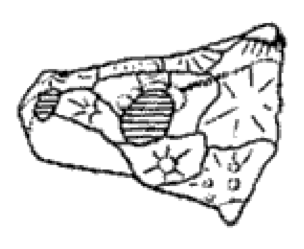
Stratigraphic range: Lower to Upper Tapinocephalus zone, Lower Beaufort Beds, South Africa



Size: Skull Length about 55 cm, Overall length about 3 m

Comments: This species was made the type for " *Dolichopareia*". As the name indicates, the skull is long and narrow. This would seem to indicate a different lifestyle or diet to other parieasaurs. More recently, it has been used as the monotypal species for the genus *Nochelesaurus* (it is not clear what the status of *Embrithosaurus strubeni* is, this may be a further transitional species) The bottom skull is about 48 cm long, and was originally described as *Brachypareia watsoni*, In cladistic analyses, this species is phylogenetically intermediate between *Bradysaurus seeleyi* and *Embrithosaurus schwarzi* MAK000124 120329

Graphics sketches of skulls of *Embrithosaurus angustus* (top) and *Bradysaurus watsoni* (bottom). These two species are considered synonyms of *Embrithosaurus alexanderi*, which indicates either artistic license or a great deal of individual variation, postmortem distortion, and so on. From Kuhn 1969 MAK120401



Embrithosaurus schwarzi Watson 1914

Stratigraphic range: Lower to Upper Tapinocephalus zone

Size: Overall length: 2.2 m

Characters: The bony dermal plates are thin and smooth. The ulna is without an olecranon process. (Zittel & Eastman 1932 p.243) MAK000124. "Anterior expansion of the iliac blade is flat rather than everted; the two iliac blades are not parallel but diverge anteriorly, making an angle of approximately 40° with the sagittal plane; pelvic symphysis is extremely thick, being almost half as deep as long." - Lee 1997

Comments: The type species. This is the most advanced species of this genus, as indicated by the teeth, which have nine cusps (in three groups of three). In cladistic analyses it is used as the monotypal species for the genus.

Graphics illustration of skull from Kuhn 1969

Deltavjatia vjatkensis (Hartmann-Weinberg 1937)

Synonyms: *Anthodon chlynoviensis* Efremov, 1933, *Anthodon rossicus* Hartmann-Weinberg, 1933, *Pareiasuchus vjatkensis* Hartmann-Weinberg, 1933, *Scutosaurus rossicus* (Hartmann-Weinberg, 1933)

Range: Severondvinskian Gorizont (= Lower Zone IV, Tatarian stage), Late Capitanian, (Latest Middle Permian) Kotel'nich locality in central Russia

Phylogeny: Velosauria : *Embrithosaurus (Nochelesaurus) alexanderi* + (*Embrithosaurus schwarzi* + ((*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + Pumiliopareiasauria))) + *)

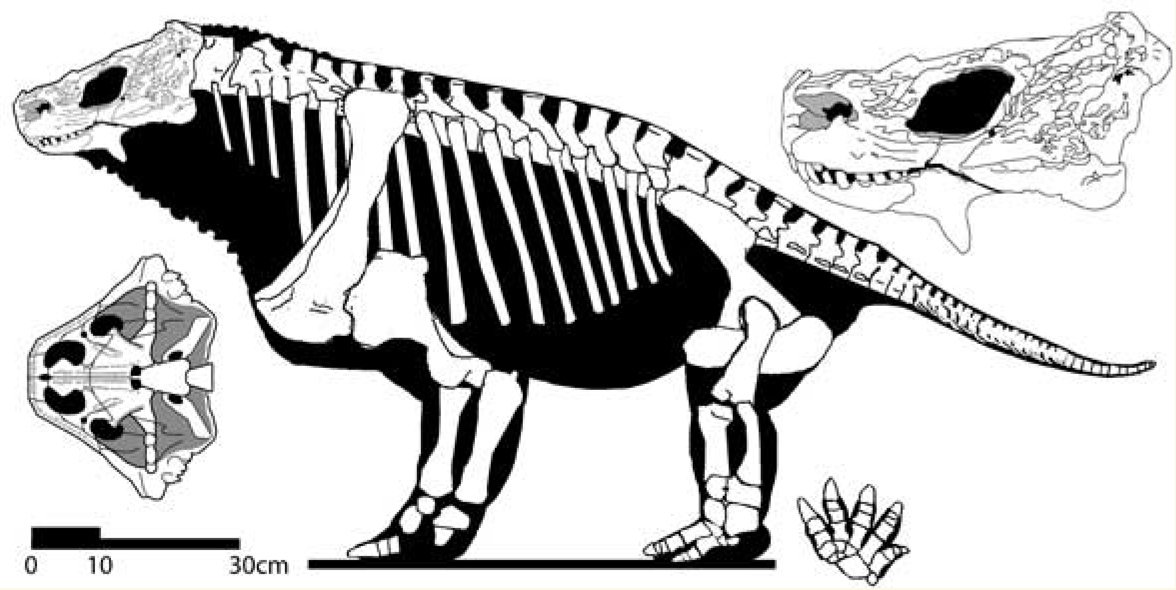
Size: 1 to 2 meters long

Characters: "the ventrolateral cheek flange terminates in a long, flattened, rectangular boss; the occipital condyle projects far behind the posterior border of the postparietal; in the largest specimen, the boss on the postfrontal is enlarged into a long conical horn" Lee 1997

Comments: Originally placed in *Pareiasuchus* (Hartmann-Weinberg 1933) this smallish pareiasaur is distinct enough to warrant its own genus. The only pareiasaur known from the lower Tatarian of Russia, *Deltavjatia* is an important taxon that bridges the large morphological and stratigraphic gap separating primitive South African *Tapinocephalus* zone pareiasaurs from the more derived forms characteristic of the overlying *Cistecephalus* zone and later deposits. It retains the long tail and feeble dermal armour of more primitive pareiasaurs, but possesses many skeletal traits characteristic of more advanced species Lee 1997. From above, the skull resembles the letter V, hence the name *Deltavjatia* (from the Greek letter Delta).

In spite of the large eye sockets, the eyeballs were small, as is shown by the size of the sclerotic ring that reinforced the cornea. Skulls of pareiasaurs with the sclerotic ring preserved are very rare. As with all pareiasaurs, the surface of skull is uneven. being covered with horn-like bumps and ossicles (bony plates) of different sizes. The largest of these are usually on the cheek, parietal and nosal bones. Sometimes there are large bosses on the frontal bones, and almost always on the lower jaw where it articulates with the skull. Attached to the largest dermal ossicles are nodules or bosses of various sizes. The spaces between the dermal ossicles probably contained skin glands, which exuded specific muscus for keeping the skin moist, or even, as with some toads, poisonous warts to deter predators. (Vyatka Palaeontological Museum)

As with all pareiasaurs, the skull does not contain a separation of mouth and nose cavities. The animals had to bolt their food without chewing, because when the food was in mouth cavity, there was impossible to breathe. (Vyatka Palaeontological Museum)



These animals were probably highly gregarious, occuring in large numbers. As with many of the similarily abundant South African Bradysaurs, most of the *Deltavjatia* found at the Kotelnich fossil locality were recovered as complete skeletons found fossilised in standing posture. The usual explanation is that they became bogged in mud died as a result of heavy rain fall, and were buried by silt and sediments carried by the flood water. Another explanation is that these water-loving animals were crowded in small ponds when there was not enough water to swim through but the ground became series of mud traps. The deltavjatias preserved this way show not only the smallest bones of the feet and tail, but also the dermal ossicles. (Vyatka Palaeontological Museum)

No doubt because of its primitive nature relative to the later and more advanced *Scutosaurus*, Golubev 2000 places this genus in a stratigraphic table of Russian Permian tetrapod families under the "Bradysauridae". *Deltavjatia* is also more lightly built than Scutosaurus, and may have been a more active animal. Despite its primitive status, it is still characterised by numerous turtle-like skull features (e.g., a very high palate), limbs, and girdles, and lateral projections flaring out some of the vertebrate in a very shell-like way. (Transitional Vertebrate Fossils FAQ by Kathleen Hunt); This relatively small species lived immediately after the mid Capitanian extinction event and represented the start of a new paraeiasaur adaptive radiation MAK120331

Graphics Photograph of *Deltavjatia vjatkensis* © Albert Khlyupin and Vyatka Palaeontological Museum - original page (Parareptilia), used with permission. Skeletal reconstruction © David Peters

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Anapsida: Pareiasauridae (3)

Pareiasaurinae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--Millerettidae
   |--Mesosauridae
   `--+--Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            |      |==Bradysaurus
            |      `--Velosauria
            |         |==Embrithosaurus
            |         `--+--Deltavjatia
            |            `---+--+--Shihtienfenia
            |                 |   `--Pareiasaurus
(Pareiasuchus)
            |                 `--+--Pareiasaurus
serridens
            |                    `--+--Scutosaurus
            |                        `--+--Elginia
            |                           `-
-Pumiliopareiasauria
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
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1. *Pareiasaurus* X
2. *Scutosaurus* X
3. *Shihtienfenia* X

Descriptions

Shihtienfenia permica Young and Yeh 1963

Synonym: *Honania complicidentata* Young, 1979, *Huanghesaurus liuliensis* Gao, 1983, *Shansisaurus xuecunensis* Cheng 1980, *Tsiyania simplicidentata* Young, 1979

Stratigraphic range: Shihtienfeng series / "pareiasaur fauna" / Shiqianfeng Formation of Shansi province and Shihezi Formation of Henan (Late Capitanian/Early Wuchiapingian age) China

Phylogeny: Velosauria **:** *Embrithosaurus* + (*Deltavjatia* + ((*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + Pumiliopareiasauria)) + (*Pareiasuchus* + *)))

Characters: "rounded expansion on the anterior margin of the scapula blade, near the dorsal end; and the acromion process is a smoothly contoured, semicircular flange" - Lee 1997

Comments: The skull of this pareiasaur is unknown. It is known originally from a number of isolated vertebrae, jaws, and limb-bones and an incomplete skeleton, all from a single locality (Shiqianfeng Formation at Baode, Shansi). *Shihtienfenia* is unusual because of the presence of 6, rather than the usual 4, sacral vertebrae, and may belong in a separate subfamily, although Oskar Kuhn includes it under the Pareiasaurines in his monograph (Kuhn 1969). As with the Pareiasaurines the upper margin of the ilium is flat. No dicynodonts are found in association, so these animals obviously lived in a separate environment. MAK000124

Shansisaurus xuecunensis, from the Shihezi Formation of Henan, differs only in possession of a more robust humerus, which is not enough to justify taxonomy separation; *Huanghesaurus liuliensis* known from a lowre jaw and partial skeleton would be another synonym. (Lucas 2001). *Honania complicidentata* and *Tsiyania simplicidentata* Young, 1979, also from this locality, are based on isolated teeth and probably invalid taxa, or synonyms of *S. permica*. Lee 1997 refers to *S. xuecunensis* as a metaspecies lacking the autapomorphies of *Shihtienfenia*. Tsuji & Müller 2009 seem to consider it a valid taxon for cladistic analysis, and like Lee 1997 place the two Chinese species close to *Pareiasuchus*.

In all instances biostratigraphic correlation is difficult because of the very fragmentary nature of associated fauna (a single dorsal vertebra attributed to the amphibian *Bystrowiana*, a possible gorgonopsian, and several "procynosuchid" teeth. Bystrowianids and procynosuchids would imply a very late date (Changhsingian), but this material is so fragmentary and to be non-diagnosable. Lucas 2001 originally considered the fauna to be of dinocephalian (=Tapinocephalus zone - Capitanian) age, but later Lucas 2006 reassessed this as correlated with his Steilkransian land vertebrate age (=Cistecephalus zone) on the basis of the *Shihtienfenia* being equivalent to *Pareiasaurus*, *Pareiasuchus*, and *Scutosaurus*. Cladistic analyses however (Lee 1997, Jalil & Janvier 2005, Tsuji & Müller 2009) shows that *Shihtienfenia* (coded as two species) is more basal than all three of those taxa, but more derived than *Deltavjatia*. It is likely therefore to be either a contemporary of, or slightly later than *Deltavjatia*, which would put it at Late Capitanian or Early Wuchiapingian age MAK120330

Pareiasaurus Watson 1914

Synonyms: *Pareiasuchus*, *Propappus*

Stratigraphic range and localities: Early Tropidostoma to Middle Dicynodon zone (Ward et al 2005, supplem. info, range data;), (previously referred to as Endothiodon to Daptocephalus zones) Lower Beaufort Beds, Karoo basin, (latest Wuchiapingian to Middle Changhsingian age), Lower Beaufort Beds, Karoo basin, South Africa; Luangwa valley Zambia; Ruhuhuh valley, Tanzania. (Early Wuchiapingian to Early Changhsingian age)

Phylogeny: Velosauria **:** *Embrithosaurus* + (*Deltavjatia* + ((*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + Pumiliopareiasauria)) + (*Shihtienfenia* + *)))

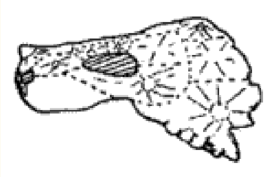
Length: about 2.5 meters long

Weight: about 600 kg

comments: This genus includes a number of large Pareiasaurs. The skull is broad and the snout short. There are 4 sacral vertebrae. The phalangeal count of the fore-foot is 2,3,3,3,3,2. The armour is well developed, with several rows of heavy scutes. There are 14 pairs of low, broad-crowned teeth, each with 9 to 13 or more cusps (depending on the species). MAK000124

[2] Most species have since been moved to *Pareiasuchus*, which is now considered more derived than the Chinese *Shansisaurus* and *Shihtienfenia* it shares the clade with (note that these two latter taxa are considered synonyms by Lucas 2001). Lee 1997 suggests the self-explanatory name Pareiasuchidae for this clade, although an -inae suffix would be less coinfusing as -idae is the linnaean family rank suffix. Because of the incomplete knowledge of the Chinese pareiasaur(s), only a single unambiguous synapomorphy is currently known to diagnose the group: **$** Extremely long scapula blade. However, further finds might reveal that other traits, currently interpreted as autapomorphies. Alternatively, this character may simply be the result of convergence - e.g.

the need for increased shoulder muscle attachment due to feeding habits, intraspecific behaviour or environmental factors. Moreover, since a very long scapula is a feature found not only in *Shihtienfenia* but typical for pareiasaurs as a whole (Lucas 2001 p.80, consider for example this this photo of *Deltavjatia*) the validity of this synapomorphy may be questioned. Another thing that should be considered is paleogeography. Were pareiasaurs uniform across pangea, or were they evolving separately in geographically endemic clades? For now we find it more parsimonious to consider that *Deltavjatia*, *Shihtienfenia*, primitive *Pareiasaurus* (*Pareiasuchus*, perhaps a subgenus) and advanced *Pareiasaurus* as part of a single evolutionary (and hence paraphyletic) continuum. MAK120330



Pareiasaurus nasicornis (Haughton and Boonstra 1929)

Synonym: *Pareiasuchus nasicornis* Haughton & Boonstra, 1929 is more commonly used in literature today, to avoid a paraphyletic *Pareiasaurus*

Stratigraphic range: Endothiodon Zone, Karoo basin, South Africa

Characters: large descending cheek flanges project backwards, gving the the skull a delta-shape in dorsal view; ridge bearing internal trochanter extends to the preaxial tibial facet (convergence with *Bradysaurus baini*). - Lee 1997

Comments: This early form is one of the first representatives of the genus. It was originally included under the genus *Pareiasuchus*. The snout is heavily armoured, and bears a horn-like boss. The teeth are equipped with 11 (or possibly 13 or 15) cusps. This is a large animal; the skull is about 50 cm in length. This species might be ancestral to *Pareiasaurus peringueyi*. MAK000124

Pareiasaurus peringueyi (Haughton and Boonstra 1929)

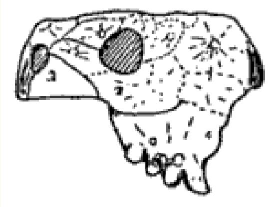
Synonyms: *Pareiasuchus peringueyi* Broom & Haughton, 1913 more commonly used in literature today, to avoid a paraphyletic *Pareiasaurus*; *Pareiasaurus pulcher* Broom, 1935 is an old synonym no longer current

Stratigraphic range: Cistecephalus Zone, Karoo basin, South Africa

Characters: lateral flange of the exoccipital forms a distinct, dorsally-oriented crest along the posterior margin of the paroccipital process; small median tubercle on the internal surface of the mandible, directly above the symphyseal ‘hook’; angular boss a large, blunt knob - Lee 1997

Comments: **[1]** This species was the type species for *Pareiasuchus*. It is represented by a nearly complete skeleton from the Zak River, South Africa . It is a medium-sized animal, the skull being 36 cm long. It is distinguished especially by the large quadrato-jugal region inclined far outwards and forwards so that its lower border makes an angle of about 120^{o} with the maxillary border; this cheek bears large bony bosses. There are at least 13 pairs of teeth in the upper jaw, each with 13 or possibly 15 cusps (Zittel & Eastman 1932 p.243)

[2] *Scutosaurus* from the Dvina river, northern Russia was originally included under *Pareiasuchus* (Hartmann-Weinberg 1933) but is a more advanced genus



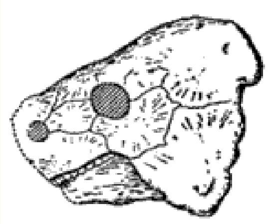
Pareiasaurus serridens Owen 1876

Synonyms: Anthodon gregoryi Broom, 1930, Anthodon nesemanni Broom, 1940, Brachypareia rogersi (Broom, 1912), Bradysaurus rogersi (Broom, 1912), Pareiasaurus minor Seeley, 1892, Pareiasaurus omocratus (Seeley, 1888), Pareiasaurus pinnatus Olson & Broom, 1937, Pareiasaurus rubidgei Broom, 1940, Propappus omocratus Seeley, 1888, Propappus serridens (Owen, 1876), Propappus rogersi Broom, 1912,

Stratigraphic range: Daptocephalus Zone, Karoo basin, South Africa

Characters: cranial sculpturing consists of a reticulate network of fine pits and grooves but there is no boss on the centre of each element; dorsal flange on the anterior margin of the proximal end of the paroccipital process - Lee 1997

Comments: This late species is the type species for *Pareiasaurus*, and represents the culmination of this lineage. The armour is well developed. There are 14 pairs of teeth, each with 9 to 11 cusps. The short deep skull is about 40 cm in length. Note the extended quadrato-jugal region (cheek bones). MAK000124



As befits such a popular and charismatic secies the list of synonyms is out of control, although it may be that some of these represent chronospecies, others would be growth stages, individual variation, etc. *Pareiasaurus omocratus* (Seeley 1888), from either the Endothiodon or Cistecephalus Zone, was the type species for *Propappus*. Only fragments of the skull are known. The back thickly covered with large, slightly sculptured, bony scutes. There does not appear to be ventral (belly) armour (Zittel & Eastman 1932 p.243) . This species is now considered a synonym of *Pareiasaurus serridens*. *Anthodon gregoryi* Broom 1930 (right) from the Middle? Cistecephalus zone, Karoo was attributed to the advanced genus *Anthodon*, but would be a large species for that genus, known from an incomplete skull almost 30 cm wide. The teeth only have have 8 cusps each. It is now also considered a synonym of *Pareiasaurus serridens* MAK000124 120329

Scutosaurus karpinskii (Amalitzky, 1922)

Scutosaurus skeleton, American Museum of Natural History. Author p_a_h, Flikr, copied at Wikipedia, Creative Commons Attribution. This photograph nicely illsutrates the stocky and hevay build of this animal

Scutosaurus - life reconstruction from Lambert et al 2001

Life reconstruction of same, from Lambert et al 2001 pp.72-3 via Prehistoric wiki

synonyms: *Pareiasaurus karpinskii* (or *karpinskyi* (see note)) Amalitzky, 1922, *Pareiasuchus elegans* Amalitzky, 1922, *Pareiasuchus horridus* Amalitzky, 1922, *Pareiasuchus tuberculatus* Amalitzky, 1922, *Scutosaurus itilensis* Ivachneko & Lebedev, 1987 and possibly also *Proelginia permiana* Hartmann-Weinberg, 1937 and hence also *Scutosaurus permianus* (Hartmann-Weinberg, 1937), but see note

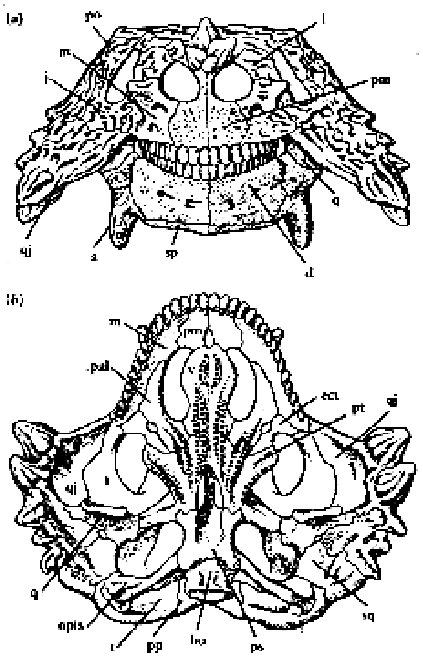
Stratigraphic range: classically, upper part of Zone IV (Tatarian stage), of Sokolki, Malaya Severnaya Dvina River, Arkhangelsk Region, northern European Russia (mathematical com), but this is a widespread index fossil found widely throughout late Wuchiapingian to Middle Changhsingian age assemblages of the Perm region of Russia and thereabouts. Earlier occurances (early to mid Wuchiapingian) are attributed to *Proelginia permiana* by Russian biostratigraphers, this may be either a synonym of *S. karpinskii* or a chronospecies (*S. permianus*) that evolves into it, given the large span of time involved, we have tentatively gone with the latter option

Phylogeny: Velosauria :*Deltavjatia* + (*Shihtienfenia* + *Pareiasuchus*) + (*Pareiasaurus* + ((*Elginia* + Pumiliopareiasauria) + *)))

Size: length 2 to 3 meters, mature (3 meter) specimens would have a live weight of at least a tonne

Characters: small median boss on the basioccipital between the basal tubera, crowns of the teeth on upper jaw point slightly outwards, radiating ridges covering the skull are very coarse. - Lee 1997, p. 210

The skull (left) is very broad, flat, and strongly sculptured, and bears bony protuberances in the jugal (cheek) and rear regions. As with some species of *Pareiasaurus*, with which it is clearly related, the quadrato-jugal or cheekbones extend outwards and forwards, makings an angle of about



Left: *Scutosaurus* skull, front and palatal view from Carroll, 1988, p.205*above*: *Scutosaurus* skull, top (dorsal) view Kuhn, 1969, p.79

120^{o} with the maxillary border.
The skull shown on the left is about 50 cm wide. MAK000124

The post-cranial skeleton is well known. There are 6 cervical, 13 dorsal, 5 (or 4?) sacral vertebrae, and only a few tail vertebrae

Comments: [1] This very large pareiasaur occurs at a later time than *Deltavjatia vjatkensis*. Originally known from several skeletons found together in a flood channel sand deposit, it is a common and widespread index taxon. It is an advanced form with upright limb posture, this being an adaptation for supporting the weight of the body (Cox et al 1988) although it has also been interpreted as semi-aquatic (e.g. Golubev 2000 p.S221) (and hence presumably sprawling). The skin is heavily armoured with osteoderms.

[2] Stratigraphically earlier specimens are consistantly referred to as *Proelginia permiana* and used by Russian paleontologists in biozonation, which implies it is a morphologically distinct species (Golubev 2000, Tverdokhlebov et al 2005, Sennikov & Golubev 2006, Newell et al 2010). Western paleontologists consider it a synonym of *S. karpinskii*. We have tentatively considered these as the chronospecies *Scutosaurus permianus* (Hartmann-Weinberg, 1937) and *Scutosaurus karpinskii* respectively

[3] due to problems of transliteration from Russian cyrillic, the species name is variously spelt with one or two "i"'s.it is occaisonally also spelt "yi"; according to MSY Lee (2001), the "karpinskyi" variant was inadvertently published prematurely by Watson in 1917 when the full description was delayed by war and the death of Amalitzky, but "karpinskii " should be retained; We have adopted this latter spelling as the correct one

[4] With *Scutosaurus* and other pareiasaurs, spikes and horns developing on the snout and from the lower jaw only develop with age, and may have been used in mating displays or other intraspecific behaviour (Lambert et al 2001 p.73)

[5] The genus name, "Shield Reptile" refers to the large plates of armor scattered across its body. (Wikipedia)

[6] Perhaps the most popular of the pareiasaurs, *Scutosaurus* features both in the *Walking with Monsters* speculative documentary series and the*Primeval* sci fi TV series. In *Walking with Monsters* it is shown as a social animal that migrated in groups. Certainly pareiasaurs did seem to have been gregarious and social creatures (as indicated by large numbers found together, often mired in swamps in standing position), their status as migratory animals is purely speculative In paleo art and dramatisations Scutosaurus is depicted as being preyed upon by large gorgonopsids. While it is not impossible that animals such as the lion- or bear-sized *Inostrancevia* could have taken on these ox-sized animals, they would have obviously preferred to pick off juveniles or sick or oilder individuals, rather than challenge an Scutosaurus, which was both heavily armoured and the largest and strongest animal in its environment. MAK120402

Links: *Scutosaurus karpinski* web page (mathematical com); Paleobiology database; *Scutosaurus* at Palaeocritti; Scutosaurus - Prehistoric Life; Scutosaurus - Daily Fossil, Scutosaurus - all about reptiles; Deviant art, Wikipedia; Scutosaurus - Wikimedia Commons (photos and art); and many many more links (many short pages with the same art, photos, and text content)

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Anapsida: Pareiasauridae (4)

Elginiidae and Pumiliopareiasauria

Abreviated Dendrogram

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REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--Millerettidae
   |--Mesosauridae
   `--+--Lanthanosuchidae
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            |      |==Bradysaurus
            |      `--Velosauria
            |         |==Embrithosaurus
            |         |?--Provelosaurus
(biostratigraphy and large scale evolution)
            |         `--+--Deltavjatia
            |            `--+--Pareiasaurus
            |               `--+--Scutosaurus
            |                  `--+--Elginia
            |                      `-
-Pumiliopareiasauria
            |                          |?-
-Provelosaurus (morphology only)
            |                          `--+-
-Nanopareia
            |                             `--+-
-Anthodon
            |                                `-
-Pumilopareia
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
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1. *Anthodon* X

2. *Elginia* X
3. *Nanopareia* X
4. *Provelosaurus* X
5. Pumiliopareiasauria X (or not, depending on your point of view)
6. *Pumilopareia* X

The enigma of *Provelosaurus*

Reconstruction of *Provelosaurus brasilienses*, from Bagé-Aceguá highway, Western Rio Grande do Sul State. Length: 2.5 meters. From Some Fossil Vertebrates From Southern Brazil - Laboratory of Paleovertebrates

The Brazilian pareiasaur *Provelosaurus americanus* (Araújo, 1985), known from the nearly complete skull and postcranial elements of at least four individuals, from the Rio do Rasto Formation, Paraná Basin, Rio Grande do Sula, Brazil. Originally described as a South American representative of the genus *Pareiasaurus*, it was assigned to a new genus *Provelosaurus* by Lee (1997), who noted it shows more affinities with the small, highly derived, South African dwarf pareiasaurs (called Pumiliopareiasauria by Jalil & Janvier 2005) than with the more typical Pareiasaurus. According to Lee, Provelosaurus bridges the morphological gap between the advanced South African and the more generalized pareiasaurs. So far so good, African and Brazilian fauna often are very similar, look at *Mesosaurus*; that is just more evidence of them being adjacent pieces of the ancient supercontinent of Gondwana.

What *is* strange though is the date of this fauna. The Rio do Rasto Formation, which occurs at a number of different outcrops, contains a rich assemblage of classic Middle Permian tetrapods, including Platyoposaurine and Melosaurine archegosaurs and Rhinesuchoid temnospondyls among the amphibians, and such anteosaurid and titanosuchid dinocephalians and a new basal anomodont among the therapsids. Exccept fro the rhinesuchid, the otehr taxa put the minimum age limit of this fauna as mid Capitanian, and some taxa would seem to push it back to Wordian (Cisneros et al 2005, Dias-da-Silva 2012)

Yet while *primitive* pareiasaurs are known from the Capitanian, *Provelosaurus* seems anything but. It has a reduced body size, and specializations in the humerus otherwise found only in pumiliopareiasaurs and turtles, although it also retains more generalised features such as a plate-like scapula blade, unfused osteoderms, and a prominent cnemial crest. (Lee 1997 p.267). Autapomorphies in the shape of the squamosal and the morphology and placement of the quadratojugal bosses are quite unlike contemporary Tapinocephalus Assemblage Zone fauna such as *Bradysaurus*, *Embrithosaurus*, and instead show similarity with advanced forms such as *Scutosaurus* and *Pumiliopareia* (Cisneros et al 2005). A Wuchiapingian stem- pumiliopareiasaur would nicely bridge the ghost lineage and verify Lee (1997)'s and Jalil & Janvier 2005's Velosauria **:** Therischia + Pumiliopareiasauria hypothesis. But an early Capitanian, still less a Wordian age, Pumiliopareiasaurian makes about as much sense as a Connecitect Yankee in King Arthur's Court. Even if we assume a very early (Wordian-Capitanian) origin for a monophyletic dwarf-pareiasaur lineage, with Pumiliopareiasaurs originating in West Gondwana before migrating south-east to Africa, this does not explain why no further Pumiliopareiasaurs appear for another ten million years, in the latest Permian Latest Wuchiapingian - Changhsingian, or the otherwise sequential evolution of the pareiasaur group, nor why everything else found in the Rio do Rasto formation is very mundanely and cosmopolitanly Middle Permian, with absolutely no other evidence of endemism or precocious taxa. As with the early advanced Australian lycopod, *Barragwanatha*, which apparently (on the basis of associated graptolite index fossils) predates even the most primitive land plants such as *Cooksonia*, *Provelosaurus* appears to be a time travelling taxon that is much too early for its own advanced evolutionary status.

It would perhaps be too much to expect the creationists - who are so concerned to refute the fossil record that they depend on Paluxy man tracks and dinosaurs on Noah's Ark - to show any interest in rare genuine enigmas that challenge common sense by placing apparently more advanced forms earlier than more primitive ones, although noncladistic evolutionists might, as shown by argument by critics of birds from dinosaurs used regarding the temporal paradox of *Archaeopteryx* occuring earlier than its "ancestor" *Deinonychus*; this has bnow been resolved with the discovery of maniraptoran dinosaurs older than *Archeopteryx*. Of course, we may actually be dealing with an authentic time travelling *Anthodon*, perhaps a Time Lord pareiasaur and his Tardis. Apart from this, we might consider (and/or discard) the three possible rational explanations.

(1) The least controversial possibility that *Provelosaurus* occurs at a latest Permian stratigraphic date (Barberena 1985) or level (Langer 2000) , as originally suggested, has now pretty much been refuted by further discoveries, which have firmly cemented the age of the tetrapod fauna as middle Permian (Malabarba et al 2003, Cisneros et al 2005, Dias-da-Silva 2012).

(2) The usual approach in current vertebrate paleontological literature is to take morphological abnalysis as absolute. There were pumiliopareiasaurs in the Capitanian, whether we like it or not. Almost all pareiasaur evolution is hidden from us, and can only be traced with ghost lineages, which means that ecological crises such as the late Capitanian extinction event, and any follow up adaptive radiation, were pretty insignificant, and that the fossil record is not a reliable guide to the evolutionary history of life through deep time. This phylopessimistic morphology-only approach of much of paleoherpetology-based cladistics asserts that the fossil record is so incomplete that no useful phylogenetic signal can be extracted from stratigraphy (or for that matter, geography). Cladistics still adopts a sort of atomistic idealism approach, assuming that morphological traits occur in some ideal mathematical platonic world unfettered by such mundane and messy details as stratigraphic sequence, paleogeography, and paleoecology. Moreover, the presence or absense of individual traits are considered in atomistic isolation from that of other traits, rather than considering the whole organism, its development, and its possible environment holistically. But conflicting phylogenies from molecular phylogeny alone should be enough to show that a morphology-only approach can not provide the complete story. Clearly, homoplasy and reversals play a much larger than role than is usually considered in parsimony or even maximum likelihood analyses. This is not to deny the usefulness and validity of the phylopessimistic morphoilogy-based approach, only to suggest that it should be used as complementary to other approaches, not as the only way.

(3) It may well be that, as with the evolution of life in general, pareiasaur evolution is strongly homoplastic, and *Provelosaurus* developed advanced characteristics by convergence with later groups. Indeed, these convergences may simply be due to small size (suggested in passing on Palaeocritti), in the same way that lepospondyls and early amniotes appear to belong to the same clade for the same reason (Carroll, 2009). Although this is not a perfect explanation, as it does not explain the more primitive morphology of the similarly diminutive *Deltavjatia*, it at least has the advantage of a hypothesis in keeping with biogeographic and stratigraphic factors. Pending further developments therefore, we have decided to follow this more "holistic" approach. MAK120331

Descriptions

Elginia mirabilis Newton 1892

Stratigraphic range: Elgin Formation of Scotland (*Dicynodon* biochron ((Lucas 2001 pp.85-7) *Gordonia* being a junior synonym), so Changhsingian in age)

Phylogeny: Velosauria **:** *Embrithosaurus* + (*Deltavjatia* + (*Pareiasaurus* + (*Scutosaurus* + (Pumiliopareiasauria + *))))

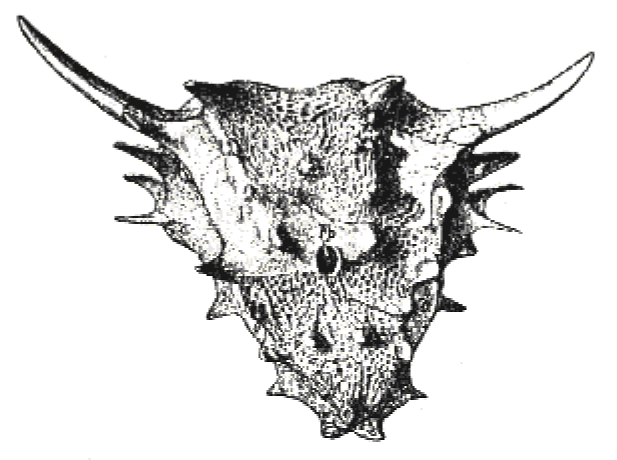
Estimated overall size: length 60 cm long, weight about 8 or 10 kg

Characters: long conical horns over the skull and along cheek margins; notched skull table with supernumerary bones enlarged and contacting medially, forming a frill at the rear; median depression just behind the nasal bosses;

posteroventral embayment of the orbital margin - Lee 1997

Comments: For a long time this was the only species of the monotypal family or subfamily Elgininiinae Cope 1895. This is a small specialised late lineage, characterised by large spikes or backwardly curved "horns". Despite the number of times it has been illustrated and referred to, Elginia is known only from a single skull, which is about 15 cm long, triangular, coarsely sculptured, and armed with a number of paired bosses or spines. The upper jaw bears 12 pairs of teeth, each with 9 or 10 cusps. The teeth are slightly constricted at the base and serrated at the crown. Zittel & Eastman 1932 p.243;

Recently, elgininiine pareiasaurs have been reported from the late Dzulfian age of Northern Pangea (Scotland and Russia). In the Moscow Basin (middle part of the Vyatskian horizon), associated with therapsids like *Nanocynodon* and *Dicynodon*, proterosuchid archosaurs, and bystrowianid amphibians, and representing a later time period than that of the giant Scutosaurs (Ivachnenko 1992). These include two partial skeletons of adults, and a young individual 25 cm long from the Vyazniki assemblage of the Vladimir region (Russian Wikipedia) A new species, *Obirkovia gladiator* Bulanov & Jashina 2005, was described based on a quadratojugal from the Obirkovo locality (Upper Tatarian Substage, Vologda region). Elginiids first appear in Eastern Europe in the middle of the Vyatkian Regional Stage (Scutosaurus karpinskii Zone) (Bulanov & Jashina 2005) which would be latest Wuchiapingian or Earliets Changhsingian age (Newell et al 2010, fig2 (stratigraphic correlation table)). In comparison with the earlier and abundant scutosaurs, they represent a rare element of Russian Vyatskian faunas (Golubev 2000). It may be that, as with the contemporary gondwanan pumiliopareiasaurs, these laurasian dwarf parieasaurs represent the specialised end of the line for these great herbivores.



Elginia mirabilis, *left*: illustration from Zittel & Eastman 1932 p.242, right, side view, sketch from Kuhn, 1969, p.74

As with many pareiasaurs, precise phylogenetic placement is uncertain. *Elginia* shares with *Scutosaurus* elaborate cranial ornament, which may imply they are related (Boonstra, 1932), although this is more likely to be the result of simple convergence. It was also thought related to the very primitive taxon 'Dolichopareia' (=Nochelesaurus) on the basis of a deeply notched skull table shared with the latter (Walker 1973) , but this turned out to be the result of taphonomic distortion (Lee 1997). Cladistic analyses tend to place it as more derived than the earlier giant *Pareiasaurus* and *Scutosaurus*, but evidence of actual phylogenetic relationships is obscure, and phylogenies differ according to whether Elginia is the most highly derived Therischian (Lee 1997, Jalil & Janvier 2005) or intermediate between *Scutosaurus* and Pumiliopareiasaurs (Tsuji & Müller 2009).

Links more on Elginia

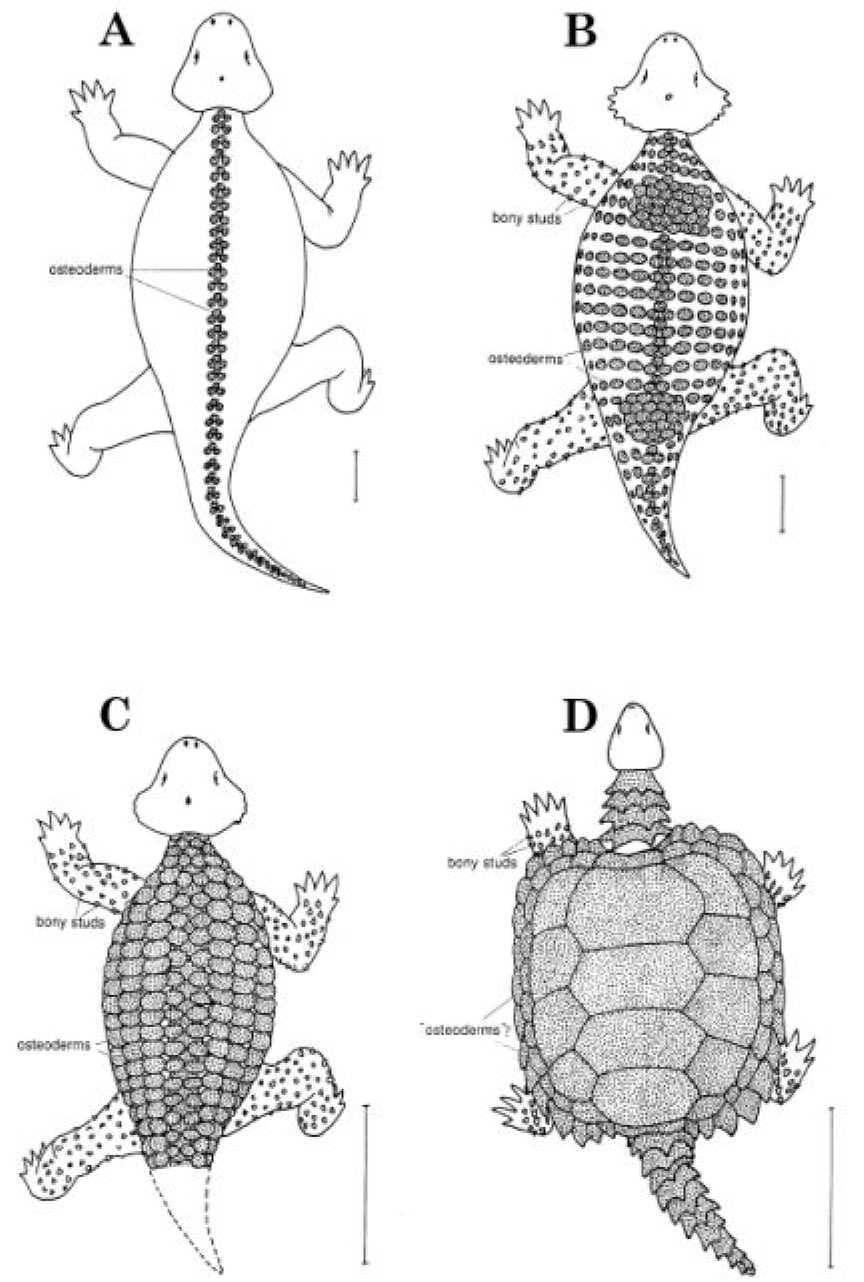
Image *Elginia* life reconstruction, artwork by Dmitry Bogdanov, Wikipedia, public domain.

Pumiliopareiasauria Jalil and Janvier 2005 : *Anthodon*, *Nanoparia*, and *Pumiliopareia*

Range: Latest Permian of Sth Afr

Phylogeny: Velosauria **:** *Embrithosaurus* + (*Deltavjatia* + (*Pareiasaurus* + (*Scutosaurus* + (*Elginia* + * **:** *Nanopareia* + (*Anthodon* + *Pumilopareia*)))))

Comments: [1] These are the dwarf pareiasaurs, the most highly derived, the heavily armoured, and turtle-like of the group, that only appear at the end of the Permian. *Anthodon* and *Pumiliopareia* share numerous and striking postcranial traits with turtles, these would be synapomorphies if they are turtle ancestors (Lee 1997, pp. 267-8) and convergences if they are not



Pareiasaurs and turtles - from Lee 1997 fig.19. showing dorsal dermal armour and bony studs over limbs, and overall similarity in body proportions. Dorsal reconstructions of (A) the large primitive pareiasaur *Bradysaurus* (Middle Permian of South Africa), (B) the large advanced paraeiasaur *Scutosaurus* (Late Permian of Russia), (C) the small advanced pareiasaur *Anthodon* (Latest Permian of South Africa), and (D) the stem chelonian *Proganochelys* (Late Triassic of Germany). Scale bar 30 cm

[2] The idea that turtles are actually highly derived pareiasaurs was strongly argued on cladistic grounds by Michael Lee in a series of innovative papers (Lee, 1993, 1995, 1997, 2001), and supported by Jalil & Janvier 2005. Thus, pareiasaurs had turtle-like cranial features, and it is not hard to imagine dermal ossicles and scutes, embedde din the skin or attached to the skull, vertebrae, progressively evolving into bony plates,and finally fusing into a turtle shell. There is also a progressive morphological sequence, as illustrated in the diagram at the right, showing pareiasaurs becoming progressively more heavily armoured and then, after a series of giant forms, progressively smaller. Pareiasaurs evolving into turtles also has a coolness factor rather like dinosaurs evolved into birds. Significantly, both came about through the new science of cladistics. It would also mean, cladistically speaking, that turtles *are* pareiasaurs, although surely this is no worse than alternatives such as turtles are plesiosaurs! (well, sauropterygians, but let's not quibble!) But whereas dinosaurs to birds is as solid a phylogenetic hypothesis as any that could be formulated, the question of a pareiasaur origin for turtles and tortoises is a lot more controversial, and, unlike dinosaurs to birds, there are some strong rivals. deBraga & Rieppel, 1997 argue that pareiasaur scutes are not homologous with the turtle shell and show that many features of turtles, especially the limbs, suggest sauropterygia and lepidosauromorph relationships. Meanwhile molecular phylogeny consistently places turtles among the archosaurs. Recently the eunotosaur ancestry hypothesis has been revived. None of these hypotheses is without controversy, but if pareiasaurs are not rturtle ancestors, than irather than evolving *into* turtles, pareiasaurs were evolving parallel to them. As such, pareiasaurs would represent "prophetic forms" rather than true ancestors. MAK120331

[3] The middle Permian *Provelosaurus americanus* is commonly placed as the most basal pumiliopareiasaur, but stratigraphically this makes no sense, see our comments above

[4] on a much more trivial level, here at *Palaeos com* we need to reconsider our colour attribution; having orange for extinct clade sor taxa and yellow for extant ones is not very useful if it is not even clear whether a clade is actuallyextinct or extant or extant. If MSY Lee is correct then all the dendrogram links and headings dfeaturing pareiasaur clades need to be change dfrom orange to yellow (and otehrs such as procolophonidea etc from yellow to orange) . One controversy-proof option (albeit a bit colourful) would be to introduce a colour coding based on earliest appearance of the taxon in question a la the geological timescale; but to change everything would be so much work, given thousand and thousand of entries, it is not presently considered practical MAK120402

Nanoparia luckhoffi Broom 1936

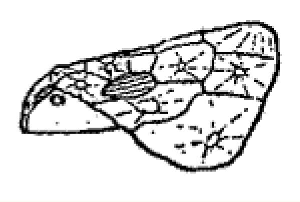
Stratigraphic range: Dicynodon (previously called Daptocephalus) Zone, Lower Beaufort Beds, Karoo basin, South Africa (Changhsingian age)

Phylogeny: Pumiliopareiasauria **:** *Nanopareia* + (*Anthodon* + *Pumilopareia*)

Size: length 60 cm, weight about 8 or 10 kg

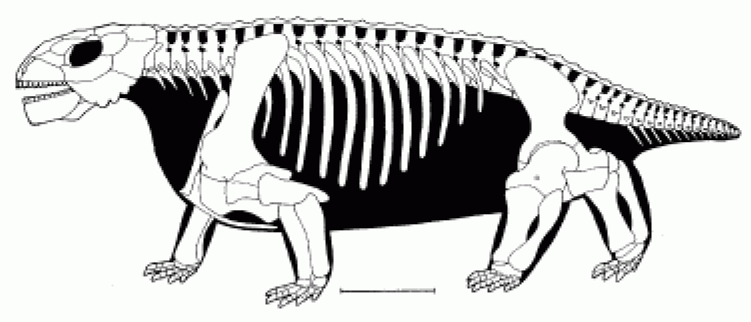
Characters: snout very pointed in dorsal view, superficial element present between the squamosal and quadratojugal. Lee 1997, p. 210

Comments: This is an unusual small, spiny specialised form. The skull is very similar to that of *Pareiasaurus* and Romer considered it a synonym of the latter. Orlov however (in *Osnovy Paleontology*, the monumental multi-volume Russian textbook of Paleontology) placed it in the Elginiinae. Kuhn 1969 however argues that while resembling *Elginia* in the ossifications at the rear of the skull, it differs completely in proportions and would notseem to be related. Lee 1997 considers it a basal member of the dwarf pareiasaurs.



Anthodon serrarius Owen 1876

Synonyms: *Propappus parvus* Haughton, 1913, *Pareiasaurus parvus* (Haughton, 1913)



Stratigraphic range and localities: late Early to early Late Dicynodon (=Daptocephalus) zone (Ward et al 2005, supplem. info, range data;), Lower Beaufort Beds, Karoo basin, (latest Wuchiapingian to Middle Changhsingian age)

Phylogeny: Pumiliopareiasauria **:** *Nanopareia* + (*Anthodon* + *Pumilopareia*)

Size: Skull length 30 cm, overall length 1.2-1.5 m long, estimated weight about 80 to 100 kg

Characters: marginal teeth do not form a continuous cutting edge, but separated by small gaps; the cranial sculpture consists of fine, widely-spaced pits and weakly developed bosses. - Lee 1997, p. 210

Comments: this small form combines the primitive feature of interpterygoid fenestra with an advanced feature of turtle-like armour. The skull is small and quite lightly built. The cheekbones form very large quadratojugal "horns" that extend downwards to a great degree, but with a smooth unornamented surface. . The mandible has ventral protrusions (further "horns"). The postparietals are fused and, along with the tabulars, located on the skull roof, as in more primitive diadectomorphs. Small dermal ossicles covered the body, while the pattern of armour plates on the back reminiscent of a turtle shell. There are 11 to 14 pairs of overlapping teeth, of small and uniform size, each with 8 to 15 cusps, giving them, as with all pareiasaurs, a leaf-like or flower like appearance, hence the genric name "flower tooth". The tail was further shortened relative to less derived forms.

The Holotype (BP/1/548) consists of an incomplete skull and several anterior vertebrae. The teeth are regularly spaced and have at least 9 cusps each.

Anthodon minusculus Haughton 1932 from the Daptocephalus zone, Ruhuhuh valley, Tanzania is known from a single humerus and would be a nomen dubium

Graphics Sketch of skull from from Kuhn, 1969 Skeletal reconstruction from Lee 1997

Links Palaeocritti - Anthodon serrarius, David Peters - Anthodon,

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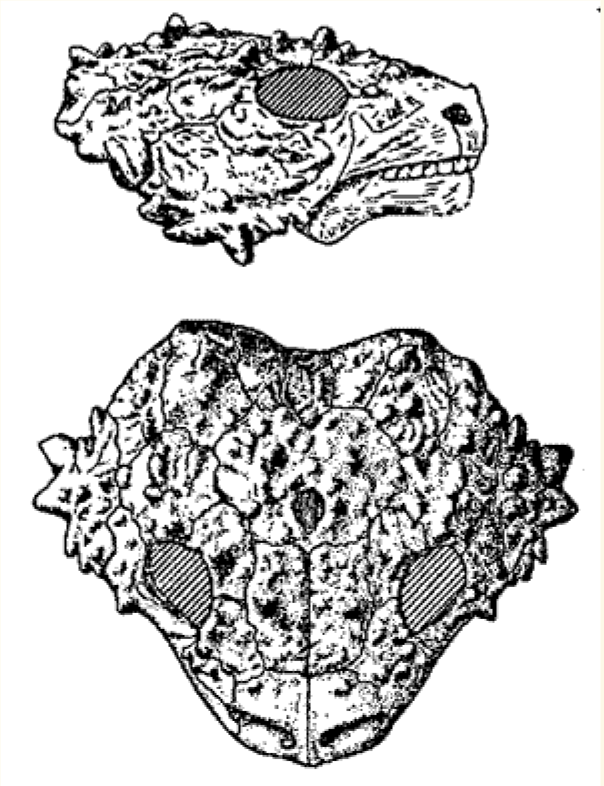

Pumiliopareia pricei (Broom and Robinson 1948)

Synonyms: *Nanoparia pricei* Broom and Robinson 1948, *Pareiasaurus pricei* (Broom & Robinson, 1948),

Range: Dicynodon zone of Sth Afr (Changhsingian)

Phylogeny: Pumiliopareiasauria **:** *Nanopareia* + (*Anthodon* + *Pumilopareia*)

Size: Length of skull 12 cm; overall length about 50 cm.

Characters: skull table and cheeks completely covered by densely-spaced, conical bosses; orbits perfectly round; only approximately 9 teeth on each upper jaw and 7 on each lower jaw; ribs very wide, abutting, the intercostal spaces thus being almost non-existent. Lee 1997, p. 210

Comments: Known from a complete skeleton with osteoderms, *Pumiliopareia* is the smallest known member of the pareiasaurs, measuring only a fifth the linear dimensions of its larger relatives. Like Anthodon, its body was entirely covered with osteoderms. In analyses that support a pareiasaur origin of turtles, the sister taxon of the testudines. However it specifically shares with shares with turtles a single triat only: Ribs greatly expanded anteroposteriorly (i.e. wide) Originally included under the genus *Nanoparia*, it was given its own name by Lee 1997 who found it did not form a clade with *Nanoparia luckhoffi*, the type species of that genus, and preferred to have monophyletic genera. Nanoparia may still be a paraphyletic genus, which is allowed in Linanean binomial taxonomy, or it may be that all three Pumiliopareiasaurs are similar enough to belong to single genus. For now we have retained Lee's monotypal genus; the name, taken from the Latin *pumilio* - dwarf , appropriately refers to the diminutive size of these animals. Lee 1997 p.268 MAK120401

Links Palaeocritti - Pumiliopareia pricei

Graphics: Illustration of skull from Kuhn, 1969, p.79

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Anapsida: Procolophonoidea

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--Nyctiphruretus
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |  |--Barasaurus
               |  `--+--Owenetta
               |     `--+-- Candelaria
               |        `--"Owenetta"
kitchingorum
               |?--TESTUDINES
               `--+--Sauropareion
                  `--Procolophonidae
                     |--Procolophoninae
                     `--Leptopleuroninae
```

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2. *Candelaria* X
3. *Owenetta rubidgei* X
4. *Owenetta kitchingorum* X
5. Owenettidae X
6. Procolophonoidea
7. *Sauropareion* X

Descriptions

Procolophonoidea:

Range: P-T.

Phylogeny: Procolophonia **:** *Nyctiphruretus* + ((Nycteroleteridae + Pareiasauridae) + * **:** Owenettidae + Procolophonidae.)

Characters: Close to Testudines. Post enlargement of orbit, exposing jaw musculature; concave ventral edge of skull in postorbital area. Caudal ribs not fused to centra. 3 sacral ribs. T forms had many broad or peg-like teeth, probably herbivorous. Deep quadrate emargination (? Carrol says tympanum supported by squamosal) & slender stapes. Later forms have long processes from lower cheek - like Pareiasaurs?

Links: link; link; Triassic Skulls; PANJAEA - Bone fossils gallery.

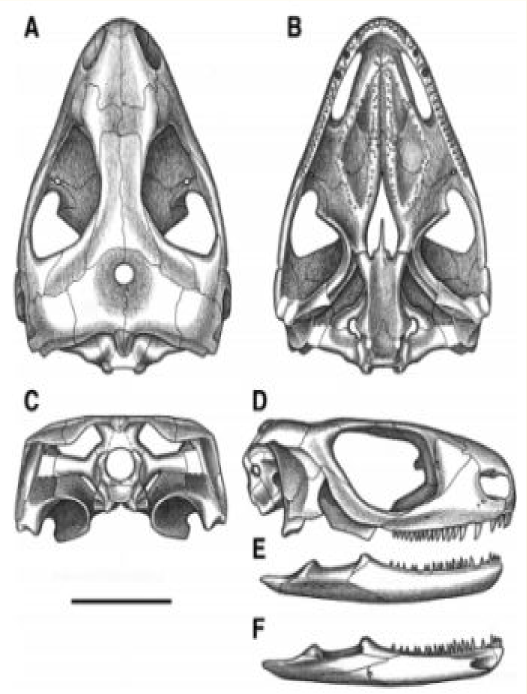
Owenettidae: Broom, 1939

Range: Permian and Triassic of South Africa, Madagascar, and South America

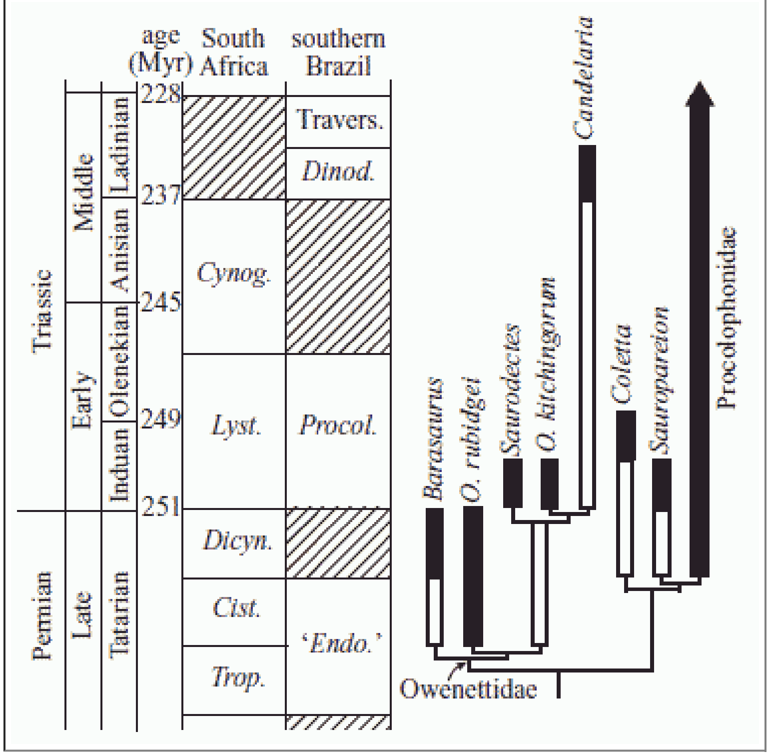
Phylogeny: Procolophonoidea **:** (*Sauropareion* + Procolophonidae) + * **:** *Barasaurus* + (*Owenetta* + (*Candelaria* + *"Owenetta" kitchingorum*)).

Characters: large pineal foramen as in therapsids; small sharp teeth (probable insectivorous diet). ATW020412. Relatively small procolophonians with broad heads and robust bodies. The family shares several synapomorphies that separate it from other related procolophonomorphs. The absence of an entepicondylar foramen is diagnostic to all members from which the humerus is known. In regards to cranial anatomy, there is no contact between the postorbital and parietal bones as a result of enlarged postfrontal bones, and the skull table is formed partly from large supratemporals lateral to the parietal bones (Reisz & Scott 2002). Smokeybjb090614 Wikipedia

Comments: *Barasaurus* and *Owenetta* have frequently been grouped with Nyctiphruretus (e.g.Romer, 1966, Ivachnenko et al 1979) but this is on the basis of shared primitive features Lee 1995. Although Owenettids seem to be more primitive than procolophonids, and appear earlier in time. Lee 1995, Reisz & Scott 2002 and subsequent workers retreive them as a monophyletic taxon, which asks the question where are the intermediaries between nyctiphruretids/nycteroleterid grade basal procolophonia and adavanced procolophonidae to be found? So it is likely that either Owenettids will turn out to be an intermediate, paraphyletic grade, at least at their base, and their apparent monophyly as sister group to their more advanced cousins (the Ceratosaur effect) or new more basal proto-procolophonids will be discovered. MAK120324



From Wikipedia: The family was constructed in 1939 for the type genus *Owenetta*. Since then several other genera have been assigned to Owenettidae, including *Barasaurus* and *Saurodektes*. The oldest known owenettid, *Owenetta rubidgei*, dates back to the Wuchiapingian stage of the Late Permian. It and two other owenettids, *Barasaurus* and *Saurodektes*, have been found from the Beaufort Group in the Karoo Basin of South Africa. These strata



Stratocladogram of procolophonoid interrelationships, including ghost lineages. The Owenettidae is here considered a monophyletic taxon that includes *Candelaria*, while the Early Triassic taxa *Coletta* and *Sauropareion* are transitional forms between the Owenettidae and Procolophonidae proper. From Cisneros et al 2004 p.1544. Note that this is a chronogram, not an example of stratocladistic analysis

span the Permo-Triassic boundary and provide evidence for the great faunal change that occurred as a result of the Permian-Triassic extinction event. Although most owenettids lived during the Permian, remains of some taxa such as "Owenetta" *kitchingorum* (soon to be placed within its own genus (Modesto et al 2003) extend the temporal range of the family into the Triassic. The youngest known owenettid is *Candelaria* from the Santa Maria Formation of Brazil, which lived during the Ladinian stage of the Middle Triassic (Cisneros et al 2004) Smokeybjb 090614

Graphic: *Owenetta kitchingorum* by Smokeybjb, Wikipedia graphics page

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Owenetta rubidgei: Broom, 1939

Range: Late Permian of Sth Afr

Phylogeny: Owenettidae **:** *Barasaurus* + ((*Candelaria* + *"Owenetta" kitchingorum*) + *)

Characters: prefrontals contacting one another medially, hence no frontal-nasal contact (convergent with derived pleurodiromorph and cryptodiromorph turtles), enlarged, V-shaped emargination on the ventral border of the cheek between the jugal and quadratojugal; extremely slender humerus (convergent with romeriids) (Lee 1997)

Comments, suggested as a possile turtle ancestor or turtle relative (Reisz & Laurin 1991)

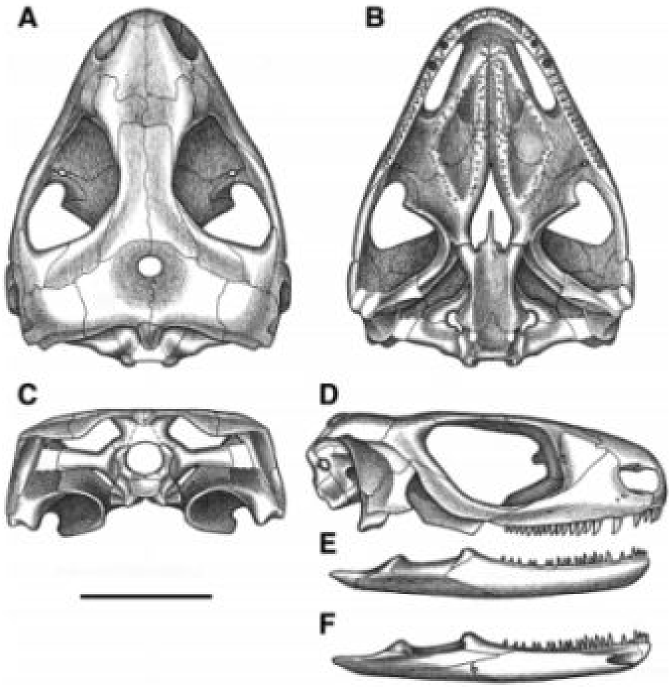
"Owenetta" kitchingorum:

Range: Palingkloof Member of the Balfour Formation, just above the P-T Boundary (Earliest Induan) of Sth Afr (Botha &Smith 2006 fig.7) extending into the lowest Katberg formation (Botha et al 2007 fig.3)

Phylogeny: Owenettidae **:** *Barasaurus* + (*Owenetta* + (*Candelaria* + *)).

Comments: Known from two nearly complete, articulated skeletons which for the first time provided detailed information on the postcranial structure of these small reptiles. On the basis of similarities with the somewhat earlier *Barasaurus*, the new clade Owenettidae was erected, although *Owenetta* differs in that the upper leg bones (humerus and femur) are long and slender compared to

Barasaurus. *O. kitchingorum* was originally placed with *Owenetta rubidgei*, indicating that the genus spanned the P-T transition (Reisz & Scott 2002). Later cladistic analysis imply that the species doesn't belong in the genus, although this is not to reject the possibility that it may have evolved from it (or the genus *Owenetta* may include bothe species but be paraphyletic). It is now placed closer to *Candelaria*, indicating a derived clade that survived the P-T extinction event (Cisneros et al. 2004, Tsuji & Müller 2009) MAK120323.



Owenetta kitchingorum. Skull reconstruction in (A) dorsal, (B) palatal, (C) occipital, and (D) right lateral views. Reconstruction of mandible in (E) lateral and (F) medial views. Scale equals 1 cm. Drawing and caption from Reisz & Scott 2002 fig.6

Candelaria barbouri (Price 1947)

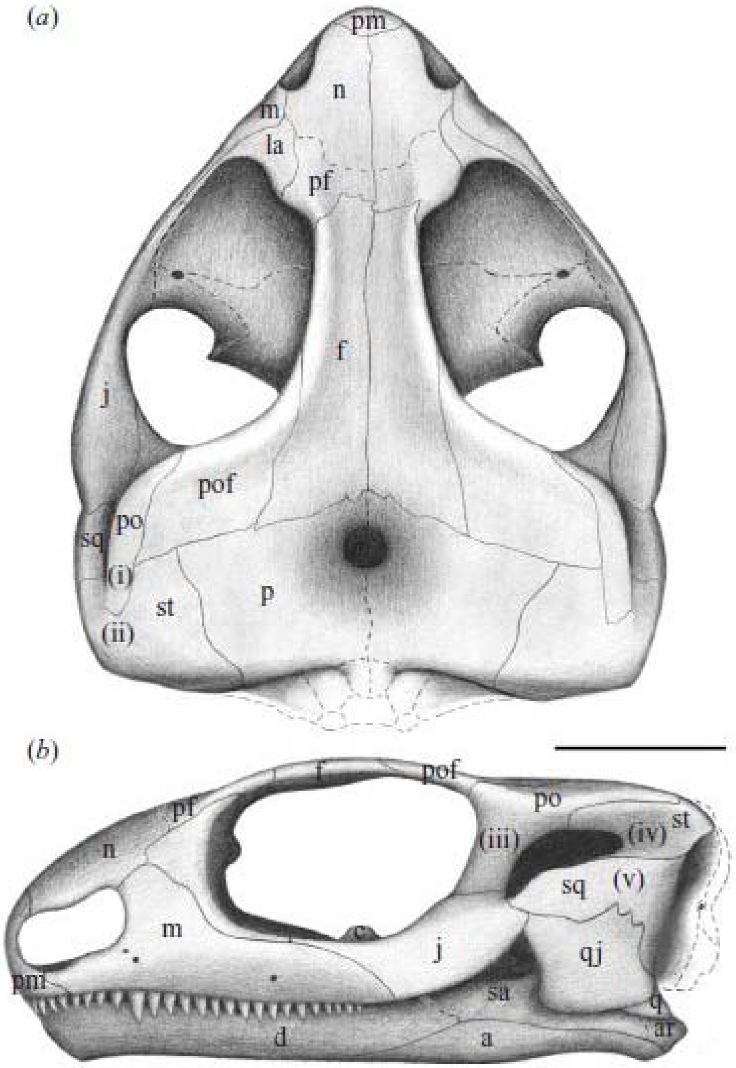
Range: Candelaria County, Rio Grande do Sul State, Brazil. Dinodontosaurus Cenozone of the Santa Maria Formation (Parana Basin), Ladinian (late Middle Triassic) age

Phylogeny: Owenettidae **:** *Barasaurus* + (*Owenetta* + (*"Owenetta" kitchingorum* + *)).

Reconstruction of the skull of *Candelaria barbouri* (Price 1947) (a) Dorsal view; and (b) left lateral view. from Cisneros et al. 2004, Cisneros 2006. Characters (i)-(v) relate to the temporal fenestra (see diagram).

i. posterior process of the postorbital present, which extends well into the supratemporal;
ii. lateral notch of supratemporal absent;
iii. thin concave temporal bar present posterior to the orbitotemporal fenestra;
iv. supratemporal expanded ventrally;
v. squamosal dorsoventrally narrow but anteroposteriorly elongate.

Abbreviations: a, angular; ar, articular; c, coronoid process; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal. Scale bar, 1 cm.



Comments: the most recent owenettid, which shows that the group survived well into the Triassic. This fills in some of the stratigraphic gap between the last owenettids and the first turtles, which supports the idea of chelonians descending from an owenettid-type reptile (Reisz & Laurin 1991)., although *Candelaria* itself is too specialised to be an actual ancestor. *Candelaria* is distinguished from all other owenettids by its relatively large size (at least 30% larger than all other known owenettids) and by a suite of characters related to the presence of a temporal fenestra Cisneros et al. 2004, see diagram and text at right

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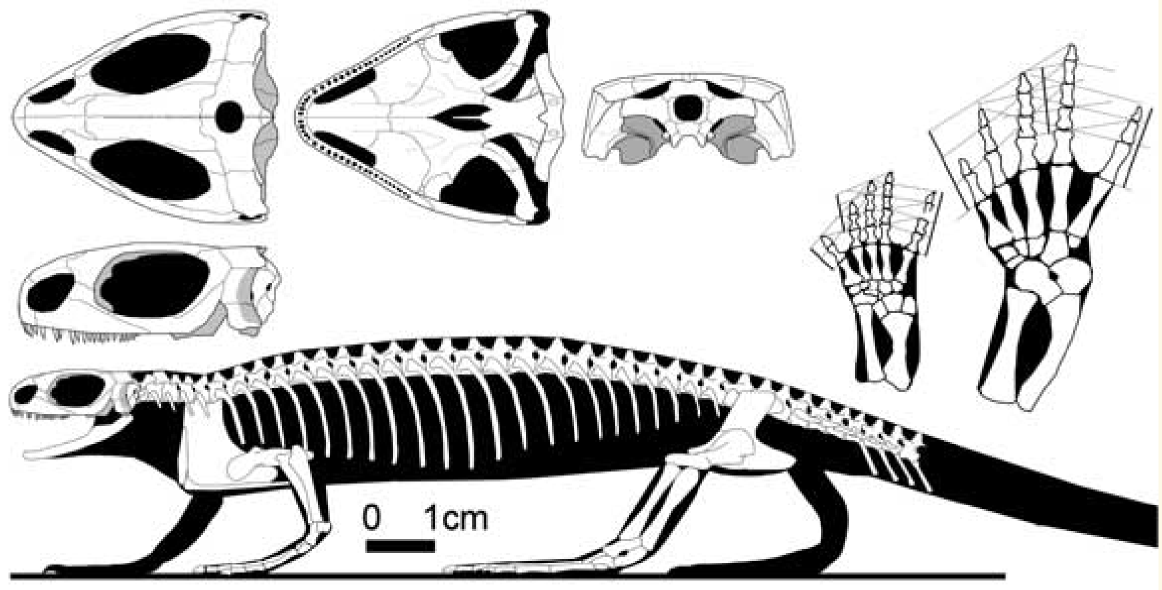

Barasaurus besairiei Piveteau 1955

Range: Late Permian of Madagascar

Phylogeny: Owenettidae : (*Owenetta* + (*Candelaria* + *"Owenetta" kitchingorum*)) + *.

Comments: An unusual, small-headed form, with a longer torso and larger hands and feet than earlier anapsids, indicating herbivorous specialisations similar to those of caesids and other big-bodied plant eaters. Although similar to *"Owenetta" kitchingorum* (Reisz & Scott 2002), cladistic analysis reveals it to be a more basal Owenettid (Cisneros et al. 2004, Tsuji & Müller 2009). The Barasaurus and the owenettids would then represent a distinct and parallel evolutionary lineage, one of a number of parallel experiments in herbivory among the procolophonids, and distinct from the more specialised later forms. MAK120323

Graphics Skeletal reconstruction © David Peters, used with permission

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Anapsida: : Procolophonidae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
                  |--Sauropareion
                  `--+--Phaanthosaurus
                     `--+--Theledectinae
                        `--+--Tichvinskia
                           `--"Horned
procolophonids"
                               |--Procolophoninae
                               |  |--Eumetabolodon
                               |  `--Procolophon
                               `--Leptopleuroninae
```

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7. *Sauropareion* X
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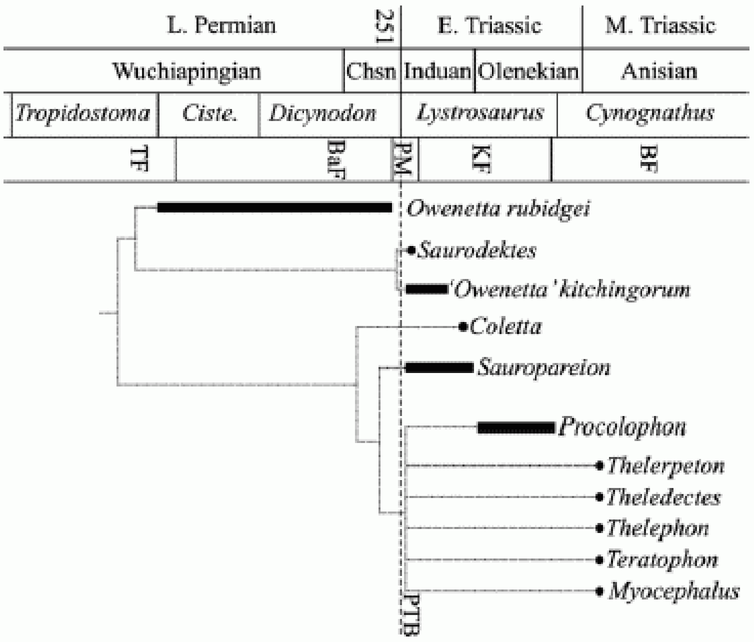
The Procolophonids - tough survivors in a harsh new world

The Procolophonidae are a group of early herbivorous reptiles of the anapsid lineage that attained a world-wide distribution during the Triassic period. They were small stocky creatures, with blunt chisel-like teeth and triangular skulls. They seemed to come from nowhere following the P-T extinction event, to dominate the Triassic microvertebrates niche.

In fact, the procolophonids had three things going for them: the ability to feed on tough fibrous vegetation, an armour of defensive spines, and the ability to dick and burrow, which, as with modern burrowers, would have surved both to hide from predators and to survive the excessive heat of the day

A Triassic success story

Although there are a number of fragmentary Permian remains attributed to procolophonids, the family only is known with certainty from the earliest Triassic. Along with temnospondyls, cynodonts, and the dicynodont Lystrosaurus, earliest Triassic owenettids and procolophonids were important components of the post-extinction recovery fauna. In South Africa three species of procolophonoids (the owenettids *Owenetta kitchingorum* and *Saurodektes rogersorum* and the procolophonid *Sauropareion anoplus*) are known only from the Palingkloof Member of the Balfour Formation, the very lowest part of the Lystrosaurus zone, no more than 30 m above the Permo-Triassic boundary (Botha et al 2007). We are looking at a sudden and amazing evolutionary radiation occuring within only tens of thousand sof years of the main extinct event, perhaps less.



Cladogram of procolophonoids plotted against the South African Permo-Triassic biostratigraphy. Vertical bars and solid circles indicate taxon ranges and single specimen occurrences, respectively. Abbreviations: Chsn, Changhsingian; Ciste., Cistecephalus Assemblage Zone; PTB, Permo-Triassic boundary. Numbers indicate millions of years ago. Diagram and caption from Botha et al 2007

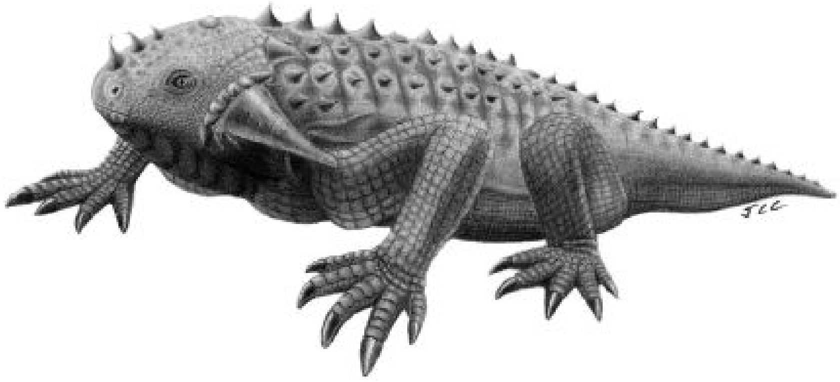
But these sorts of logarithmic differences in timescales are hard to represent diagramatically. This is the reason why the stylised chrono-cladogram, whilst providing very useful information regarding the stratigraphic range of the various taxa, it does not do justice to the suddeness of the procolophonid story. Because logarithmic distinctions in timescales are hard to present against a uniform geological timescale (which deals with increments millions of years or more), the diagram shows what look like (if it is taken literally), a number of ghost lineages reaching back into the Permian. But it is more reasonable to assume that the great procolophonian adaptive radiation really only occurred *after* the P-T extinction event, in the earliest Triassic. The same thing happened with earliest Cenozoic mammals, as the fossil record unambiguously shows.

It may even be that the evolutionary radiation of survivors into suddenly totally empty niches may have been so rapid as to have taken mere centuries or millennia, or at most tens of thousands of years immediately after the P-T event (or between several extinction pulses). At this scale, where direct ancestors-descendent reklationships are involved, there is no need to avoid paraphyly the way standard cladistics does, because every instance of speciation is by its very nature a paraphyletic process. We know that species can give rise to other species by several means, perhaps the most common being budding (when geographically isolated populations undergo rapid genetic drift); less common would be anagenesis (where one species slowly evolves into a another) and splitting (like anagenesis but with several descendent species). Reading the diagram from a gradist perspective therefore, we would speculate that at the PT-boundary, still in the midst of the extinction event, there is an immediate evolutionary radiation, where *Owenetta rubidgei* quickly evolves into both *Saurodektes rogersorum* and *Owenetta kitchingorum* (which implies that *S. rogersorum* should perhaps be renamed *Owenetta rogersorum*). Procolophonids may also have appeared as part of this same adaptive radiation, beginning with a number of early types, before the rise of the very successful, indeed ubiquitous and cosmopoliton *Procolophon trigoniceps*. A quantum leap beyond its predecessors, larger, better armoured, able to digest tougher plant material, *P. trigoniceps* dominated Gondwana for all of the middle and late Early Triassic, before giving rise to further species which, although here oversplit in a bewildering array of genera, should probably just beconsiderd further species of the genus *Procolophon*. In the northern part of Pangea meanwhile, a rival development emerged, the Leptopleuronines. Between them, these two groups would be the rabbits of the Triassic, abundant small burrowing herbivores, pre-adapted to harsh conditions, able to flourish wherever they go MAK120402

Dig baby dig

The procolophonid's first line of defence was a protective burrow. The hypothesis that procolophonids were burrowers is a popular and persuasive one. It was first suggested with the discovery of *Procolophon trigoniceps* remains found within a burrow-cast (Groenewald 1991). Since then, many other suggetsions and observations have been made. *Leptopleuron lacertinum* possesses several morphological traits that are associated with a burrowing mode of life (Säilä 2010a). The related *Hypsognathus fenneri* lacks cranial kinesis, which may reflect a burrowing lifestyle (Sues et al. 2000). All three known specimens of *Koiloskiosaurus coburgensis* are preserved together, dorsal up and in the same orientation, which makes sense if the three individuals were occupying a burrow (Botha-Brink and Modesto (2007)). The wide flat body of *Procolophon* is proportionally quite similar to that of the extant horned lizard *Phrynosoma* which burrows in loose sand (deBraga 2003). But these are all advanced species. What is most intersting is that from the very start, their most primitive and earliest forms, procolophonids were burrowers. this is evident from *Sauropareion anoplus*, which we have already seen is one of those little animals that appeared suddenly in the imediarte aftermath of the P-T exutinction event. It exhibits skeletal modifications such as the presence of a spade-shaped skull, robust phalanges, and large unguals, all associated with digging and burrowing (MacDougall et al 2012). While neither large nor armoured, it could certainly conceal itself from preditors.

Prickly customers



Life reconstruction of *Procolophon trigoniceps* from Cisneros 2006 p.58. In this illustration the quadratojugal processes (cheek bones) are covered by long keratinous spines, and there are also large digging-claws. Keratinous spines are common in large or stocky-bodied modern lizards like *Iguana, Phrynosoma*, and *Uromastyx*, and *P. trigoniceps* and other advancxed procolophonids probably were similarly equipped. Long quadratojugal and supratemporal spines on *Procolophon* and on leptopleuronines doubtless served as anti-predatory mechanism, as with extant phrynosomatid lizards (Young et al., 2004, cited in Cisneros 2006).

Two recent equivalents of the procolophonidae: (1) the Thorny Devil *Moloch horridus* (Squamata - Agamidae), central and western Australia. Length upto 20cm. These reptiles live almost exclusively on ants
Photograph by Wouter!, aka Retuow, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

(2) the American Desert Horned Lizard or "horny toad" *Phrynosoma platyrhinos* - (Squamata - Iguania - Phrynosomatidae) of western North America. Length about 10 cm. An ant-eater like Moloch (by means of convergent evolution, as the two are only distantly related)
Photo by Chris Brown USGS, (via wikimedia), Public domain

If you look at a life reconstruction of *Procolophon* you wonder how such a soft plump looking little animal, easy pickings for a hungry *Thrinaxodon*, could have survived and flourished worldwide for several millions of years (and the family overall for 50 million). In fact, *procolophon* probably looked much more like modern spiny desert lizards like the Australian Thorny Devil and American Horned Lizard, shown above.Spines would have provided protection from preditors, and in addition, there was the ability to burrow. Procolophonids had a low broad body, very much like like *Phrynosoma* but several times as long. In addition, unlike modern thorny or hormed lizards, but like the iguana, they were herbivores; the larger size was probably required for food processed

Eats roots and leaves

More efficient food processing was certainly one the keys to procolophonid success. This is revealed in the evolution of progressively more efficient teeth, which doubtless accompanied many soft-body physiological adaptions. While early forms (e.g. *Tichvinskia vjatkensis*) were still omnivores that would have fed on hard skinned insects as well as tough plant matter, the development of labiolingually expanded crowns enabled a diet of high-fiber plant matter, a niche thatr was convergently exploited by several different evolutionary lines. In the case of the bigger and more advanced forms such as most procolophonines and leptopleuronines, large molar-like teeth developed for processing tough, fibrous foods (Cisneros 2006 p.101) MAK120326

Descriptions

Procolophonidae: Lydekker 1890 (or Cope, 1889)

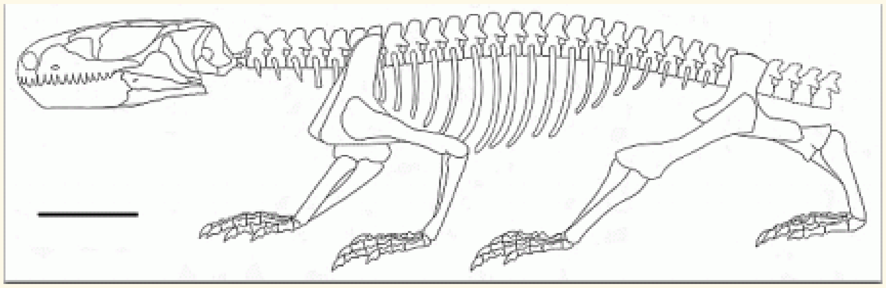
Phylogenetic definition: All taxa more closely related to *Procolophon trigoniceps* Owen 1876 than to *Owenetta rubidgei* Broom 1939. (Cisneros 2006 p.92)

Range: Late Perm? Triassic, Cosm.

Phylogeny: Procolophonoidea **:** Owenettidae + * **:** *Sauropareion* + (*Phaanthosaurus* + (Theledectinae + (*Tichvinskia* + (Procolophoninae + Leptopleuroninae)))).

Comments: Here based on cladistic systematics. Of the three traditional subfamilies, Procolophoninae and Leptopleuroninae are monophyletic, Spondylolestinae is paraphyletic (Cisneros 2006 p.108)

Saurопareion anoplus Modesto, Sues and Damiani 2001



Range: Palingkloof Member of the Balfour Formation and lower strata of the Katberg Formation, Beaufort Group, Karoo Supergroup, Induan portion of the Lystrosaurus Assemblage Zone, just above the P-T Boundary (Earliest Induan) of Sth Afr

Phylogeny: Procolophonidae **:** (*Phaanthosaurus* + (Theledectinae + (*Tichvinskia* + (Procolophoninae + Leptopleuroninae)))) + *.

Size: skull length ~3 cm.

Characters: deep posteromedian emargination of the skull table, deep occipital shelves of the parietals and supratemporals, posteroventral facial process of the quadratojugal. (Modesto et al 2001)

Comments: Known from three partial skeletons from Vangfontein, Middelburg District, South Africa. The proportions of the body are similar to those of extant digging animals, and the animal seems to well represent burrowing abilities that would have characterised the procolophonidae as a whole. These include a spade-shaped skull (suitable for moving and packing soil, as with various extant mammals, such as the golden mole, marsupial mole, and mole-rat). While the limbs are not heavily modified for digging, possessing none of the modifications that would increase the mechanical advantage of the limb, such as elongated acromion and olecranon processes found in moles, ground squirrels and aardvarks, which provide a larger area for muscle attachment. But the unguals are relatively large, making them suitable for digging. The non-terminal phalanges are short and robust, which makes the fore and hind feet rigid so they can endure mechanical forces when digging; the modern gopher tortoise has a similar adaptation. While not having the extreme limb modifications seen in some mammals, this would not prevent burrowing abilities (MacDougall et al 2012). Apart from or along with the related *Coletta seca* (known froma single skull found somewhat higher in the Katberg Formation (Lystrosaurus zone) (Botha &Smith 2006, Botha et al 2007)) this is the most basal procolophonid (Cisneros 2006, Cisneros & Ruta 2010, MacDougall et al 2012). These animals, like the contemporary *Owenetta kitchingorum*, show that owenettids happily survived the P-T extinction event (Modesto et al 2001).

Graphics Skeletal reconstruction from MacDougall et al 2012. Scale bar equals 2 cm

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Phaanthosaurus ignatjevi Tchudinov & Vjuschkov, 1956

Range: Vokhmian Gorizont, Induan, Russia

Phylogeny: Procolophonidae **:** *Sauropareion* + ((Theledectinae + (*Tichvinskia* + (Procolophoninae + Leptopleuroninae))) + *).

Theledectinae Cisneros 2006 **:** *Theledectes perforatus*, *Eumetabolodon dongshengensis* and the Arcadia procolophonid.

Range: Early Triassic of China and Aus,

Phylogeny: Procolophonidae **:** *Sauropareion* + (*Phaanthosaurus* + ((*Tichvinskia* + (Procolophoninae + Leptopleuroninae)) + *)).

Comments: Cisneros (2006)'s analysis recovered a previously unrecognized clade of procolophonids from south and east Pangaea. This includes a new unnamed procolophonid from the Arcadia Formation of Australia. The Theledectines are small procolophonids distinguished by enlarged, monocuspid marginal teeth with circular bases. These are different from those of *Nyctiphruretus* or the owenettids, which although they also have circular bases are thinner and sharper (Cisneros 2006 pp.93-4)

Tichvinskia vjatkensis Tchudinov & Vjuschkov, 1956

Range: Rybiskian Gorizont, Olenekian, Russia

Phylogeny: Procolophonidae **:** *Sauropareion* + (*Phaanthosaurus* + (Theledectinae + ((Procolophoninae + Leptopleuroninae) + *))).

Size: length: 25 cm,

Link: Palaeocritti

Unnamed clade ("Horned Procolophonids") **:** "crown group" [1] procolophonids

Phylogenetic definition: Procolophoninae and Leptopleuroninae (node based) (Cisneros 2006)

Range: Triassic, Cosm.

Phylogeny: Procolophonidae **:** *Sauropareion* + (*Phaanthosaurus* + (Theledectinae + (*Tichvinskia* + * **:** Procolophoninae + Leptopleuroninae))).

Comments: This unnamed clade might perhaps be called "Ceratoprocolophonia", as its members can be readily identified by the presence of quadratojugal horns. Also characterized by a more robust build, notably a wide rib cage, and a considerably larger size in comparison to earlier procolophonids and owenettids. (Cisneros 2006 pp.94-5). This clade (including *Tichvinskia*) showed a significant shifts in diversification rates relative to other anapsids (parareptiles) (Tsuji & Müller 2009), indicating the success of the procolophonid adaptive radiation during the Triassic. MAK120329

Notes: [1] using the cladistic term "crown group" here in a non-anthropocentric and non-neontological context

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Procolophoninae Procolophoninae Lydekker 1890 Procolophoninae Seeley, 1888 emend. Romer, 1956, Ivakhnenko, 1979 **:** *Procolophon*, *Eumetabolodon*, *Thelerpeton*, *Teratophon*

Phylogenetic definition: All taxa more related to *Procolophon trigoniceps* Owen 1876 than to *Leptopleuron lacertinum* Owen 1851. (Cisneros 2006 p.92)

Range: Eartly to Mid Triassic, Sth Afr, China, Ant, Sth Am.

Phylogeny: Procolophonidae **:** *Sauropareion* + (*Phaanthosaurus* + (Theledectinae + (*Tichvinskia* + ("Horned procolophonids" **:** Leptopleuroninae + * **:** *Eumetabolodon* + *Procolophon*)))).

Characters: Snout deep and short, postfrontal contacts frontal and parietal only. (Cisneros 2006)

Comments: By inclusion of *Procolophon* this group represents "typical" procolophonids of the early Triassic. The clade recovered by Cisneros 2006 is not well supported, requiring only one step to collapse. Some of the taxa, such as *Kapes*, have elsewhere been assigned to the Leptopleuroninae (Säilä, 2008). MacDougall et al 2012 recovered four members of this clade: *Procolophon trigoniceps*, *Thelerpeton (Thelegnathus) oppressus*, *Teratophon (Thelegnathus) spinigenis* (these three of the Early-Middle Triassic Cynognathus zone, (Olenekian-Anisian) of South Africa), and *Eumetabolodon bathycephalus*. This is also the same as a one-step suboptimal scenario by Cisneros 2006 ("clade L").

Eumetabolodon bathycephalus Li, 1983

Horizon: Upper He Shang Gou Formation (Early Triassic), Shaanxi and Nei Monggol, Inner Mongolia, North China.

Phylogeny: Procolophoninae **:** *Procolophon* + *).

Size: skull length: 6 cm

Characters: short high skull, short snout, forward positioned pineal foramen ("third eye") partially bordered by frontals, and long, posterior (rearward) located jaw articulation are all unique features among procolophonids (Lucas 2001 p.99).

Comments: Known from numerous skulls and skull fragments, *Eumetabolodon bathycephalus* is a typical member of the Procolophonid family, similar to the Gondwanan *Procolophon* and the European *Koiloskiosaurus*, all charactrerised by classic features such as triangular skull, large orbits, and a small number of transversely broad, bicuspid teeth. The 18 known skulls of *Eumetabolodon* fall into four size classes and allow tooth replacement during ontogeny to be analyzed. The study by Li (1983) shows evidence of tooth replacement during growth, in which conical teeth postcanine teteh in juveniles (implying an insectivorous diet) were replaced by transversely broad, bicuspid teeth in adults (implying a herbivorous lifestyle); hence the name "changeable tooth". (Lucas 2001 p.99). Two species have been placed here; *E. bathycephalus* is the best known taxon, whilst another species, *E. dongshengensis* has also been described based on a poorly preserved partial skull. Cladistic analysis by (Cisneros 2006 indicates that *Eumetabolodon* is a paraphyletic or polyphyletic genus: *Eumetabolodon bathycephalus* is a procolophonine, whereas *E. dongshengensis* is a theledectine and must be placed in a new genus (Cisneros 2006 p.108)

Link: Palaeocritti

Procolophon: Owen 1876

Synonyms: *Procolophon baini* Broom 1905, *Procolophon brasiliensis* Cisneros and Schultz 2002, *Procolophon cuneiceps* Seeley 1878, *Procolophon griersoni* Seeley 1878, *Procolophon laticeps* Seeley 1878, *Procolophon minor* Owen 1876, *Procolophon platyrhinus* Seeley 1905, *Procolophon pricei* Lavina 1983, *Procolophon sphenorhinus* Seeley 1905 (ref Paleobiology Database)

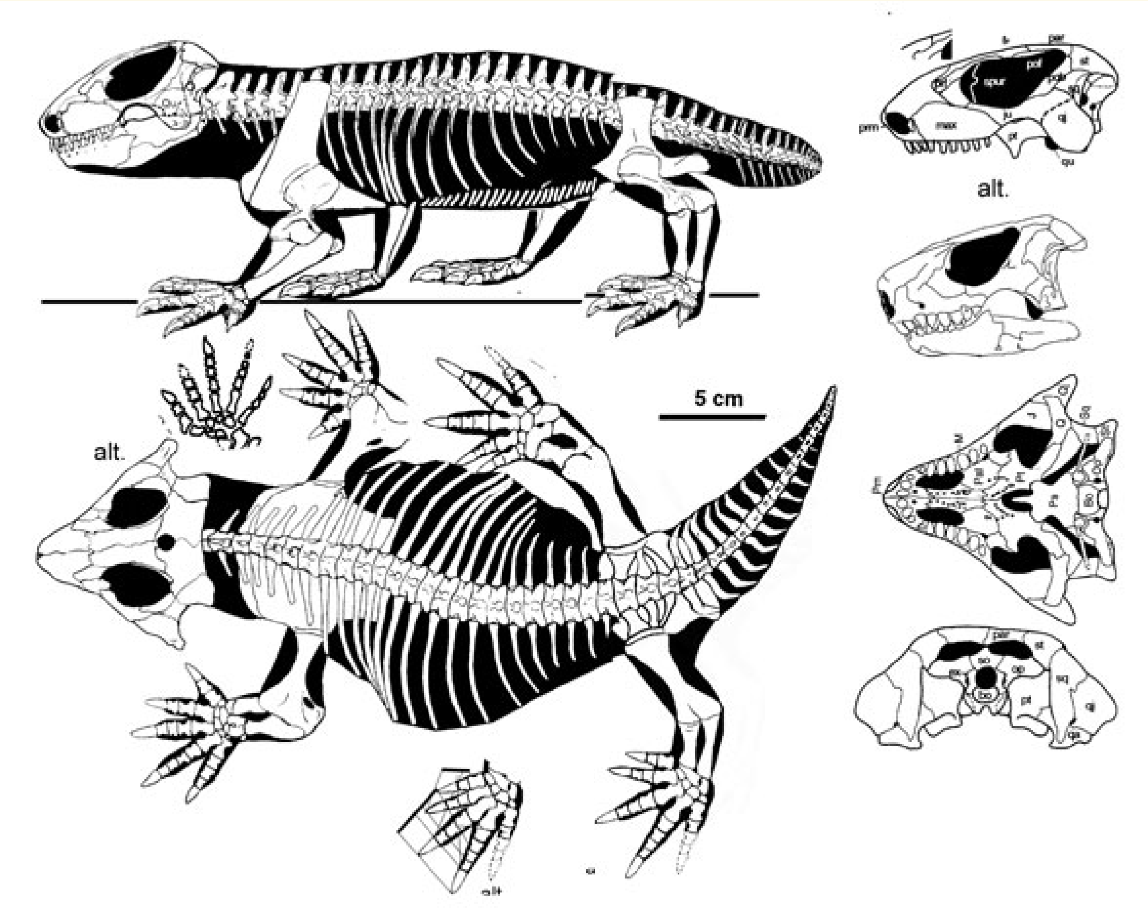
Range: Early Triassic (Middle Lystrosaurus zone, Induan to Early Cynognathus zone, Olenkian), South Africa, Antarctica, and Brazil (pan-gondwanan).

Horizons. Lower Katberg Formation (upper Lystrosaurus zone) to lower part of the Burgersdorp Formation ((Cynognathus Subzone A = lowermost Langbergia Subzone, Late Induan-Olenekian). of the Karoo Basin, Fremouw Formation of the Transantarctic Basin (Kitching et al. 1972; Colbert and Kitching 1975) and the Sanga do Cabral Formation of the Parana Basin in Brazil (Barberena et al. 1981; Lavina 1983). (Cisneros 2006 pp.35, 47-8)

Phylogeny: Procolophoninae **:** *Eumetabolodon* + *.

Size: Length: 30 cm

Comments: The eponymous representative of the Procolophonidae (to say nothing of the Procolophonoidea, the Procolophonia, and the Procolopnonomorpha...), known from hundreds of specimens, most of them found in the Lower Triassic sediments of the South African Karoo, where it is outnumbered only by the ubiquitous *Lystrosaurus*, this long-lived and widespread species can quite plausibly be assumed to have evolved from smaller, more primitive, stratigraphically earlier Triassic forms like *Sauropareion*, which it would have replaced or supplanted.



In the past included under paraphyletic orders like the Cotylosauria (Watson 1914, Colbert, 1969, Kuhn, 1969) and Captorhinida Carroll, 1988 it is now considered a representative of the anapsid or parareptile lineage. While too specialised to be directly ancestral to turtles, it still may be close to the turtle line in the interpretation we have followed here (Reisz and Laurin 1991), although the question of turtle origins remains controversial and it may be that the procolophonoidea alone (Lee 1995) or the parareptilia as a whole Rieppel & deBraga 1996 are an entirely extinct lineage

Like other advanced procolophonids, *Procolophon* possesses a robust, wide torso (imagine an oversized desert horned "toad") and enlarged chisel-like teeth, suggesting a high-fibre diet (Gow, 1977, Hotton et al. 1997). Limb adaptations show *Procolophon* was capable of burrowing (deBraga 2003), and this species is most likely the author of burrows whose solidified casts have been recovered from the Lystrosaurus Assemblage Zone (Groenewald 1991).

The prominent horn-like quadratojugal processes on the side of the skull give the head a distinctive triangular shape. Unusually but not uniquely for early anpasids, some individuals have temporal openings, which have in the past been interpreted as different species (Hamley & Thulborn 1993).

As fossils are known across a wide geographical range, from the South African Karoo to the Transantarctic Mountains to the Parana Basin in Brazil, it can reasonably be assumed that the actual distribution of the living animal was across the whole of in Gondwana. *P. trigoniceps* persists into the latest Early Triassic (Early *Cynognathus* Zone), co-existing with the diapsid *Palacrodon* and the temnospondyl amphibian *Trematosuchus*. Although more than half a dozen species have been recognised in the past, including recently *P. pricei* and *P. brasiliensis* from the contemporary (Lystrosaurus assemblage age) Sanga do Cabral Formation of Brazil (Cisneros & Schultz 2002), these are now understood as synonyms or variants of a single species, *P. trigoniceps*

Later in the *Cynognathus* zone (early Anisian, earliest middle Triassic), *Procolophon*'s place is taken by a confusion of poorly described and repetitatively named taxa such as *Theledectes*, *Thelegnathus*, *Thelerpeton*, *Thelephon*, with a single *Teratophon* to add a little nomenclatural diversity to the mix. Cladistic analysis (Cisneros 2006) resolves *Thelerpeton*, and *Teratophon* as close to Procolophon, so it is not unlikely that would represent variations of a single chronospecies. *Theledectes* appears in tehs ame analysis as an unrelated, more primitive form. *Thelephon* seems to be part of a transitional clade related to or a basal member of the the leptopleuronines, and *Thelegnathus* is a polyphyletic taxon or a nomen dubium.

References: Cisneros 2006 pp.35, 47-8, 95-6,

Links: Palaeocritti, Wikipedia, Paleobiology Database MAK120327

Graphics Skeletal reconstruction © David Peters, used with permission

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Anapsida: Procolophonidae: Leptopleuroninae

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |  `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |  `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

|--Procolophoninae `--Leptopleuroninae |--*Anomoiodon* `--+--*Phonodus* |--*Neoprocolophon* `--+--*Sclerosaurus* `--Leptopleuronini |--*Leptopleuron* `--*Hypsognathus*

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2. *Hypsognathus* X
3. *Leptopleuron* X
4. Leptopleuronini X
5. Leptopleuroninae X
6. *Neoprocolophon* X
7. *Phonodus* X
8. *Sclerosaurus* X

Descriptions

Leptopleuroninae Ivakhnenko 1979 = Telerpetontidae Lydekker, 1888

Phylogenetic definition: All taxa more closely related to *Leptopleuron lacertinum* Owen 1851 than to *Procolophon trigoniceps* Owen 1876 (Cisneros 2006)

Range: Triassic of Eur, Nth Am, China, Brazil

Phylogeny: Procolophonidae **:::** "Horned procolophonids" **:** Procolophoninae + * **:** *Anomoiodon* + (*Phonodus* + *Neoprocolophon* + (*Sclerosaurus* + Leptopleuronini))

Phylogeny: Leptopleuronini **:** *Leptopleuron* + *Hypsognathus*.

Comments: the most specialised of the procolophonoids, they seem to have evolved in northern Pangea, and hasd supplanted or replaced procolophonines by the late Triassic. Telerpetontidae is the older term and perhaps should be used instead, even if *Telerpeton* is the junior synonym for Leptopleuron (see comments regarding Podokesauridae and Coelophysidae); for now we have retained the more familiar term as that is the one used in current literature MAK120328

Anomoiodon liliensterni von Huene, 1939

Horizon: Lowest layer of the Chirotherium Sandstone (Middle Bundsandstein) of Reurieth, near Hildburghausen, Germany, Late Olenekian.

Phylogeny: Leptopleuroninae **:** (*Phonodus* + *Neoprocolophon* + (*Sclerosaurus* + Leptopleuronini)) + *

Phylogeny: Leptopleuronini **:** *Leptopleuron* + *Hypsognathus*.

Size: overall length 10 cm

Comments: Known from two partial skeletons, this poorly known tiny procolophonid was thought to be synonym of *Kapes* of Russia (Spencer & Storrs, 2002). Cisneros 2006 recovered an unexpected procoplophonine clade consisting of the South African *Thelephon* (or *Thelegnathus*) *contritus* and the Laurasian genus *Kapes*, known only from tooth bearing fragments. Tsuji and Müller 2009 in their review of the Parareptilia include a very large cladogram, incorporating Cisneros' data for procolophonoids, in which *Kapes* and *Anomoiodon* are sister taxa in the aforementioned unnamed clade But before this, when a mold of the holotype of *Anomoiodon liliensterni* resurfaced in the Berlin Museum. Laura K. Säilä 2008 studied the specimen and, although likewise concluding that *Anomoiodon* is a sister taxon of *Kapes*, placing it at the base of the Leptopleurinae rather than the Procolophoninae. (Palaeocritti). It may well be then that *Anomoiodon* and its relatives are true transitional forms, procolophonines in the process of becoming leptopleuronines MAK120328

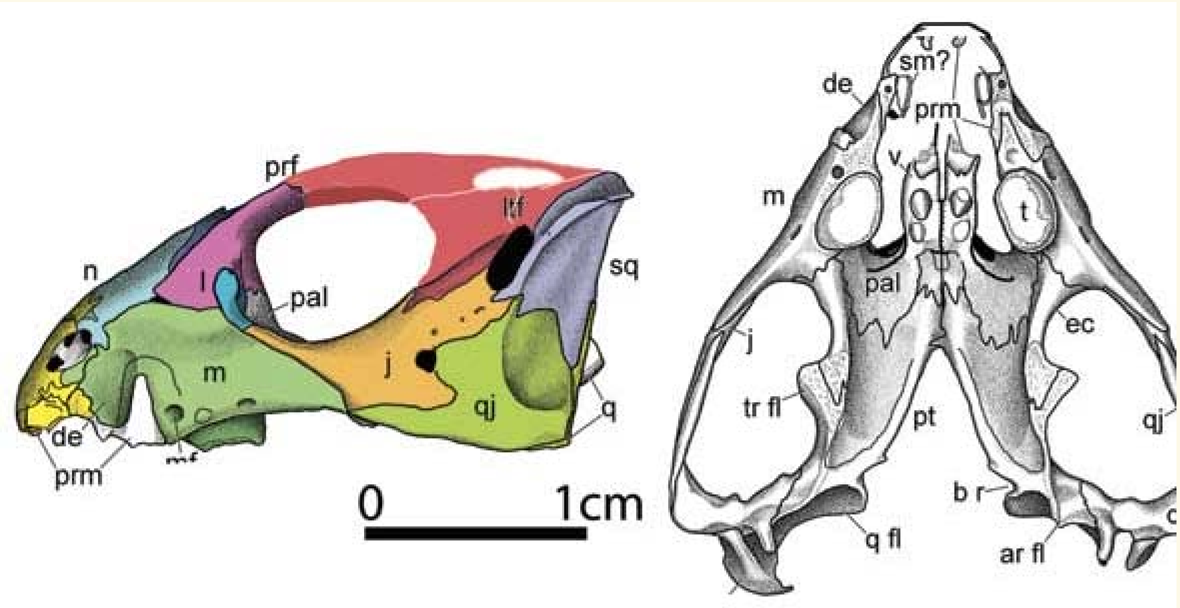
Phonodus dutoitorum: Modesto et al. 2010

Range: Katberg Formation in South Africa (Induan - Early Triassic)

Phylogeny: Leptopleuroninae **:** *Anomoiodon* + (*Neoprocolophon* +

(*Sclerosaurus* + Leptopleuronini) + *).

Size: skull length ~2cm



Comments: Known only from a single tiny skull, reminiscent of miniature placodont such as *Placodus* or *Paraplacodus*. On this basis, David Peters argues that *Phonodus* actually *is* a basal placodont. Since placodonts are themselves highly derived in respect to the original sauropterygian condition (which was more of a standard long-necked marine lizard type thing) we feel that such simlarities in the shape of the skull of , these can be much better explained as convergences. *Phonodus* is the oldest known member of the subfamily Leptopleuroninae, and was likely the result of a procolophonid migration into the Karoo Basin from Laurasia after the Permo-Triassic extinction event. Because *Phonodus* had large maxillary teeth underneath a large antorbital buttress (a bony prominence in front of the eye), and a lack of ventral temporal emargination along the side of the skull, it probably had a durophagous diet. (Modesto et al. 2010) Wikipedia, which might explain the placodont convergences, although there is no guarantee that placodonts themselves even were mollusc eaters (Diedrich 2011)

Graphics Skull reconstruction copied from David Peters

Neoprocolophon asiaticus Young, 1957

Range: Yushe, Shanxi, China; Ningwuan land vertebrate faunachron, Anisian (Lucas 2001)

Phylogeny: Leptopleuroninae **:** *Anomoiodon* + *Phonodus* + ((*Sclerosaurus* + Leptopleuronini) + *)

Comments: known from a single skull which closely resembles that of *Procolophon*, but differs in the very anterior (towards the front of the skull) placement of the gradatojugal "horns" (Lucas 2001 p.103). Stratigraphically younger than the procolophonid *Eumetabolodon*. Cisneros 2006 found the Chinese procolophonids *Pentaedrusaurus ordosianus* and *Neoprocolophon asiaticus* resolved as the most primitive members of the Leptopleuroninae, with *Pentaedrusaurus* being more basal than *Neoprocolophon*. MAK120329

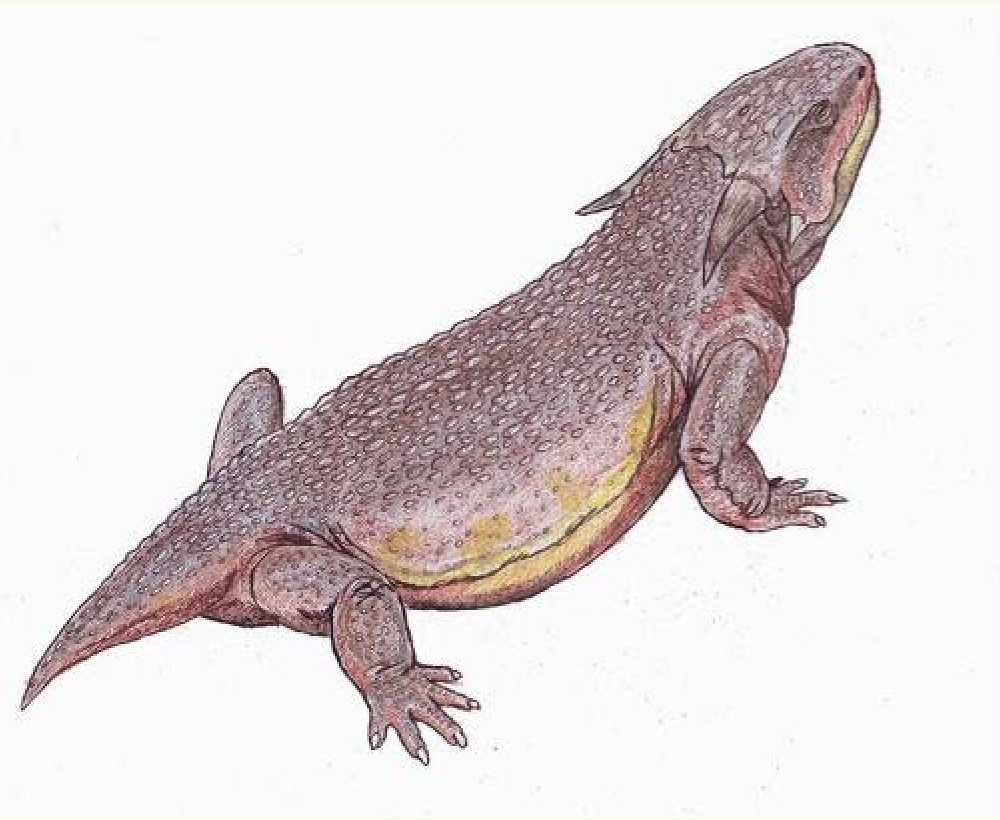
Unnamed clade : *Sclerosaurus, Leptopleuron, Hypsognathus*

Range: Triassic of Eur, Nth Am & Sth Am

Phylogeny: Leptopleuroninae **:** *Anomoiodon* + (*Phonodus* + *Neoprocolophon* + * **:** *Sclerosaurus* + Leptopleuronini)

Characters: Two or more quadratojugal spines; two jugal spines; convex temporal ventral margin; no maxillary depression. (Cisneros 2006 p.98).

Comments: Cisneros 2006 found the the sclerosaurines (Sclerosaurus armatus + Scoloparia glyphanodon) and the leptopleuronines (Leptopleuron lacertinum, Soturnia caliodon and Hypsognathus fenneri.) to be the best supported clade within the Procolophonidae ("Clade P"). It consists of derived leptopleuronines with very distinctive characteristics, such as the presence of multiple cranial spines. MAK120328



Sclerosaurus armatus: von Meyer in Fischer, 1857; monotypal family Sclerosauridae

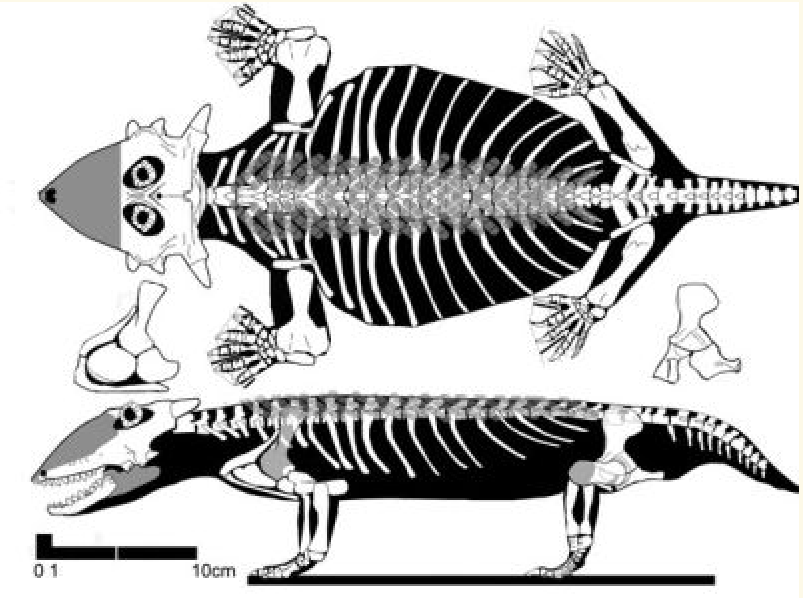
Synonyms *Labyrinthodon ruetimeyeri* Wiedersheim, 1878; *Aristodesmus ruetimeyeri* (Wiedersheim, 1878) Seeley, 1896.

Range: Upper Middle to Upper Buntsandstein (Olenekian-Anisian) of southern Germany and northern Switzerland

Phylogeny: Leptopleuroninae : *Anomoiodon* + *Phonodus* + (*Neoprocolophon* + (Leptopleuronini + *)).

Characters: distinguished from other known parareptiles by the possession of long, posterolaterally projecting spikes formed by supratemporals, posterior dentary teeth with mesiolingually aligned and slightly imbricating crowns, and a narrow band of dorsal dermal armor comprising two or three rows of sculptured osteoderms on either side of the midline. - Sues & Reisz 2008

Size: Length 30 cm



Comments: a problematic genus that has been interpeted as either a procolophonoid (von Huene, 1912; Colbert, 1946; Carroll, 1988), or a pareiasaur (Romer, 1966). Lee 1995 and Jalil & Janvier 2005 found that *Sclerosaurus* resolves as the sister taxon of Pareiasauria (the two together constituting the Pareiasauroidea) Redescription and reassessment of this taxon by Sues & Reisz 2008 returned it to the Procolophonidae. Apomorphic character states such as the presence of three spines on the quadratojugal, support its referral to the Leptopleuroninae, a placement also given by Cisneros 2006 in his detailed study of the Procolophonidae. Stratigraphically, an early to mid Triasisc age makes pareiasaur affiliations less likely. Although *Sclerosaurus* resembles pareiasaurs in the presence of an intercondylar canal on the distal end of the femur, the absence of gastralia, larger size (albeit still very small by pareaisaur standards) and having a short tailSues & Reisz 2008 and dorsal armor consisting of rows of osteoderms (there are also two spikes protruding from the back of its head) (Palaeocritti) these would be the result of convergences, and even occupying the ecological niche left vacant by the pareiasaurs as a result of the P-T extinction event. Cisneros 2006 finds that *Sclerosaurus* and *Scoloparia* (Carnian of Nova Scotia) group together in an unnamed clade (Sclerosaurini?). Considering the long stratigraphic between the two and absense of intermediate forms this would imply that Triassic microverterberate evolution is as yet still poorly known. Or similarities may have been the result of convergences. These are also the only two procolophonid species where the presence of osteoderms is known. It is however quite likely that osteoderms will be discovered elsewhere. Since the common ancestors of pareiasaurs and procolophonids were not armoured, this is clearly an example of convergent evolution, although a tendency to develop osteoderms may still be a shared ancestral trait of the procolophonia (like proto-feathers for dinosaurs)

The wide and rather flat body (proportionally as wide as a pareiasaur) means that *Sclerosaurus* may have looked something like an overgrown horned lizard, *Phrynosoma* (David Peters), although if Juan Carlos Cisneros' suggestion is correct, the Australian thorny devil would be a better metaphor, and perhaps more similar in appearance. Phrynosoma also burrows in loose sand, and in this regard it would be like procolophonids such as *Procolophon* and *Sauropareion* , the wide flat body aiding in burrowing (deBraga 2003). MAK120324.

Graphics life reconstruction by Dmitry Bogdanov, Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike; skeletal reconstruction © David Peters, used with permission

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Leptopleuronini : *Leptopleuron, Hypsognathus*

Range: Triassic of Eur, Nth Am, Sth Am

Phylogeny: Leptopleuroninae **:** *Anomoiodon* + (*Phonodus* + (*Neoprocolophon* + (*Sclerosaurus* + * **:** *Leptopleuron* + *Hypsognathus*.)))

Comments: an unnamed procolophonid from the Owl Rock Member of the Chinle Formation may belong here; although poorly preserved, it shares some apomorphies known elsewhere only in *Leptopleuron*, *Soturnia* and *Hypsognathus*, such as the presence of a single dentary incisiform (Fraser et al., 2004 cited in Cisneros 2006 p.98). According to Cisneros 2006, *Soturnia caliodon*, from the Late Triassic of Brazil, is the only known Gondwanan leptopleuronine, and sister taxon to Hypsognathus. The otherwise absense of leptopleuronines from Gondwana may be due to preservational or collecting biases, or it may mean that leptopleuronines only spread southward during the late Triassic MAK120328

Leptopleuron lacertinum Owen, 1851

Synonym: *Telerpeton elginense* Mantell, 1852

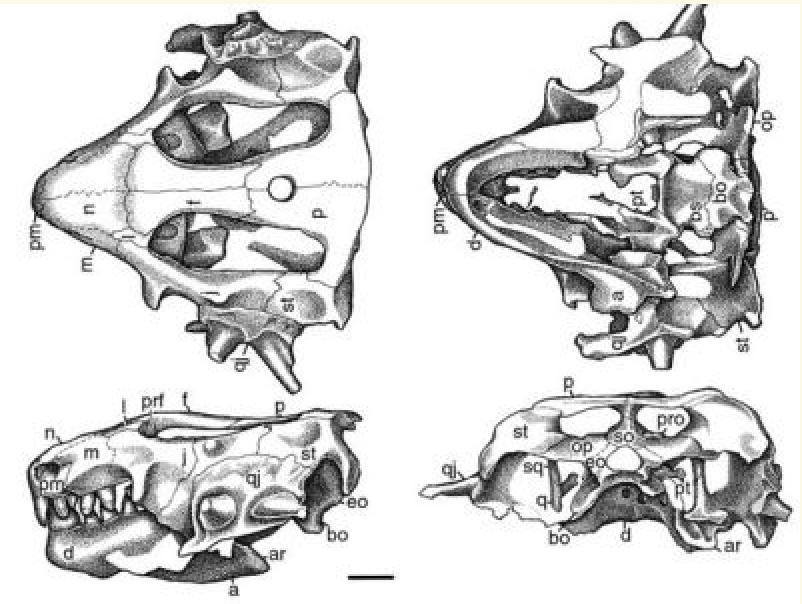
Sratigraphic range: Lossiemouth Sandstone Formation of Grampian, Scotland (early Norian).

Phylogeny: Leptopleuronini **:** *Hypsognathus* + *

Comments: similar to Procolophon, but with wider molar-like teeth, no gastralia, and hind limbs more slender

Links Palaeocritti MAK120330

Hypsognathus fenneri Gilmore, 1928



Sratigraphic range: Brunswick (now upper Passaic) Formation, Clifton, New Jersey, Newark Supergroup of eastern North America (late Norian–Rhaetian); Blomidon Formation of Nova Scotia and upper part of the New Haven Formation of Connecticut, Passaic Formation of the Newark basin in southeastern Pennsylvania. Palaeocritti

Phylogeny: Leptopleuronini **:** *Leptopleuron* + *

Size: length: 33 cm, skull width up to 12.5 cm

Comments: widely regarded as the most derived procolophonid. The dorsally open orbit extends deeply into the parietal, posterior to the pineal opening. Presumeably the eyeball occupied only the anterior half of this opening with jaw muscles filling the rest. The quadratojugal is ornamented with "horns." The postcranial portion was low and wide, as in the distantly related Sclerosaurus. - David Peters. Like procolophon, a herbivore with chisel-shaped teeth designed for dealing with tough vegetation (Colbert, 1946;)

Graphics *Hypsognathus fenneri*, reconstruction of skull, from Sues et al 2000. Abbreviations: a, angular; ar, articular; c, coronoid process; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal.

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Anapsida: Classification

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

Contents

The following rather hasty and hence somewhat incomplete page uses Linnaean taxonomy, but is rather dramatically modified from our usual refernce source of Carroll 1988. We have replaced the old Cotylosauria here with three orders: Eunotosauria, Mesosauria, and Procolophonomorpha. The predominance of monotypal taxa show that either early anapsids showed great morphological diversity, early paleobntologists loved to coin new high rank taxa or, more likely, both. For the cladistic equivalent, see the dendrogram page MAK120328

Subclass Anapsida Osborn, 1903 (= Anapsida Williston, 1917) [1] (cont.)
 Order Eunotosauria Watson, 1917 [2] (= Superfamily Millerosauroidea Romer, 1966)
  Family Millerettidae Romer, 1945 small, insectivorous, lizardlike forms, Mid to Late Perm of SAfr
  Family Eunotosauridae Haughton & Brink, 1954 monotypal family for *Eunotosaurus*, convergent with turtles, Mid Perm of S Afr
 Order Mesosauria Seeley, 1892 monotypal order for Mesosauridae only
  Family Mesosauridae Baur, 1889 monotypal family of small aquatic reptiles - Early Permian of SAfr & Sth Am
 Order Procolophonomorpha [3] Romer, 1964 an assemblage of primitive, mostly lizard- or amphibian-like Permo-Triassic reptiles, with a few aberrant large forms
  Suborder Lanthanosuchida Carroll, Kuhn & Tatarinov, 1972 (= Superfamily Lanthanosuchoidea)
  Family Acleistorhinidae Daly, 1969
  Family Lanthanosuchidae Efremov, 1946

Suborder Bolosauroia Kuhn, 1959 *monotypal for Bolosauridae only*

Family Bolosauridae Cope, 1878 faculatively bipedal, insectivorous, lizardlike forms, Early Perm of WEur, EEur, NAm, & EEas

Suborder Procolophonia Seeley, 1888

Superfamily "Nyctiphruretoidea"[4] Lee 1995 - ancestral procolophonians

Family Nyctiphruretidae Efremov, 1938 - monotypal family for basal taxon *Nyctiphruretus* , Mid Perm of EEur

Family Nycteroleteridae

Subfamily Tokosaurinae - monotypal subfamily for basal taxon *Macroleter* (=*Tokosaurus*), Mid Perm of EEur

Subfamily Nycteroleterinae - small, insectivorous, lizardlike forms, Mid Perm of EEur, NAm, & SAfr

Subfamily Rhipaeosaurinae Chudinov, 1955 - monotypal subfamily for *Rhipaeosaurus*, Mid Perm of EEur

Superfamily Pareiasauroidea Cope, 1869 (sensu Nopcsa, 1928) - *monotypal superfamily for Pareiasaurs*

Family Pareiasauridae Lydekker 1889 = Pareiasauridae Cope, 1869 - medium to very large armoured herbivores, Mid to Late Perm of Afr, Eur, EEur, SthAm, EAs

Subfamily Bradysaurinae Huene 1948 *Includes only the very large, primitive, early genus Bradysaurus Mid Perm of Sth Afr*

Subfamily Pareiasaurinae Nopcsa 1923. paraphyletic assemblage of large to very large, moderately armoured typical Pareiasaurs, Mid to Late Perm of Afr, Eur, EEur, SthAm, EAs

Subfamily Elgininae Cope, 1895 monotypal taxon for *Elginia mirabilis*, a smallish, spiny headed pareiasaur from the Late Perm of WEur

Subfamily Pumiliopareiasaurinae [5] Jalil & Janvier 2005 small, advanced pareiasaurs, strongly advergent with turtles - Late Perm of SAfr & SAm

Superfamily Procolophonoidea Romer, 1956

Family Owenettidae Broom, 1939 small, insectivorous, lizard-like procolophonoids, Late Perm to Mid Trias of SAfr, Mad, & SAm

Family Procolophonidae [6] Seeley, 1888

Subfamily Theledectinae Cisneros 2006 small, primitive, insectivorous forms, Early Trias of EEAs and Aus

Subfamily Procolophoninae Seeley, 1888 advanced, herbivorous procolophonids with stocky bodies, triangular skulls, and chisel-like teeth, Early to Mid Trias of SAfr, Ant, SAm, & EEAs

Subfamily Leptopleuroninae Ivakhenko, 1982 (= Telerpetontidae Lydekker, 1888) advanced herbivorous, spiny-headed procolophonids, Early to Late Trias of WEur, EAs, NAm, & SAm,

Subfamily [7] Sclerosaurinae Nopcsa, 1923 monotypal taxon for *Sclerosaurus armatus*, a large, wide-bodied procolophonid convergent with pareiasaurs, Early Trias of WEur

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Notes

[1] as paraphyletic stem taxon sensu Carroll, not a monophyletic clade sensu Gauthier, Resiz, etc. If turtles (order Chelonii) turn out to be diapsids, then Anapsida would become polyphyletic, and this subclass could appropriately be renamed Parareptilia. For now we are going with the more traditional, anapasid origin, hypothesis. MAK120326

[2] we are following Cisneros et al 2008 and Tsuji et al 2012 in including the eunotosaurs with or under the millerettids. This synonymises the Eunotosauria and the Millerosauroidea. The Order Eunotosauria Watson, 1917 also has priority over Millerosauria Watson 1957 and Promillerosauria Kuhn, 1959. Although Eunotosauridae would be included under a monophyletic family Millerettidae (Cisneros et al 2008), we have retained it as a distinct Linnaean taxon because of *Eunotosaurus*' great morphological distinction. MAK120328

[3] here expanded to include various related taxa.

[4] from the pseudomonophyletic taxon Nyctiphruretia Lee 1995

[5] Linnaeanisation of unranked clade Pumiliopareiasauria of Jalil & Janvier 2005

[6] Subfamily Spondylolestinae Ivakhenko, 1979 is usually include din taxaonomic lists, but we have not retained it as it is a polyphyletic taxon of assorted primitive forms procolophonoidsas currently defined. Some are not procolophonids (*Candelaria* is an owenettid), some are poorly known or indeterminate, and some have been reassigned to other subfamilies. Spondylolestinae coukld still be a valid taxon if applied only to *Spondylolestes* and related forms MAK120328

[7] which would make the Leptopleuroninae paraphyletic, although this is not a problem for linnaean/evolutionary systematic classifications

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Anapsida : Dendrogram

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

Contents

Editor's note: It is intended to give basic stratigraphic info for each taxon, or at least each terminal taxon, but limitations of time meant that this had to be defered, hence the incomplete nature of this page in that regard MAK120402

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA (=Parareptilia) MH
   |--+--Millerettidae  MPerm of SAfr
   |   `--Eunotosaurus  MPerm of SAfr
   |--Mesosauridae  EPerm of SAfr & SAm
   `--+--Lanthanosuchoidea
      |   |---Acleistorhinidae EPerm of NAm
      |   |   |---Acleistorhinus
      |   |   `---Colobomycter
      |   `--Lanthanosuchidae MPerm of EEur
      `--+--Bolosauridae  E to MPerm of WEur, EEur, EAs, & NAm
         |  |--Belebey MPerm of EEur & EAs,
         |  |--Bolosaurus  EPerm of NAm
         |  `--Eudibamus   EPerm of WEur
         `--Procolophonia
            |--Nyctiphruretus
            |--Nycteroleteridae
            |   |--Macroleter
```

```
|   |--+--Nycteroleter
|   |   `--Emeroleter
|   `--+--Rhipaeosaurus
|      `--Pareiasauridae (= Hallucicrania) MH
|           |--Bradysaurus baini
|           `--+--Bradysaurus seeleyi
|              `--Velosauria
|                 |--Embrithosaurus
|                 `--+--Deltavjatia
|                     `---+--+--Shihtienfenia
|                        |   `--Pareiasuchus
|                        `--+--Pareiasaurus serridens
|                           `--+--Scutosaurus
|                              |--Elginia
|                              `--Pumiliopareiasauria
|                                 |--Nanopareia
|                                 `--+--Anthodon
|                                     `--Pumilopareia
`--Procolophonoidea  MH
   |--Owenettidae
   |  |?--TESTUDINES ToL
   |  |--Barasaurus
   |  `--+--Owenetta
   |     `--+--"Owenetta" kitchingorum
   |        `--Candelaria
   `--Procolophonidae
      `--+--Sauropareion
          `--+--Phaanthosaurus
              `--+--Theledectinae
                  `--+--Tichvinskia
                      `--"Horned procolophonids"
                         |--Procolophoninae
                         |  |--Eumetabolodon
                         |  `--Procolophon
                         `--Leptopleuroninae
                            |--Anomoiodon
                            `--+--Phonodus
                               |--Neoprocolophon
                               `--+--Sclerosaurus
                                  `--Leptopleuronini
                                     |--Leptopleuron
                                     `--Hypsognathus
```

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Anapsida: References

Abreviated Dendrogram

```
REPTILIOMORPHA
|--SYNAPSIDA
`--+--EUREPTILIA
   |
   ANAPSIDA
   |--+--Millerettidae
   |   `--Eunotosaurus
   |--Mesosauridae
   `--+--Lanthanosuchoidea
      `--+--Bolosauridae
         `--Procolophonia
            |--+--Nycteroleteridae
            |   `--Pareiasauridae
            `--Procolophonoidea
               |--Owenettidae
               |   `?--TESTUDINES
               `--Procolophonidae
```

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Diapsida: Overview

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
        |
        `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
               |=="Younginiformes"
               `--+--Claudiosaurus
                   |--Weigeltisauridae
                    `--+--+--+?--Thalattosauria
                        |   |   `?-
-Saurosphargidae
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Hupehsuchia
                        `--Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

Contents

Acerosodontosaurus piveteaui, an aquatic Tangasaur from the Late Permian (Sakamena Formation) of Madagascar, and a good representation of a typical primitive diapsid (or "eosuchian"). Yet even the fossil remains of this rather unspectacular lizard-like creature were instrumental in overturning the Younginiformes hypothesis and showing that these early Diapsids didn't form a simple monophyletic lineage after all. Illustration by Nobu Tamura (Wikipedia)

This section covers a set of taxa which bridge the gap in reptile history between the amniote radiation, some time in the middle of the Carboniferous, and the flowering of the archosaur and lepidosauromorph clans in the Triassic. Although the early Eureptilia (or "Romeriida") are rather poorly known, they represent a set of taxa so wildly diverse that we can safely conclude that nothing quite like this extended family has fit under so small a roof in the entire domain of vertebrate phylospace. Many were vaguely lizard-like terrestrial forms, such as *Araeoscelis* and *Youngina*. At the other extreme, there were the ichthyosaurs, which were the most completely water-adapted tetrapods ever to evolve (however, more recently some phylogenies place the ichthyosaurs as more derived diapsids). In between, there are many shades of amphibiousness represented by *Spinoaequalis*, the Tangasaurid Younginiformes (see above illustration), *Claudiosaurus* and their cousins. There were even eureptiles which experimented with flight -- or at least gliding – among the coelurosauravids. ATW, MAK101002

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Diapsida

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
       `--o DIAPSIDA
           |==Araeoscelida
           `--o Neodiapsida
               |=="Younginiformes"
               `--+--Claudiosaurus
                   |--Weigeltisauridae
                    `--+--+--+?--Thalattosauria
                        |   |   `?-
-Saurosphargidae
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Hupehsuchia
                        `--o Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

Contents

Taxa on this Page

1. Diapsida

The Diapsids

The Eureptilia would have been a footnote in the history of turtles and mammals but for the evolution of the **diapsids**. The bulk of reptiles fall into the Diapsida. The Diapsida ("two arches") are so called because they have two (*di*-) skull openings on either side of the head, for attachment of temporal muscles (to work the jaw). However it is now known that some reptiles lost one or even both pairs of openings, so the presence or absence of this characteristic is not a completely reliable guide.

The Diapsida are divided into two important groups, the lepidosaurs (Lepidosauromorpha) and the archosaurs (Archosauromorpha). There are also a number of different lineages of early, mostly small lizard-like insectivorous forms that lived during the late Carboniferous, Permian, and Triassic periods. These have been traditionally grouped under the "Eosuchia," but it is now known that this is an artificial taxon, a "waste basket" category for any diapsid that is neither lepidosaur nor archosaur. Nevertheless the term retains some use as a synonym for "basal diapsid." MAK991026.

Depending on which phylogenetic and methodological paradigm you prefer, the Diapsida are either the single largest and most diverse subclass of class Reptilia (see Classification page), or the single largest clade of amniotes (see Dendrogram page). Either way, they are pretty important. There is even a pretty good basic phylogentic consensus, of sorts, regarding where the different groups go, which forms the backbone of the present unit. Thiis includes not only the usual terrestrial and semi-aquatic lizard-like forms, like *Acerosodontosaurus*, illustrated above, but gliders like *Coelurosauravus*, the first vertebrates to take to the air.

It is quite frustrating then, in putting up this unit dedicated to primitive (basal) diapsids, to find, once we go beyond this central and safe axis, so many small oddball , mostly aquatic, Triassic lineages here. The whole abbreviated dendrogram and table of contents ends up looking like one of those really annoying dendrograms (annoying because they contain so little phylogenetic information) which begin with an enormous list of *incertae sedis* (taxa of uncertain position) about which all that can be said is that they belong somewhre in that particular clade.

Well, that's all that can be said here. There is no doubt that thalattosaurs are neodiapsids (and they are among the more important lineages of the Triassic marine reptiles. at that) but are they more closely related to Ichthyosaurs (Bickelmann et al. 2009) or to Sauropterygians (Li et al. 2011)? Or both (assuming ichthyosausr and plesiosaurs are related) or neither?

The same can be said, and asked, of *Hupehsuchus*. It's a diapsid, but *where* on the diapsid tree does he belong? Near primitive ichthyosaurs? Or Sauropterygia? Or simply an independent line of be basal neodiapsids?

Or the mollusc (or seaweed?) eating *Omphalosaurus*. An ichthyosaur? Or (perhaps like the hupehsuchians) ichythosaur mimic? Or, if we really want to talk about odd balls, *Sinosaurosphargis*, a creature that resembled a turtle or a placodont, but about which all we can say for sure is that it wasn't a turtle or a placodont.

For that matter, where exactly *do* the ichthyosaurs and the sauropterygians - the two groups that between them pretty much embody the 19th century "antedeluvian monsters" of the Mesozoic seas? How much progress has been made in almost two centuries. We used to be pretty sure where the ichtyosaurs and the plesiosaurs (& co., i.e. the sauropterygia) went, now we aren't quite so sure.

The problem is that all these strange groups were so highly specialised, and so different from their obviously more conventional ancestors, that cladistics simply isn't any help. Without shared characteristics with which to compare, or transitional forms that had such characteristics, we simply cannot determine where a creature belongs on the cladogram, the abstract evolutionary tree. It's the reason for the uncertainty of placement of groups like mesoasurs and turtles; both of which may be anapsids or diapsids, but both are so specialised it's impossible to tell.

Here there is the choice between the fool and the coward. The fool's option is to go out on a limb and say "this group belongs with *X* and is related to *Y*." To follow this course at least gives us one assurance: that we will almost certainly be shown to be totally wrong when new discoveries turn up and new phylogenetic analyses are made. Whereas the coward's option is to say "I don't have any idea", which at least is being honest and truthful, but it makes for dendrograms that really, really, suck.

No doubt in these pages, in trying to avoid this conundrum, we have been foolish where discretion would be the better part of valour, and cowardly where there was the need to bodly state new hypotheses. MAK111108

Diapsida - History of discovery

In the 19th century, the evolution of the reptiles was mostly interpreted in terms of current groups. The Diapsida as a distinct taxon were only named in 1903 by Henry Fairfield Osborn, who distinguished between two arched (Diapsida) and single arched (Synapsida) reptiles. His system was very different to that used today; the Pelycosaurs for example were not Synapsids but Diapsids! So were the Procolophonia (perhaps because *Procolophon* sometimes displays temporal openings), mesosaurs, and ichthyosaurs). His ideas were further taken up by Watson (1917, 1957), Williston (1925), and Broom (1925), among others. While all agreed on the monophyly of the Diapsida, they argued over the relationships of the various groups, as well as the nacetsors of extant taxa like Squamata (see Benton (1985) and Evans (1984) for more on this). It was at this time that classification in terms of temporal fenestrae was developed, abd this remained standard until the cladistic revolution of the 70s and 80s. Meanwhile, back in the 1930s, Alfred Sherwood Romer, the most influential vertebrate paleontologist of his time (and perhaps of the 20th century) rejected the idea of a monophyletic Diapsida. He considered that the lepidosaurs evolved from cotylosaurs (anapsids, captorhinomorphs) via the Eosuchia/Younginiformes, and the Archosaurs likewise via the Thecodonts. Such was his influence that it was not until the 1970s that a monophyletic Diapsida was once again accepted as paleontological canon, although other authors like Colbert (1969) retained a monophyletic Diapsida with Romer's Archosaurs and Lepidosaurs as infraclasses. Interestingly, early cladists like Lovtrop 1977 and Gardiner 1982 similarly rejected a monophyletic Diapsida (on morphological grounds) in favour of a crocodile-turtle clade, ironic in favour of recent molecular studies, although Benton 1985pp.104-6 rejects most of their claims. Today, despite the almost complete consensus of molecular studies which say that turtles are crown group archosaurs, no cladist accepts such a topology, favouring instead the anapsid or the lepidosauromorph hypothesis

Romer's objection was that there wasn't any suitable ancestral form with characteristics common to both lepidosaurs and archosaurs. This changed with restudy of *Petrolacosaurus* by Robert Reisz (1977, 1981), as well as studies of various eosuchians by Carroll, Gow, and others (summarised in Benton (1982)).

With the Diapsida firmly established as a valid taxon, it seems that our understanding of reptile evolution would go smoothly from thsi point on. Unfortunately, science being science, and phylogeny being phylogeny, this was only the beginning of further controverises, explained in the following section, courtesy of the Tree of Life web project and open source science (yayy!). MAK111119

Diapsid Phylogeny

Michel Laurin and Jacques A. Gauthier

Even though diapsid phylogeny has been intensively studied, relatively few computer-assisted studies of early diapsids have been published. The large-scale phylogenetic analyses of Benton (1985), Evans (1988), and Gauthier et al. (1988) focused on lepidosauromorphs and archosauromorphs. More recently, phylogenies based on data matrices incorporating several diapsid terminal taxa (more than 20) were presented. Therefore, only simplified versions of these phylogenies are presented here (the node names are modified to be consistent with the recommended usage and do not necessarily follow the published versions).

This page deals mostly with the phylogeny between the various stem-diapsids, Lepidosauromorpha and Archosauromorpha. However, some taxa, such as ichthyosaurs and sauropterygians, have been variously thought to be stem-diapsids, lepidosauromorphs, or archosauromorphs, so their affinities are briefly discussed below. Turtles are usually not considered diapsids, but a few paleontological studies have suggested that they were closely related to sauropterygians (and to lepidosauromorphs). The results of these studies are also briefly exposed below.

Benton (1985) presented the following phylogeny:

```
        ==================================== Araeoscelidia
        |
        |                                 === Younginiformes
   =====|             ==Lepidosauromorpha=|
        ==Neodiapsida=|                   === Lepidosauria
                      |
                      ======================= Archosauromorpha
```

Evans (1988) studied more stem-diapsids, but her main conclusions are similar to those of Benton (1985) and Gauthier et al. (1988):

```
        =========================================== Araeoscelidia
        |
        |  ======================================== Coelurosauravus
        |  |
        |  |  ===================================== Sauropterygia
        |  |  |
        |  |  |==================================== Heleosaurus
        |  |  |
   =====|  |  |==================================== Galesphyrus
        ===|  |
           ===|                                  === Heleosuchus
```

```
              |                                ===|
              |           ==Lepidosauromorpha=|  === Younginiformes
              ====Sauria==|                   |
                          |                   ====== Lepidosauria
                          |
                          ========================== Archosauromorpha
```

Both of these studies, as well as Gauthier et al. (1988) suggested that younginiforms were lepidosauromorphs. Laurin (1991) argued that younginiforms were not saurians, and this conclusion has been accepted by most scientists (Rieppel, 1993, 1994; Gauthier, 1994). The phylogeny suggested by Laurin (1991) is as follows:

```
        ================================ Araeoscelidia
        |
        |             ================== Coelurosauravus
        |             |
        |             |  =============== Apsisaurus
   =====|             |  |
        ==Neodiapsida=|  |  ============ Younginiformes
                      ===|  |
                         ===|        === Lepidosauromorpha
                            ==Sauria=|
                                     === Archosauromorpha
```

Rieppel (1994), Rieppel and deBraga (1996), and deBraga and Rieppel (1997) argued that turtles (Testudines) are closely related to sauropterygians (a group of aquatic diapsids from the Mesozoic), and that both groups are lepidosauromorphs. This phylogeny suggests that turtles are actually diapsids that have lost their temporal fenestrae. While this conclusion remains controversial, it deserves to be presented:

```
       ==================================================== Araeoscelidia
       |
       |             ====================================== Claudiosaurus
       |             |
       |             |  =================================== Younginiformes
       |             |  |
   ====|             |  |                               === Sauropterygia
       ==Neodiapsida=|  |                            ===|
                     ===|        ==Lepidosauromorpha=|  === Testudines
                        ==Sauria=|                   |
                                 |                   ====== Lepidosauria
                                 |
                                 ========================== Archosauromorpha
```

Gauthier (1994) reviewed amniote phylogeny.

Caldwell (1996) did one of the first computer-assisted phylogenetic analyses of diapsids incorporating ichthyosaurs. He found that if turtles and ichthyosaurs were included in his matrix, ichthyosaurs were the sister-group of sauropterygians, and this large clade of aquatic diapsids was close to the base of Archosauromorpha, while turtles appeared to be lepidosauromorphs.

```
        ======================== Araeoscelidia
        |
   =====|  ===================== Claudiosaurus
        |  |
        ===|  ================== Younginiformes
           |  |
           ===|           ====== Lepidosauria
              |        ===|
              |        |  ====== Testudines
              ==Sauria=|
                       |     === Sauropterygia
                       |  ===|
                       ===|  === Ichthyosauria
                          |
                          ====== Archosauria
```

Without ichthyosaurs, the same matrix resulted in a topology in which turtles were the sister-group of sauropterygians, and in which this clade was part of Lepidosauromorpha (sauropterygians shifted from archosauromorphs to lepidosauromorphs).

```
        ======================== Araeoscelidia
        |
   =====|  ===================== Claudiosaurus
        |  |
        ===|  ================== Younginiformes
           |  |
           ===|           ====== Lepidosauria
              |        ===|
```

```
                 |        |  === Sauropterygia
                 ==Sauria=|  ===|
                          |      === Testudines
                          |
                          ========= Archosauromorpha
```

Finally, without turtles, ichthyosaurs were the sister-group of sauropterygians, and that clade was located outside Sauria (Sauria is identified with the wrong clade in Caldwell's figure).

```
           ===================== Araeoscelidia
           |
      =====|  ================== Claudiosaurus
           |  |
           ===|  =============== Younginiformes
              |  |
              ===|     ========= Ichthyosauria
                 |  ===|
                 |  |  ========= Sauropterygia
                 ===|
                    |        === Lepidosauromorpha
                    ==Sauria=|
                             === Archosauromorpha
```

Motani et al. (1998) reassessed the affinities of ichthyosaurs using the data matrices of Rieppel and deBraga (1996) and of Caldwell (1996) by adding ichthyosaurs (in the first case) or recoding them by incorporating data that they had recently obtained about the early (Lower Triassic) ichthyosaur *Utatsusaurus hataii*. Using the matrix of Rieppel and deBraga (1996), they obtained the following topology:

```
           ======================== Araeoscelidia
           |
      =====|  ===================== Claudiosaurus
           |  |
           ===|  ================== Younginiformes
              |  |
              ===|  =============== Ichthyosauria
                 |  |
                 ===|           === Lepidosauria
                    |        ===|
                    ==Sauria=|  === Sauropterygia
                             |
                             ====== Archosauromorpha
```

In that tree, turtles (not shown) were located outside diapsids, in their traditional location (along with other parareptiles). According to that tree, ichthyosaurs are stem- diapsids, and sauropterygians are lepidosauromorphs.

Using the data matrix of Caldwell (1996), Motani et al. (1998) obtained the following topology:

```
           =========================== Araeoscelidia
           |
      =====|  ======================== Claudiosaurus
           |  |
           ===|  ===================== Younginiformes
              |  |
              ===|  ================== Ichthyosauria
                 |  |
                 ===|           ====== Lepidosauria
                    |        ===|
                    |        |  |  === Testudines
                    ==Sauria=|  ===|
                             |     === Sauropterygia
                             |
                             ========= Archosauromorpha
```

In this tree, the position of ichthyosaurs and sauropterygians remains the same, but turtles move into lepidosauromorphs, as the sister-group of sauropterygians.

Finally, Merck (1997b) suggests that ichthyosaurs are the sister-group of sauropterygians, and that this clade is part of Archosauromorpha.

The conflicting results obtained from various authors, and sometimes, by a single author (or group of authors) using different taxa suggest that more work is needed to assess the affinities of ichthyosaurs, sauropterygians, and turtles.

Descriptions

Diapsida:

Range: from the Late Carboniferous.

Phylogeny: Eureptilia **:** Protorothyrididae + * **:** Araeoscelida + Neodiapsida.

Characters: Upper (triradiate squamosal & triradiate post-orbital) [R89] and lower temporal fenstrae; posttemporal fenestra present, bordered by narrow occipital flange of squamosal, tabular (if present), supraoccipital & paroccipital process [R89]; suborbital fenestra consisting of a relatively large hole in the palate located between palatine, ectopterygoid, and maxilla [Other taxa may have foramen in this region, but there is usually no fenestra] [R89]; ossified sternum; **$** (primitively) radius long, measuring 70 - 90% of humerus length; ridge-and-groove ankle joint between tibia and astragalus.

Links: Temporal Fenestration and the Classification of Amniotes; Introduction to the Diapsids; Reptilian Systematics; Introduction to the Diapsids; Diapsida; Basal Diapsida; Reptiles - Subclass Diapsida.

Note: Domed skull of Amniotes permits muscles to run vertically. Vertical muscles allow strong static pressure when jaws are closed or almost closed. Increase in muscle bulk would strain periosteal covering of bone. Fenestrae may have evolved as unossified attachment points. Later, evolved as openings which "bulging" of these jaw muscles. Note no obvious change in jaw musculature in primitive forms.

References: Rieppel (1989) [R89]. ATW070113.

New page MAK111108

Diapsida: Araeoscelida

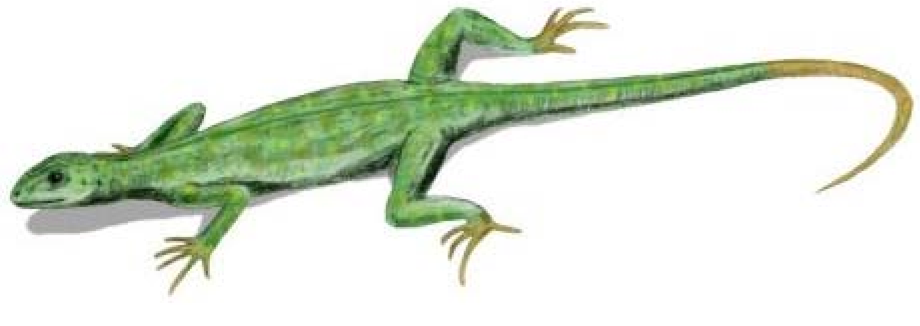
Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
             `--o DIAPSIDA
                |==o Araeoscelida
                |   |-- Spinoaequalis
(probably       |   `--+-- Petrolacosaurus
paraphyletic)   |      `-- Araeoscelis
                `--o Neodiapsida
                    |=="Younginiformes"
                    `--+?--Ichthyosauria (in Sauria?)
                       `--o Sauria
                          |--LEPIDOSAUROMORPHA
                          `--ARCHOSAUROMORPHA
```

Contents

Taxa on this Page

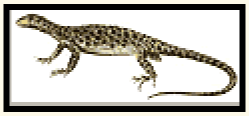
1. Araeoscelida *
2. *Araeoscelis* X
3. *Petrolacosaurus* X
4. *Spinoaequalis* X



Life restoration of *Petrolacosaurus kansensis*, the earliest known diapsid, from the Late Carboniferous of Kansas. Illustration by Nobu Tamura (Wikipedia)

* Traditionally a monophyletic clade, the present author considers that, on stratigraphica nd morphological grounds, the Araeoscelida are better understood as a grade of early diapsids. In which case, phylogenetically and cladistically speaking, Aeroscelida = Diapsida.

Descriptions



Araeoscelida: *Aphelosaurus*, *Araeoscelis*, *Kadaliosaurus*, *Petrolacosaurus*, *Spinoaequalis*, *Zarcasaurus*. Most basal diapsids?

Range: Late Carboniferous to Early Permian.

Phylogeny: Diapsida: Neodiapsida + * **:** *Spinoaequalis* + (*Araeoscelis* + *Petrolacosaurus*)

Characters: Lizard-like; some euryapsid (upper temporal fenestra only), but jugal still bifurcated; long necks, with great elongation of neck in some; gracile, presumably cursorial, limbs.

Comments: a number of poorly known very forms have been placed here, making the group something of a "wastebasket taxon". Most certainly a paraphyletic basal assemblage; also spelt "Araeoscelidia", here we are using Williston (1913)'s original spelling.

Links: Palaeocritti, Paleobiology database, Wikipedia, UCMP - Basal Diapsids (only a paragraph), MAK101001.

Araeoscelis *Araeoscelis gracilis*

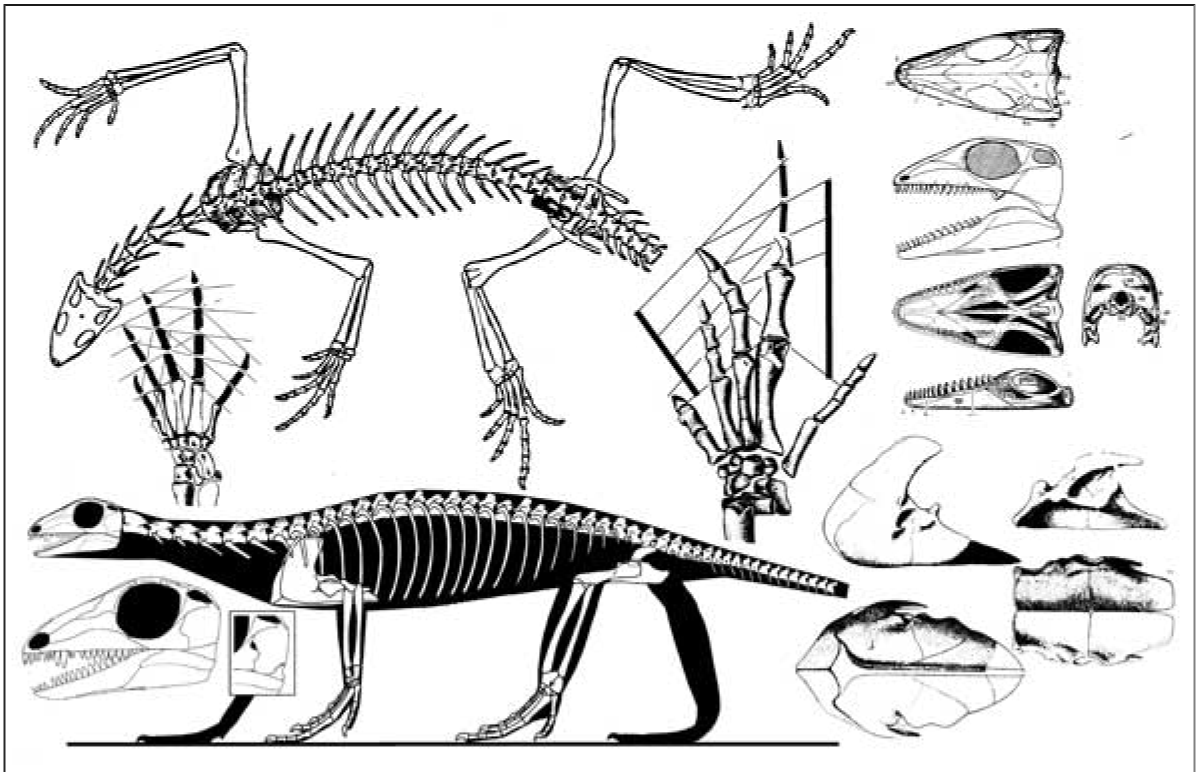
Range: Early Permian.

Phylogeny: Araeoscelida **:** *Spinoaequalis* + (*Petrolacosaurus* + *)

Characters: euryapsid (upper temporal fenestra only).

Comments: At one time considered to be the ancestor of sauropterygia, because of the euryapsid style openings.

Links: Palaeocritti, Wikipedia, About com Dinosaurs MAK101001



Araeoscelis gracilis, drawing by David Peters Reptile Evolution.

Petrolacosaurus

Range: Late Carboniferous

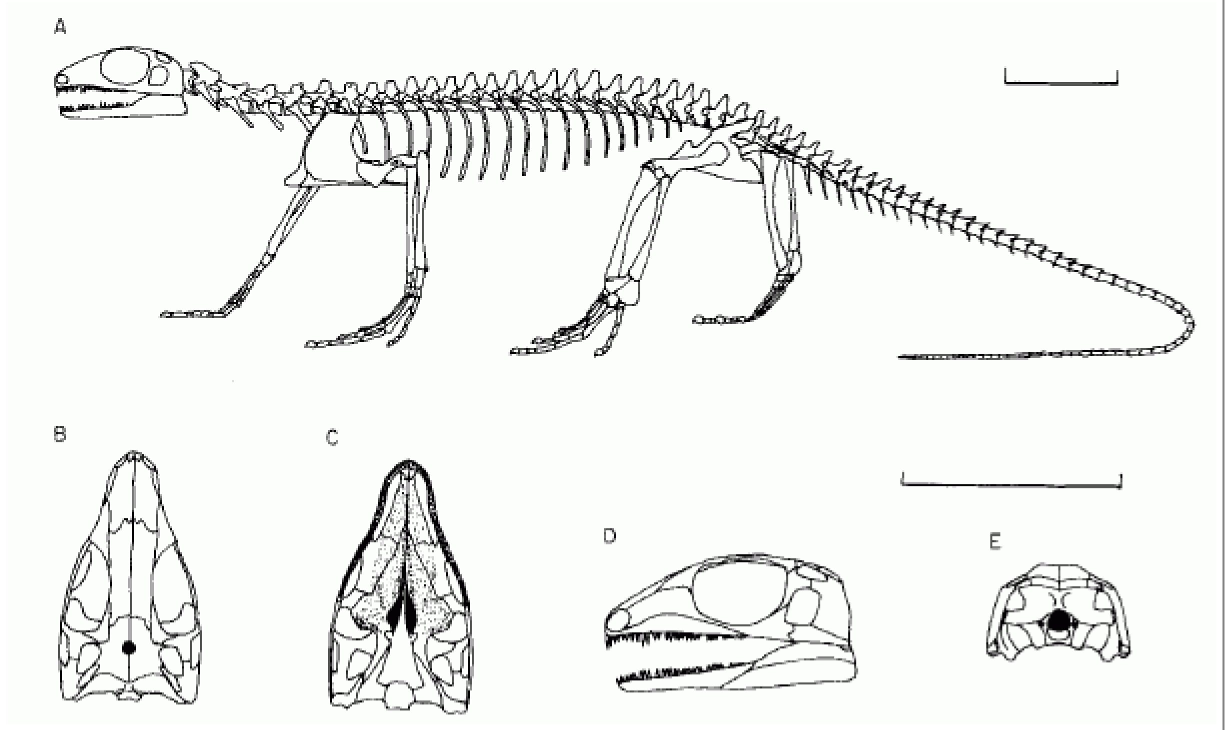
Phylogeny: Araeoscelida **:** *Spinoaequalis* +

(*Araeoscelis* + *)

Comments: The earliest known diapsid. Unlike the closely related *Araeoscelis*, it shows the typical diapsid condition with two temporal fenestrae in the skull.

Links: Palaeocritti, Wikipedia, Prehistoric Land Reptiles - Planet Dinosaur, David Peters - Reptile Evolution MAK101001

References: Reisz 1977, 1981



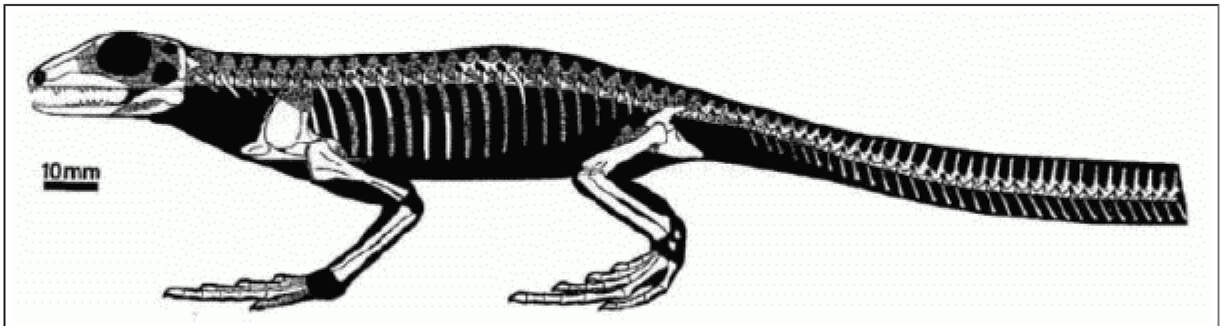
Petrolacosaurus kansensis, from the Late Pennsylvanian of Kansas. Drawing from Diapsid characters, from Benton 2000.

Spinoaequalis

Range: Late Carboniferous (Virgilian - Late Pennsylvanian) of N Am

Phylogeny: Araeoscelida : (*Araeoscelis* + *Petrolacosaurus*) + *

Characters: deep, laterally compressed tai.



Spinoaequalis schultzei, from the Late Pennsylvanian of Kansas. Note the deep (laterally compressed) tail, which would have been used as a swimming organ, the animal moving side to side in a sinuous motion. Drawing from deBraga & Reisz 1995.

Comments: The earliest known aquatic reptile. It probably swam using its flattened, fanned tail. Found in association with marine fish..

Links: Wikipedia

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Diapsida: Neodiapsida

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
       |
       `--DIAPSIDA
          |==Araeoscelida
          `--Neodiapsida
             |--Orovenator
             `--+--Lanthanolania
                |=="Younginiformes"
                `--+--Ichthyosauria
                   `--Sauria
                      |--LEPIDOSAUROMORPHA
                      `--ARCHOSAUROMORPHA
```

Contents

Taxa on this Page

1. *Lanthanolania* X
2. *Orovenator* X
3. Neodiapsida

Neodiapsida is a cladistic term for basically all Diapsids apart from a few unfortunate primitive ones lumped under the Araeoscelida. In the opinion of the present author, the Araeoscelida are a grade of early diapsids, all of which were pretty similar. One of these however was more successful than its fellows, and gave rise to the huge diapsid phylogenetic radiation, including ichthyosaurs and plesiosaurs, lizards and snakes, phytosaurs and crocodilians, prolacertifoms and pterosaurs, dinosaurs and birds, as well as other assorted forms.

Ther ancestors of this glorious evolution were agile long-legged, long-necked, lizard like forms, very much like their araeoscelidan ancestors, and differing only in minor details of the skull and skeleton (and presumably, of teh soft body physiology that isn't fossilsed).

Until recently, the earliest neodiaspids were known exclusively from the latest Permain and early Triassic. This changed with the recent discovery of two new early and middle Permian forms, *Orovenator* and *Lanthanolania*, which bridge the morphologiocal and temporal gap between the permocarbonifderous araeoscelidians and petralacosaurs and the Permo-Triassic younginiforms or eosuchians MAK111116

Descriptions

Neodiapsida: defined: younginiforms + crown diapsids [C97a], or Sauria > Araeoscelida ToL

Range: from the Middle Permian.

Phylogeny: Diapsida: Araeoscelida + * **:** *Orovenator* + (*Lanthanolania* + (Tangasauridae + (*Claudiosaurus* + Weigeltisauridae + (Ichthyopterygia + Sauria)))).

Characters: lacrimal reduced or absent [R89]; descending flange of parietal participates in UTF [R89]; quadrate laterally exposed (not covered by squamosal in lateral view) [R89]; quadrate embayed posteriorly [R89]; *retroarticular process* present [R89]; *caniniform* teeth absent [R89]; parasphenoid without teeth [R89, *dubitante*]; *olecranon* absent [R89]; femur slender & *sigmoid* [R89]; femoral distal condyles not projecting markedly beyond shaft [R89]; **$** femoral ventral ridge system reduced (without prominent ventral adductor crest for, e.g. *m. caudofemoralis*); **$** proximal carpals and tarsals small.

Links: Neodiapsida; Autapomorphies of Diapsid Clades.

References: Callaway (1997a) [C97a]; Rieppel (1989) [R89]. ATW070113. Phylogeny revised MAK111116

***Orovenator*:** *O. mayorum* Reisz et al., 2011

Range: Early Permian - Sakmarian of Oklahoma

Phylogeny: Neodiapsida **:** (*Lanthanolania* + (Tangasauridae + (*Claudiosaurus* + Weigeltisauridae + (Ichthyopterygia + Sauria)))) + *

From the abstract: The initial stages of evolution of Diapsida (the large clade that includes not only snakes, lizards, crocodiles and birds, but also dinosaurs and numerous other extinct taxa) is clouded by an exceedingly poor Palaeozoic fossil record. Previous studies had indicated a 38 Myr gap between the first appearance of the oldest diapsid clade (Araeoscelidia), ca 304 million years ago (Ma), and that of its sister group in the Middle Permian (ca 266 Ma). Two new reptile skulls from the Richards Spur locality, Lower Permian of Oklahoma, represent a new diapsid reptile: *Orovenator mayorum* n. gen. et sp. A phylogenetic analysis identifies *O. mayorum* as the oldest and most basal member of the araeoscelidian sister group. As Richards Spur has recently been dated to 289 Ma, the new diapsid neatly spans the above gap by appearing 15 Myr after the origin of Diapsida. The presence of *O. mayorum* at Richards Spur, which records a diverse upland fauna, suggests that initial stages in the evolution of non-araeoscelidian diapsids may have been tied to upland environments. This hypothesis is consonant with the overall scant record for non-araeoscelidian diapsids during the Permian Period, when the well-known terrestrial vertebrate communities are preserved almost exclusively in lowland deltaic, flood plain and lacustrine sedimentary rocks. (original url)

Links: Wikipedia

References: Reisz et al 2011 .

***Lanthanolania*:** *L. ivakhnenkoi* Reisz & Modesto, 2003

Range: Middle Permian - Wordian (upermost Kazanian) of Arkhangel'sk Province, Russia

Phylogeny: Neodiapsida **:** *Orovenator* + ((Tangasauridae + (*Claudiosaurus* + Weigeltisauridae + (Ichthyopterygia + Sauria))) + *)

Comments: Known from the holotype and only specimen PIN 162/56, a partial skull with an incomplete lower temporal bar from the Glyadnaya Shchelya locality, Mezen river in Mesen District, recently discovered to be a very primitive neodiapsid. Interpreted as possible stem lepidosauromorph by Evans & Jones 2010, reinterpreted as very primitive (basal) neodiapsid by Reisz et al 2011

Links: Wikipedia

References: Reisz et al 2011 .

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Diapsida: Younginiformes (Eosuchia)

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
        |
        `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
              |--Youngina Younginiformes
              |--Thadeosaurus
              `--+--Tangasaurinae
                  `--+--Claudiosaurus
                      |--Weigeltisauridae
                       `--+--+--Thalattosauria
                             |   `-
-ICHTHYOSAURIA
                             |?--Hupehsuchia
                             |?--Omphalosaurus
                             |?--Saurosphargidae
                             `--Sauria
                                 |?-
-CHORISTODERA
                                 |-
-LEPIDOSAUROMORPHA
                                 `-
-ARCHOSAUROMORPHA
```

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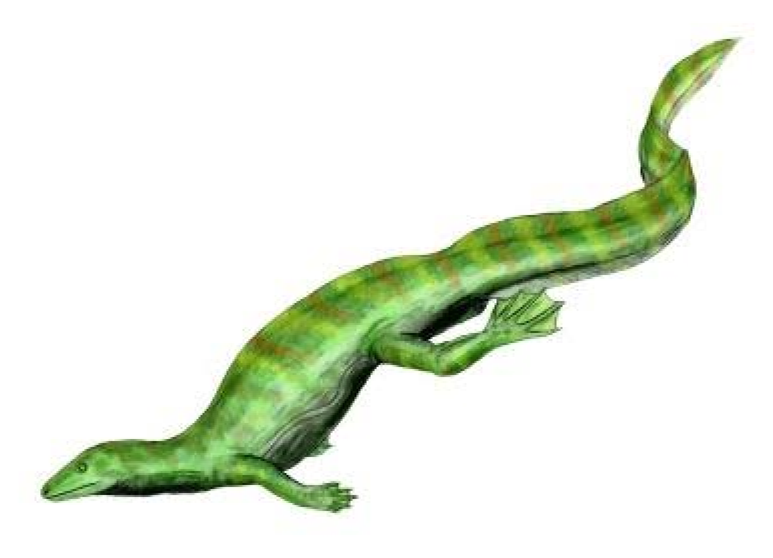
Taxa on this Page

1. Sauria
2. Tangasauridae X
3. *Thadeosaurus* X
4. *Youngina*
5. Younginiformes X



Hovasaurus boulei, a tangasaurid from the Late Permian of Madagascar. Illustration by Nobu Tamura (Wikipedia)

The Younginiformes - basal neodiapsids

The Younginiformes began life as the *Eosuchia*, a group (of ordinal rank in Linnaean taxonomy) coined by Broom in 1914 to refer to early and generalised diapsid reptiles, on the basis of *Youngina*,known from the late Permian of South Africa. The group eventually became a wastebasket taxon for any early generalised diapsids that are not obviously lepidosaurs or archosaurs. As a result, Romer suggested the order Younginiformes to be applied strictly to those forms of primitive diapsid nature. Romer was dissatisfied with this and coined the name Younginiformes is a replacement

With the rise of Hennig-based cladistic methdology, Benton 1985, Gauthier et al, and Evans 1988 placed them in the lepidosauromorphs, as the sister taxon to Lepidosauria. Laurin 1991 moved them to the base of Neodiapsida, and these findings have been accepted by other workers; see Diapsid phylogeny for more. The following synthetic consensus view, based on Carroll, 1988, Gower, 1996, Frey, Sues & Munk, 1997, and Gao & Fox, 1998, is from Mikko's Phylogeny Archive. It doesn't represent a particular cladogram, but rather a dendrogram mash-up of different Evolutionary Systematic and Cladistic sources:

```
===o Neodiapsida Gauthier, 1984 sensu Benton 1985
   |?-o †Weigeltisauridae Piveteau 1926 (†Coelurosauravus Piveteau 1926)
   `--+-- †Apsisaurus witteri Laurin 1991 (now known to be a varanopsid pelycosaur!)
      `--o Eosuchia Broom, 1924 sensu deBraga & Rieppel, 1997
         |?=o †Eosuchia Broom, 1924 [Younginiformes Romer, 1945]
         |  |?- †Acerosodontosaurus piveteaui Currie, 1980 [Acerosodontosauridae]
         |  |?- †Noteosuchus colletti (Watson, 1912) Broom, 1925 [Eosuchus colletti Watson, 1912]
         |  |-- †Galesphyrus capensis Broom 1914 [Galesphyridae Currie 1981]
         |  |--o †Younginidae Broom, 1914
         |  |  |-- †Heleosuchus griesbachi Broom 1913
         |  |  |-- †Thadeosaurus colcanapi Carroll, 1981
         |  |  `-- †Youngina capensis Broom, 1914 [Youngoides romeri, Youngopsis]
         |  `--o †Tangasauridae Haughton, 1924
         |     |-- †Hovasaurus boulei Currie, 1981
         |     |-- †Tangasaurus mennelli Currie, 1982
         |     `-- †Kenyasaurus mariakanensis Harris & Carroll, 1977
         `--+?- †Claudiosaurus germaini Carroll, 1981 [Claudiosauridae Carroll, 1981 ]
            |?-+--o †Lazarussuchus Hecht, 1992; U.Olig.-L.Mioc. Eu. [Lazarussaurus (lapsus
calami)]
            |  |  |-- †L. inexpectatus Hecht, 1992
            |  |  `-- †L. dvoraci Evans & Klembara, 2005
            |  `?- †Choristodera
            |?- †“Ichthyosauromorpha”
            `-- Sauria Gauthier, 1984
```

In recent years the hand-coded Hennigian analysis has been replaced by computer-based statistical parsimony analysis using large numbers of traits from a larger range of taxa. These result in hundreds of trees, from which the most parsimonious (the ones of shortest length) are selected. This different methodology results in very different tree topology (the shape of the cladogram; i.e. the arrangement of the nodes and taxa). When applied to the

Younginiformes this resulted in a very different, and much less tidy, arrangement. The following abstract is from Bickelmann, Müller & Reisz, 2009:

> "A restudy of the Upper Permian diapsid *Acerosodontosaurus piveteaui* from Madagascar indicates that the bone formerly identified as the quadratojugal is a fragment of a rib. This in turn implies that, in contrast to previous studies, the lower temporal arcade must be considered incomplete and derived relative to the ancestral condition. Since the phylogenetic position of *Acerosodontosaurus* is poorly understood, the taxon was entered into a modified phylogenetic data matrix of diapsid reptiles, and the purported monophyly of "Younginiformes" was tested for the first time by including all potential members of the clade as separate taxa, as well as other taxa from the same deposits. The results of the phylogenetic analysis do not support the monophyly of "younginiform" reptiles. Instead, most taxa cluster unresolved at the base of Neodiapsida, a finding that has important implications for the understanding of early diapsid evolution because it suggests that early neodiapsids represent several distinct evolutionary lineages. *Acerosodontosaurus* and *Hovasaurus* do form a clade, a finding consistent with the stratigraphic age and biogeography of these taxa."

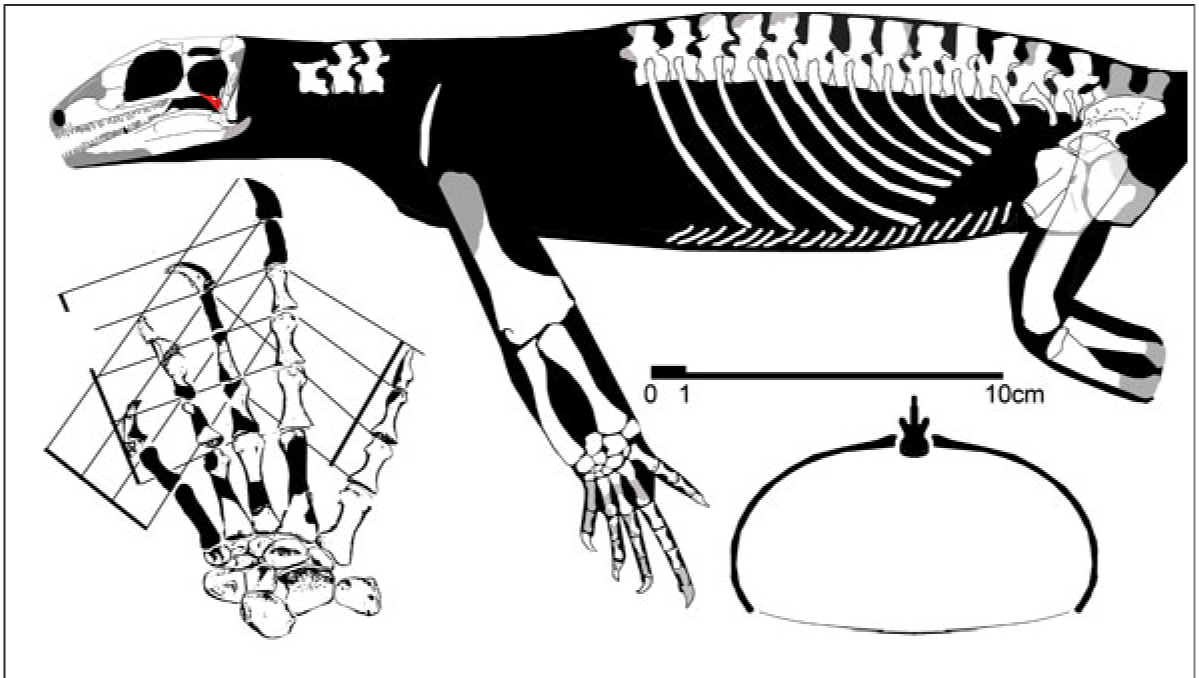


Illustration of *Acerosodontosaurus piveteaui*, by David Peters, Reptile Evolution. The quadratojugal bone, shown in red, is determined by Bickelmann et al. 2009 to be a portion of rib. This leads to a revolution in early diapsid relationships, including demolishing the monophyletic Younginiforms (Peters himself rejects this interpretation).

The resulting cladogram is represented as follows (from Mikko's Phylogeny Archive):

```
===o Neodiapsida
    |-- †Youngina
    |-- †Kenyasaurus
    |--
†Lanthanolania
    |-- †Thadeosaurus
    |-- †Galesphyrus
    `--+--+--
†Tangasaurus
       |   `--+--
†Hovasaurus
       |      `--
†Acerosodontosaurus
       `--+--
†Claudiosaurus
          `--+--+--
†Palaeagama
             |   `--
†Saurosternon
             `--+--
†Coelurosauravus
                `--o
?Sauria
                   |-
-+--
†Thalattosauriformes
                   |
`--
†“Ichthyosauromorpha”
                   `-
-+--o
Lepidosauromorpha
|  |-- †Choristodera
|  `--+--
†Sauropterygia
|      `--+--
Testudinata
|          `--+--
†Kuehneosauridae
|             `--
Lepidosauriformes
`--o Archosauromorpha
|== †“Protorosauria”
```

```
`--+--
†Trilophosauria

`--+--
†Rhynchosauria

`-- Archosauriformes
```

In contrast to the earlier work of Bentan, Evans, and Gauthier et al, the Younginiformes have become an assemblage of basal Neodiapsids, and Claudiosaurus and *Coelurosauravus* moved to a more derived position. The elimination of a monophyletic Younginiformes is ironicallty more in keeping with the premise of transitional evolutionary grades (which also helps prune away some of those excessive ghost lineages). I am reminded here also of the difference in chelonian phylogenetic studies and cladograms between the earlier, ground-breaking work of Gaffney, and the more recent phylogenies of Joyce and others. In these and other instances, use of powerful computers as well as the benefit of more recent discoveries, and tend to key in as much data as possible, creating huge data matrixes and clades that cannot be easily identified by means of a few obvious synapomorphies. In these instance, it is hard to know which methodology should be preferred. In any case it seems that the relationships of these early diapsids are a lot less clear-cut then was previously thought.

One thing that everyone does agree on now is that the younginiforms preceded the great Lepidosaur - Archosaur split, and that there was a large evolutionary radiation during the Late Permian or, perhaps, Early Triassic (the latter dating makes more sense if we assume the Diapsids radiated to occupy the evolutionary niches vacated by the Synapsids and Parareptiles folliowing the end-Permian mass extinction) . Meanwhile there are other, more phylogenetically controversial taxa, such as the ichthyopterygia, sauropterygia, and many smaller groups, which may or may not be related to each other, and which may or may not belong outside or in one of the two main Diapsida groups. MAK111120

Sauria: LCA all living diapsids [C97a]

Range: from the Middle Permian.

Phylogeny: Neodiapsida:::: Ichthyopterygia + *: Archosauromorpha + Lepidosauromorpha.

Characters: Ant. process of squamosal narrow; squamosal largely restricted to top of skull; dorsal origin of temporal musculature; no tabular; sacral ribs lateral orientation; ribs mostly single-headed; fusion of caudal ribs, small proximal carpals & tarsals.

References: Callaway (1997a) [C97a] ATW990911.

Younginiformes: *Acerosodontosaurus*, *Youngina*, *Hovasaurus, Tangasaurus*. Medium-sized lizard-like, some forms aquatic. Possibly paraphyletic as ancestral to lepidosaurs.

Range: Late Permian to Early Triassic.

Phylogeny: Neodiapsida::: (Ichthyopterygia + Sauria) + *.

Characters: Aquatic forms quite similar to terrestrial with laterally flattened tails. Single coracoid; tabular absent; quadrate not embayed; vertebrae with relatively tall neural spines; stapes large; sternum and vertebral transverse processes present; cleithrum present; olecranon process of ulna absent; primitive tarsus, pes; **$** lateral centrale not in contact with 4th distal carpal; gastroliths.

Comments: Originally considered the most basal diapsids, this view was revised after discovery of *Petrolacosaurus* and other araeoscelids. Considered next lepidosauromorphs (Benton 1985; Evans 1988), moved to the base of Neodiapsida (Laurin 1991), now seem to be a praphyletic assemblage of basal forms (Bickelmann et al 2009). From the introduction:

> The so-called "younginiform" reptiles (Benton 1985; Romer 1945) are known exclusively from the Upper Permian and Late Triassic of Madagascar and East Africa (Broom 1914; Carroll 1981;

> Currie 1980, 1981, 1982; Harris and Carroll 1977; Haughton 1924; Piveteau 1926). Originally thought to be the most basal diapsids, this view was modified after careful investigations of Petrolacosaurus and other araeoscelid reptiles (Reisz 1977, 1981; Reisz et al. 1984). Although "younginiform" reptiles were occasionally considered as lepidosauromorphs (Benton 1985; Evens 1988), Gaffney (1980), and later Laurin (1991) eventually placed them in their currently accepted position at the base of Neodiapsida. However, the in-group relationships of "Younginiformes," as well as their monophyletic status, are neither understood nor have they been tested in a modern phylogenetic framework. Currie suggested their monophyly in 1982, including *Youngina capensis* (Broom 1914), *Hovasaurus boulei* (Currie 1981), *Tangasaurus mennelli* (Currie 1982), *Kenyasaurus mariakanensis* (Harris and Carroll 1977), as well as *Thadeosaurus colcanapi* (Carroll 1981), but this interpretation was solely based on Hennigian argumentation, which was the only technique available at that time. The same methodology was also used in studies by Benton (1985) and Evens (1988) on diapsid "younginiform" phylogeny, in which both authors also included another taxon from the same deposits, *Acerosodontosaurus piveteaui* (Currie 1980). While Currie (1982) had surprisingly ignored this taxon in his phylogenetic study, both Benton (1985) and Evans (1988) placed it as sister taxon to all other "Younginiformes."

As defined here then the Younginiformes are simply a paraphyletic assemblage of broadly lizard-like (i.e. generalised reptilian) terrestrial and semi-aquatic basal Neodiapsid reptiles that flourished during the late Permian and early Triassic periods.

Links: Diapsids Phylogeny; Autapomorphies of diapsid clades. ATW010403. Palaeocritti, Wikipedia, Wikipedia Eosuchia, UCMP - Basal Diapsids (only a paragraph) MAK111118

Youngina: *Youngina capensis* Broom, 1914 (and other species?)

Synonyms: *Acanthotoposaurus, Youngoides, Youngopsis*

Range: Late Permian (Tropidostoma-Dicynodon zones) of Southern Africa.

Phylogeny: Neodiapsida/Younginiformes: *

Links: Wikipedia

Tangasauridae: *Acerosodontosaurus, Hovasaurus, Tangasaurus*

Range: Late Permian to Early Triassic (known from from the Sakamena Group of western Madagascar).

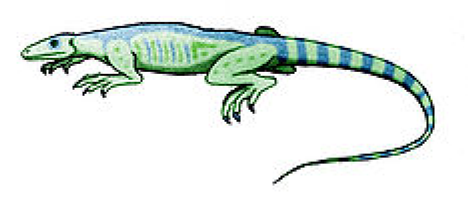
Phylogeny: Neodiapsida/Younginiformes: *

Characters: quadratojugal and jugal bones meet to form an arch in the skull, characteristic of many primitive diapsids, especially Younginiformes.. Smokeybjb 090221 (Wikipedia)

Comments: Relatively unaffected by the Permian-Triassic extinction event. (Ketchum & Barrett 2004) Benton 1985 divides the Tangasaurs into monphyletic Kenyasaurinae (terrestrial) and Tangasaurinae (aquatic). Kenyasaurinae is rejected by Bickelmann et al 2009, who however recovered a monophyletic Tangasauridae, excluding *Kenyasaurus* and *Thadeosaurus* but including *Acerosodontosaurus*. These were aquatic animals, with laterally compressed tails that allowed them to be able to swim in the freshwater lacustrine environments.

Links: Wikipedia

Thadeosaurus:



Range: Late Permian of western Madagascar).

Phylogeny: Neodiapsida/Younginiformes: *

Comments: fully terrestrial, probably a strong runner. Included with *Kenyasaurus* as a monophyletic Kenyasaurinae by Benton 1985. Analysis by Bickelmann et al 2009 rejects the Kenyasaurinae and shows it to be a paraphyletic assemblage of basal Neodiapsids

Links: Wikipedia (incl. graphic)

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checked ATW050512, revised MAK111120

Diapsida: Neodiapsida: *Claudiosaurus*

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
       |
       `--DIAPSIDA
          |==Araeoscelida
          `--Neodiapsida
              |=="Younginiformes"
              `--+--Claudiosaurus
                 |--Weigeltisauridae
                 `--+--+--+?--Thalattosauria
                      |   |  `?-
-Saurosphargidae
                      |   `--ICHTHYOSAURIA
                      |?--Omphalosaurus
                      |?--Hupehsuchia
                      `--Sauria
                         |?--CHORISTODERA
                         |--LEPIDOSAUROMORPHA
                         `--ARCHOSAUROMORPHA
```

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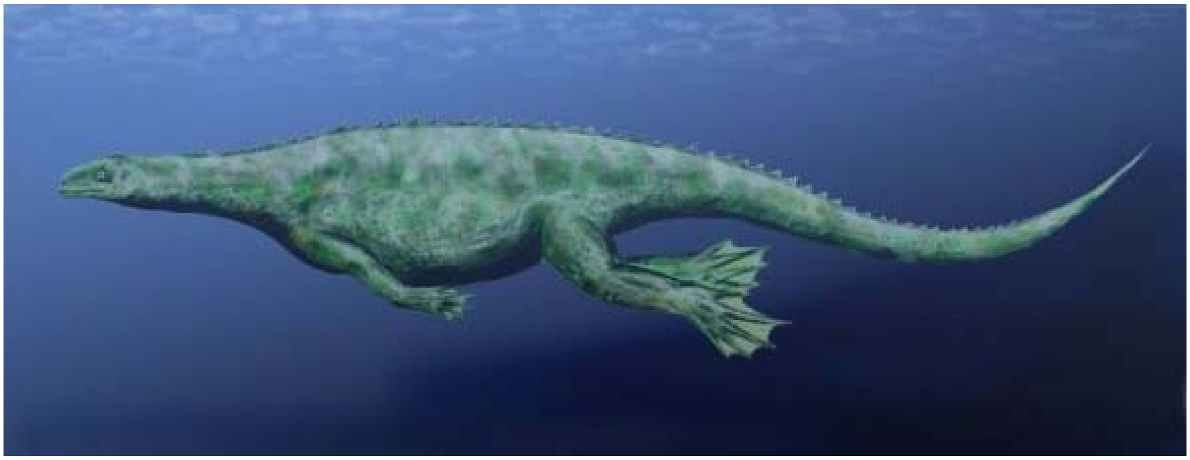
1. *Claudiosaurus* X

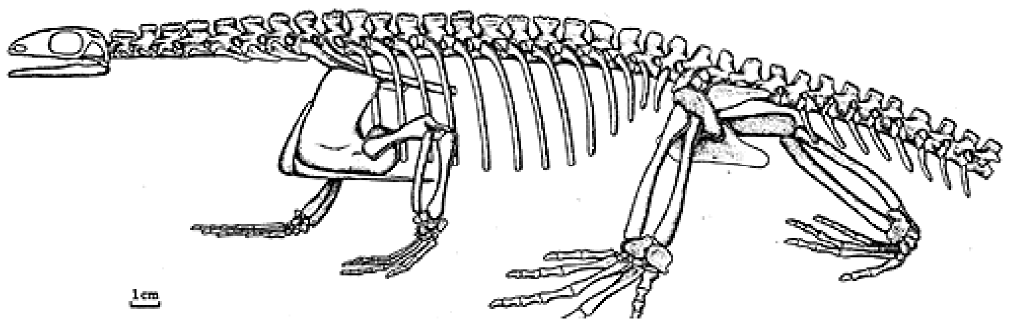


Claudiosaurus germaini, an aquatic neodiapsid from the Tangasaur from the Late Permian

(Sakamena Formation) of Madagascar.. illustration by Nobu Tamura (Wikipedia)

Claudiosaurus, Anchor Taxa, and the Illusion of Uncertainty

Claudiosaurus was a medium-sized (60 cm) low-slung reptile with a small head, fairly long neck, and a long tail. It lived by the shores of lakes or sheltered seas along a pair of rift valleys in what is now Madagascar in the Late Permian -- just before whatever event(s) it was that killed off most life forms on Earth at the end of the Paleozoic. As discussed elsewhere, many of the basal diapsids are rather scrappy; and this has led to some rather odd phylogenies. *Claudiosaurus* is an exception. It is well known from a number of good specimens. Even better, it seems rather clear that, as Carroll (1981) pointed out in his original description, *Claudiosaurus* is closely related to a group of neodiapsids now known as the **Younginiforms**.



Claudiosaurus germaini in left lateral view. From Carroll (1981).

Claudiosaurus was almost certainly amphibious. Caldwell (1994). This is not really obvious from a first glance at the skeleton, but has been quite convincingly shown by Carroll and Caldwell. Its most enigmatic feature is the skull. As in snakes, there seems almost nothing holding the skull together. The lower temporal bar is completely absent, the post-orbital skull is full of large holes, and the pre-orbital skull was weakly bound and may not even be completely ossified. It is hard to make sense of all the data, but at least there is no lack of data to make sense of.

In spite of this wealth of information, it has proven no easier to get an exact placement for *Claudiosaurus* than it has been for *Paliguana*. Most of the confusion may be due, in addition to the inclusion of taphonomic detritus, to inconsistencies in nomenclature. The most logical definitional benchmark in this area is clearly that of Jacques Gauthier. The benchmark clade is the crown group Sauria = the last common ancestor of birds and snakes. Then Lepidosauromorpha = all Saurians closer to snakes than birds; and Archosauromorpha = all Saurians closer to birds than snakes. "Closer" in this parlance means "having a more recent common ancestor with." We can't use a "diapsid" benchmark because the diapsid condition is a physical character. It has no phylogenetic meaning. We can't really use Reptilia (= turtles + turtledoves) because of the continuing concern that turtles might turn out to be inside Sauria after all. Thus, if our discussions are to be tied to reality at all, it is quite important that the Saurian anchor be firmly in place. In spite of this logical necessity, many phylogenies -- including, until recently, these Notes -- have allowed each member of this crown-stem triad (*see* Sereno (1998)) to live a wild, free life of its own. See, *e.g.* Caldwell (1996); Motani *et al*. (1998) and (to a far lesser extent) deBraga & Rieppel (1997).

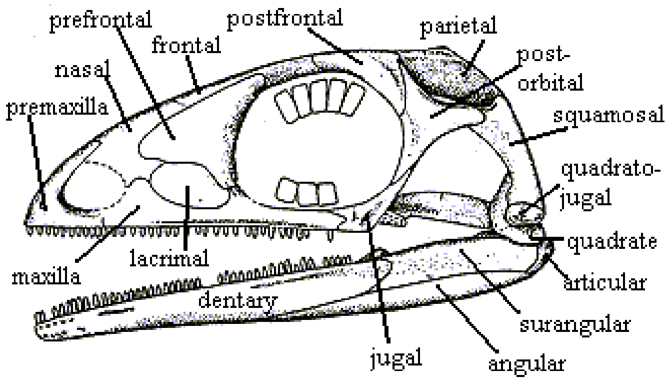
Interestingly, when we apply a consistent nomenclature and simply remove the uncertain bits and pieces, *everyone's* cladogram looks like this:

```
"Diapsida" (any arbitrary definition)
|--Araeoscelida
`--+--Claudiosaurus
   `--+--Younginiformes
      `--+--Ichthyosauria
         `--SAURIA
            |--Archosauromorpha
            `--Lepidosauromorpha
               |--Sauropterygia
               Lepidosauriformes
```

The only genuinely unsettled points are (a) whether turtles are in this mix somewhere and (b) the position of the Coelurosauravidae. The latter have variously been placed between *Claudiosaurus* and the Younginiformes, or as a sister to Ichthyosauria. (I have chosen the former alternative for no particular reason.) In truth, the original results of Caldwell (1994) are not quite consistent with this scheme, but Motani et al. (1998) *do* obtain this pattern with the same data set when they recode Ichthyosauria to incorporate more recent information. ATW010415

Descriptions

Claudiosaurus:



Claudiosaurus skul in left lateral view. Modified from Carroll (1981).

Range: Late Permian of Madagascar.

Phylogeny: Neodiapsida: (Coelurosauravidae + (Younginiformes + (Ichthyopterygia + Sauria))) + *.

Characters: About 60cm. Head small; ~50 small, sharp marginal teeth (none procumbent); shagreen of denticles on palatal bones; Meckelian canal partly open; transverse pterygoid flange undifferentiated and weak; interpterygoid vacuities reduced or absent; small suborbital fenestra present; anterior skull poorly known; premaxillae with long, thin nasal process; nasals large; prefrontal (?) large; lacrimal is an odd, oval element probably excluded from orbit; orbit large; large upper temporal fenestra; lower temporal bar and posterior process of jugal absent; quadrate strongly supported by pterygoid (unlike squamates); stapes unknown (?); no stapedial foramen on quadrate; posterior margin of parietal sculpted and may have supported postparietals, tabulars, etc.; long neck (from posterior displacement of pectoral girdle?), with 8 cervical vertebrae; 25 presacral vertebrae, all except atlas with ribs; dorsal centra ~twice as long as wide; intercentra present; neural arches in trunk well-developed and articulate; rib cage probably complete (in cartilage); ribs not pachyostotic; 2 sacral vertebrae with partial incorporation of a 3rd; tail slender & not specialized for aquatic locomotion; caudal vertebrae not specialized; sternum not ossified but clearly present; scapulocoracoid ossified as single plate-like units, forming complete plate with large interclavicle; glenoid quite far posterior and angled posteriorly; digit 3 is longest on manus; ilium elongated; no thyroid fenestra; calcaneum with distinct lateral flange (gastrocnemius?); some indication that proximal and distal tarsals were partially locked together; lateral centrale reaching fourth distal tarsal. Amphibious?

Links: Icarito Interactivo - dinosaurios (Spanish); Autapomorphies of diapsid clades, Wikipedia (stubby), UCMP - Basal Diapsids (only a paragraph), .

References: Carroll (1981).

Note: determinate growth of long bones, but ossification of distal limb and some cranial bones continued throughout life. Carroll (1981) makes a fairly good case that *Claudiosaurus* was a derived relative of *Thadeosaurus*, now classified as a younginiform.

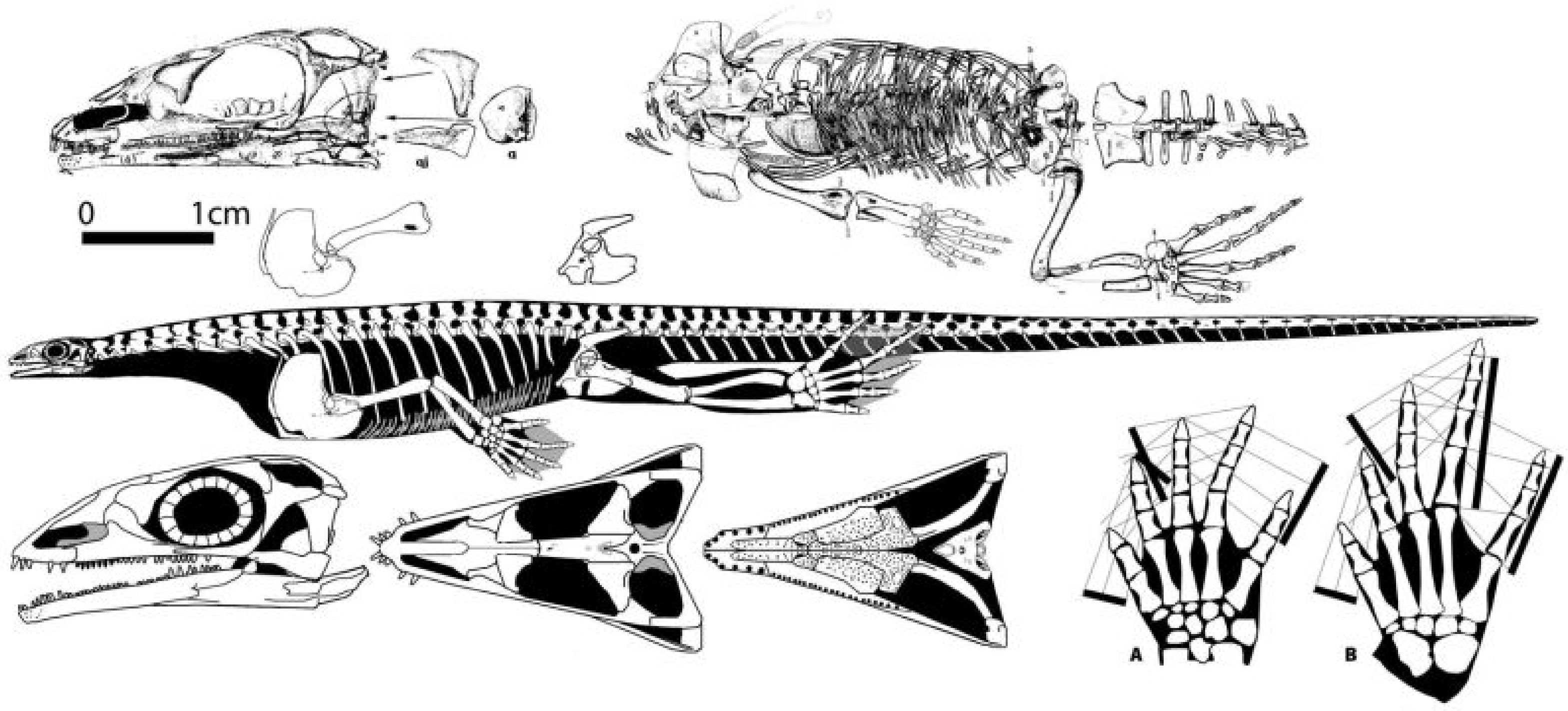


Illustration of skeleton of *Claudiosaurus germaini*, by David Peters, Reptile Evolution.

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checked ATW050512, new page MAK111116

Diapsida: Neodiapsida: Weigeltisauridae

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
        |
        `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
              |=="Younginiformes"
              `--+--Claudiosaurus
                 `--+--Coelurosauravidae
                    `--+--+--Thalattosauria
                       |  `--ICHTHYOSAURIA
                       |?--Omphalosaurus
                       |?--Saurosphargidae
                       |?--Hupehsuchia
                       `--Sauria
                          |?--CHORISTODERA
                          |-
-LEPIDOSAUROMORPHA
                          `-
-ARCHOSAUROMORPHA
```

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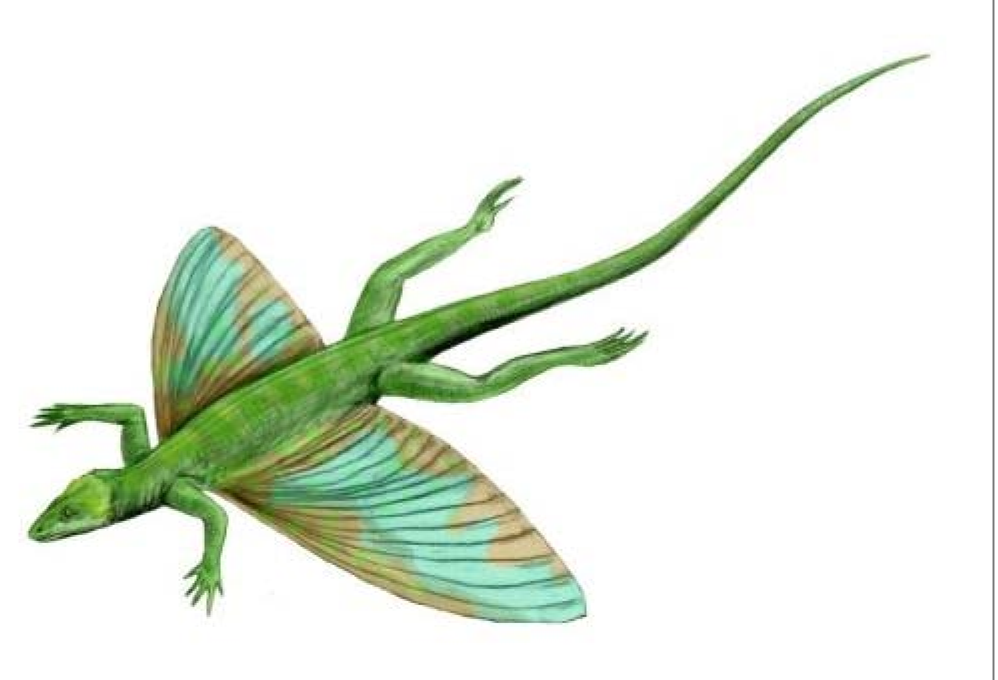
1. Weigeltisauridae X

Descriptions

Weigeltisauridae: *Coelurosauravus*, *Rautiania*, *Weigeltisaurus* arboreal gliding forms.

Synonyms: Coelurosauravidae.



Coelurosauravus jaekeli, a gliding reptile from the Late Permian of Germany. illustration by Nobu Tamura (Wikipedia)

Range: Late Permian of Europe, Madagascar, Russia and Canada

Phylogeny: Neodiapsida:: (Younginiformes + (Ichthyopterygia + Sauria)) + *.

Characters: *Coelurosauravis*: elongate, horizontal ribs – gliding membrane like *Draco*? Sues (1997) says not ribs: different support for gliding membrane. Loss of lower temporal bar, elaborate squamosal frill. *Megalancosaurus* had (1) osteological correlates for the existence of a birdlike prepatagial membrane; (2) elbow joints that, similar to many birds, "locked" at about 165 degrees extension (i.e., about 25 degree short of full extension); (3) fusion of dorsal vertebrae into a somewhat birdlike/pterosaur-like notarium; (4) lightened, externally "hollowed-out" long bones; (5) extremely long forelimbs, and possibly other flight or gliding adaptations. (Ruben, J. (2000) pers. comm on dinosaur listserver 4/6/00).

Links: UCMP - Basal Diapsids (only a paragraph), Wikipedia (stubby), link; link

Comments: very primitive forms with protorothyridid like characteristics in limb proportions and number of presacral vertebrae Currie, 1981 p.162, very basal relative to, and not closely related to, younginiformes (Currie, ibid, Benton 1985) though Bickelmann et al. 2009 gve them the opposite placement, not primitive than, but more advanced than younginiformes. This difference is certainly due to different cladistic methodologies (computer-statistical, supermatrixes and so on) used now, in contrast to the hand-drawn approach of the 1980s. One needs to ask whether the statistical approach using parsimony analysis of hundreds of trees, and with large numbers of atomistically distinct traits, better reveals or conceals phylogenetic relationships, in comparison to the approach used by early workers in the field.

Coelurosauravus elivensis Piveteau 1926

Synonyms: *Daedalosaurus magagascariensis* Carroll 1978 cospesific or distinct species?

Range: Late Permian of England and possibly Madagascar

Phylogeny: Weigeltisauridae **:** + *.

Coelurosauravus jaekeli (Weigelt 1930)

Synonyms: *Palaeochamaeleo jaekeli* Weigelt 1930; *Gracilisaurus ottoi* Weigelt 1930; *Weigeltisaurus jaekeli* (Weigelt 1930) Kuhn 1939] - ref Mikko's Phylogeny Archive

Range: Late Permian of West Germany

Phylogeny: Weigeltisauridae **:** + *.

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Thalattosauria

Diapsida: Overview

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
        |
        `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
              |=="Younginiformes"
              `--+--Claudiosaurus
                 |--Weigeltisauridae
                   `--+--+-
-Thalattosauria/Thalattosauriformes
                        |   |   |-
-Askeptosauroidea
                        |   |   |  |-
-Endennasaurus
                        |   |   |  `-
-Askeptosauridae
                        |   |   `-
-Thalattosauroidea
                        |   |      |--+-
-Nectosaurus
                        |   |      |  `-
-Xinpusaurus
                        |   |      `-
-Thalattosauridae
                        |   |         `--+-
-Thalattosaurus
                        |   |            `-
-Claraziidae
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Saurosphargidae
                        |?--Hupehsuchia
                        `--Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

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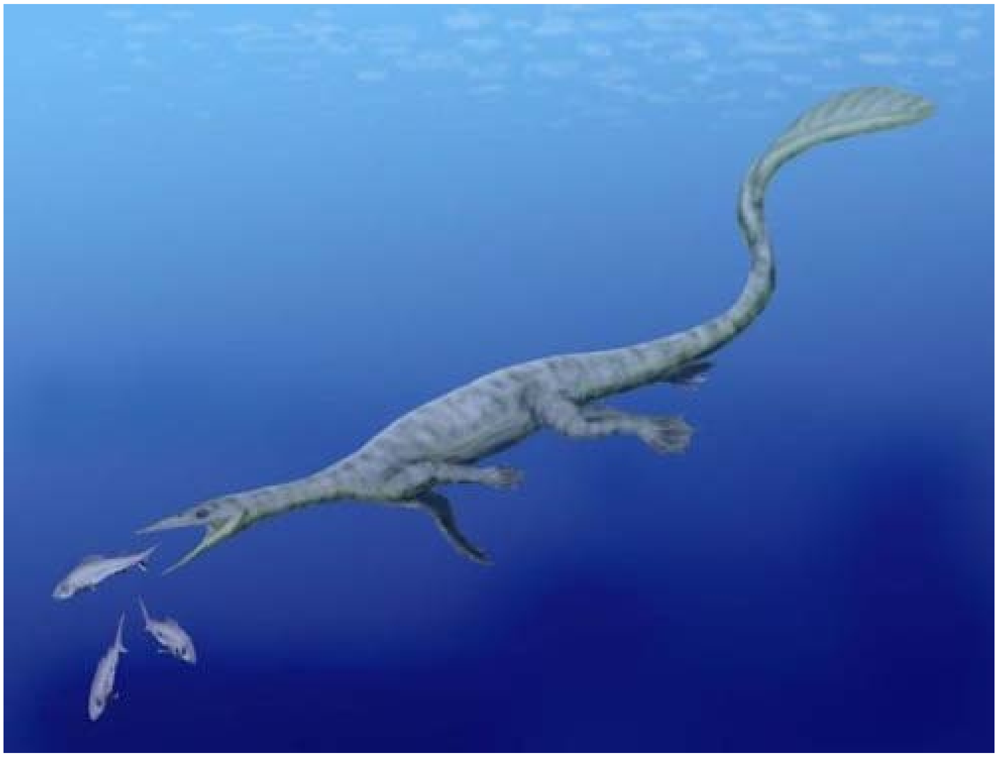
6. Thalattosauridae X
7. Thalattosauriformes X
8. Thalattosauroidea X
9. *Thalattosaurus* X
10. *Xinpusaurus* X



Endennasaurus acutirostris, an Askeptosaurian thalattosaur from the Late Triassic of Tethys Italy, Illustration by Nobu Tamura (Wikipedia). Thalattosaurs were only one of a number of diverse groups of marine diapsid reptiles that evolved in parallel during the Triassic period.

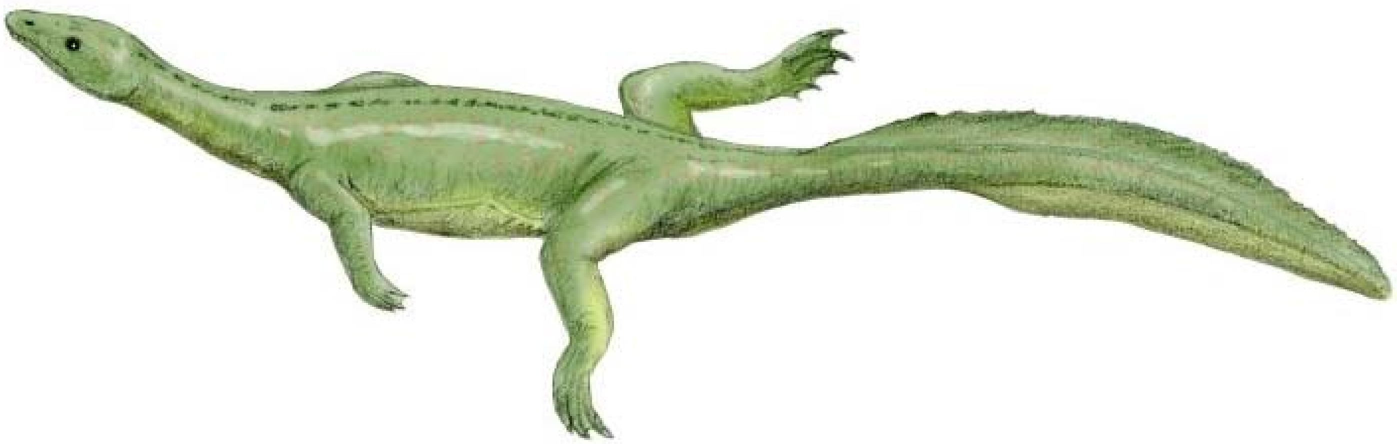
The Thalattosaurs

Thalattosaurs (meaning "ocean lizards") are marine diaspids of uncertain affinities. They resembled large (upto two to four meters or more in length) aquatic lizards, with long, flexible bodies and short but stocky limbs (see Zachary Miller When Pigs Fly Returns). They were among the more successful of the Triassic marine reptiles, and evolved along a number of distinct lines, although all appeared to be near-shore types, like the contemporary early ichthyosaurs, pachypleurosaurs, nothosaurs, helveticosaurs, proto-turtles, and trematosaur amphibians and other animals they shared the marine environment with.

Thalattosaurs are divided into two main groups: Askeptosaurs and Thalattosaurs. While quite diverse and widespread (being known from Europe, North America, and China) they are not common as fossils; recently (2011) a rare almost complete skeleton was discovered in Alaska (link, Google search). The following cladogram is from Mikko's Phylogeny Archive, 2004, modified according to Wu et al 2009

```
Thalattosauriformes
   |--Askeptosauroidea
```

```
|    |--Endennasaurus
|    `--Askeptosauridae
|         |--Askeptosaurus
|         `--+--Anshunsaurus (Wikipedia - detailed page)
|            `--Miodentosaurus
`--Thalattosauroidea
     |--+--Nectosaurus
     |  `--Xinpusaurus
     `--Thalattosauridae
          |--Agkistrognathus
          `--+--Paralonectes
             `--+--Thalattosaurus
                `--Claraziidae
                     |--Clarazia
                     `--Hescheleria
```



Miodentosaurus brevis, a thalattosaurian from the Late Triassic of China, Illustration by Nobu Tamura (Wikipedia). Although this reconstruction shows a tail fin (see also) it is equally possible that the tail was long and tapering like that of a modern marine iguana.

Phylogenetic relationships

As with most of the other lineages of specialised Triassic marine reptiles, larger relationships are unclear. Thalattosaurs have been variously included under "Eosuchia" (Romer 1966), "rhynchocephalia" (Sphenodontia) (Kuhn 1969), with sauropterygians (Reippel 1998, Nosotti & Rieppel, 2003, Li et al 2011), with ichthyosaurs as stem Sauria (Bickelmann, Müller & Reisz, 2009) and with ichthyosaurs as stem euryapsida within basal archosauromorpha (Merck, 1997, Borsuk-Bialynicka & Evans 2009). Ass often the case, different toplogies are proposed by different workers in the field. Since two different sources have linked them with ichthyosaurs, we have tentatively followed suit here, although the sauropterygian option may be just as viable. Alternatively, they could be related to neither of these major groups, and the similarities simply due to convergence. MAK101003, 111125

Descriptions

Thalattosauriformes (= Thalattosauria)

Range: Middle to Late Triassic.

Phylogeny: Younginiformes ::: (?Ichthyopterygia + * : Askeptosauroidea + Thalattosauroidea

Askeptosaurus italicus, Middle Triassic of Tethys Europe, Illustration by Nobu Tamura (Wikipedia)

Characters: elongate rostrum (snout) and premaxillae, nostrils set back, premaxillae contact frontal bones, upper temporal fenestra slit like or closed, lower temporal fenstra open below, limbs paddle like (Benton, 1985 p.151; Rieppel, 1987)

Comments: The terminology varies, with the larger thalattosaur-askeptosaurid group being called either Thalattosauria (Cheng et al 2007) or Thalattosauriformes (Müller et al., 2005), whilst the name Thalattosauroidea has been used for the more exclusive thalattosaur group (Rieppel et al., 2000).

Note on phylogeny: As with most of these early specialised groups, the actual evolutionary relationships of the thalattosaurs is unclear. They have been associated with lepidosaurs, ichthyosaurs, and archosauromorphs. It is even possible that the ichthyosaurs are related to archosauromorph (although the fish-lizards are such a specialised group it is hard to know for sure where they belong), which would make it possible for thalattosaurs to be related to both. For now we have tentatively (hence the question amrks in the menu-cladogram) placed them near the base of the ichthyosaur lineage, without making any further judgment on the overall topology of the diapsid tree. Hopefully further research will give a better understanding of the evolutionary relationships and origins of these little known but intriging Triassic reptiles. MAK101011 110923

Link: Wikipedia, UCMP - Basal Diapsids (only a paragraph),

Askeptosauroidea

Range: Middle to Late Triassic.

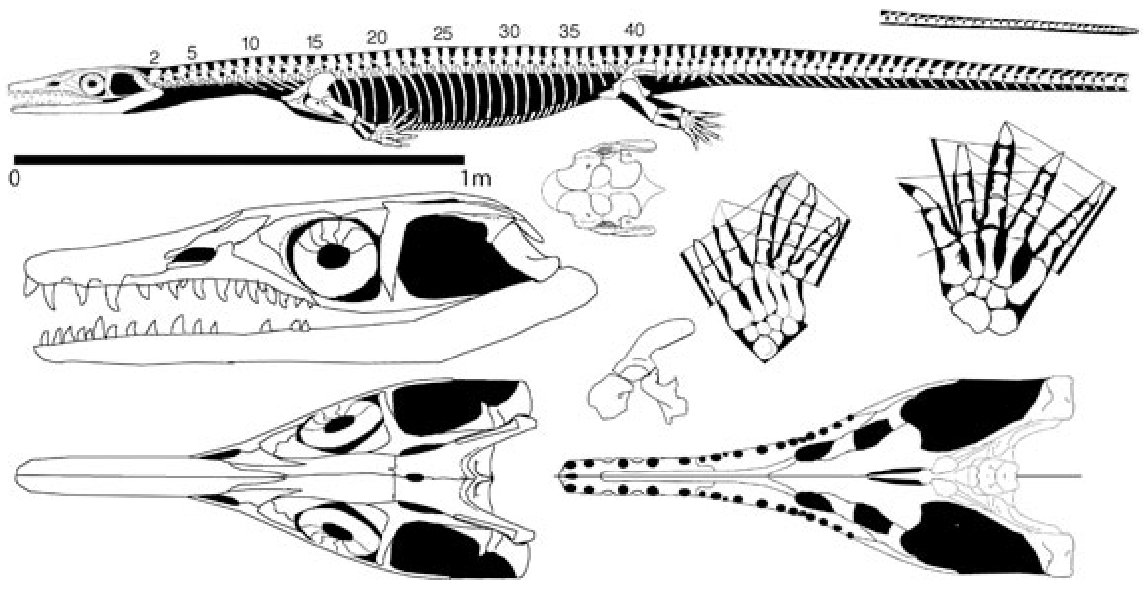
Phylogeny: Thalattosauriformes **:** Thalattosauroidea + * **:** *Endennasaurus* + Askeptosauridae

Comments: generally unspecialised forms, without the paddle-like feet. MAK101003

Askeptosauridae : *Askeptosaurus*, *Anshunsaurus*, *Miodentosaurus*

Range: Middle (Anisian/Ladinian) to Late (Carnian) Triassic of Europe and China.

Phylogeny: Askeptosauroidea **:** *Endennasaurus* + * : *Askeptosaurus* + *Miodentosaurus*



Reconstruction of skull and skeleton of *Askeptosaurus italicus*. The original animal was about 2 meters long. Drawing copyright © David Peters - Reptile Evolution - original url, reproduced with permission.

Askeptosaurus:

Range: Middle Triassic (Anisian/Ladinian) of central Europe.

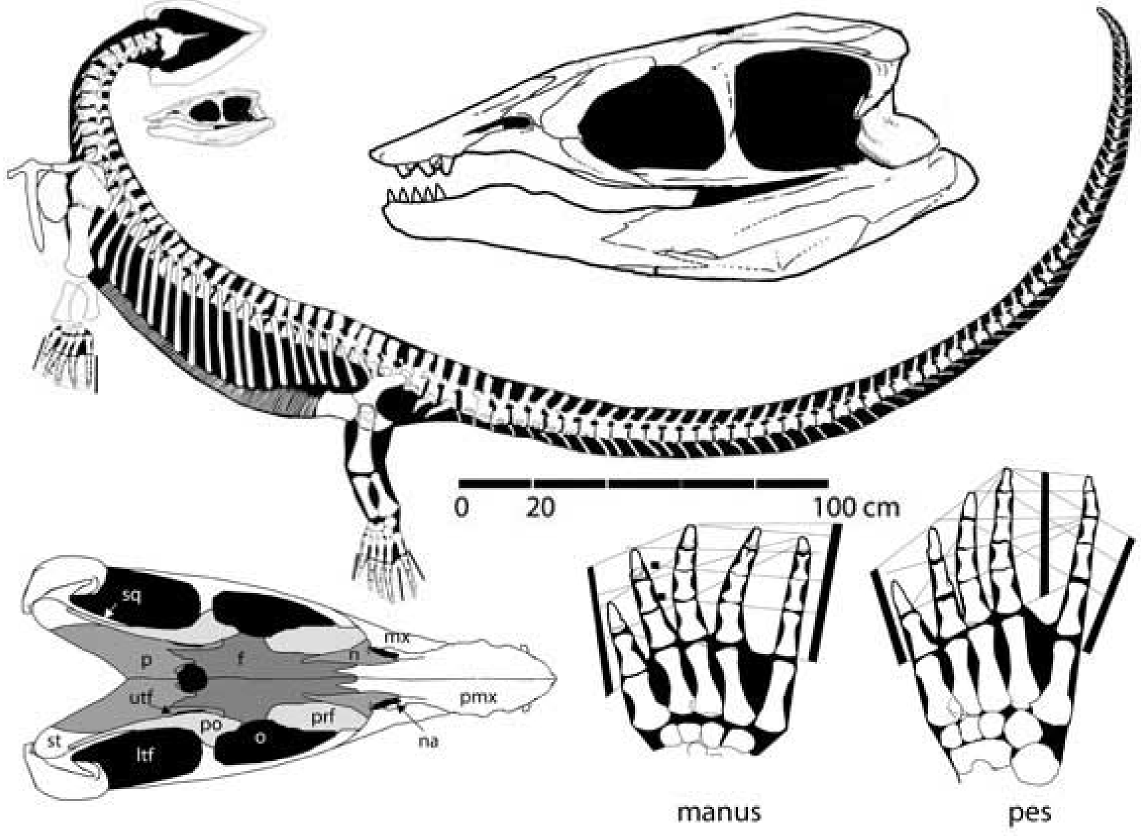
Phylogeny: Askeptosauridae **:** *Miodentosaurus* +*

Characters: elongate, parallel-sided rostrum that terminates in a blunt tip (Rieppel et al 2005), thecodont dentition, rhomboidal interclavical (also in Tanystrophid prolcertiformes) (Rieppel, 1987 p.128), no teeth on vomer or pterygoid, pleurothecodont teeth, neck longer and limbs less paddle-like than than *Thalattosaurus* (Benton, 1985 p.152); elongated eel-like body, very long tail about half the animal's total length, size 2 to 2.5 metres, large eyes with protective bony ring, suited to dim light and deep water (Wikipedia - Askeptosaurus) MAK101003

Comments:

Askeptosaurus was originally classified with *Thalattosaurus* as the Thalattosauridae, currently these are considered representatives of two distiinct lineages

Link: David Peters - Reptile Evolution, Wikipedia



Reconstruction of skull and skeleton of *Miodentosaurus brevis* from the late Triassic of China. From the scale bar (see also photo) the original animal was about 5 meters long, which makes it among the biggest of the Thalattosaurs. Note, the skull at the lower left is too narrow, compare with photo (previous link). Drawing copyright © David Peters - Reptile Evolution - original url, reproduced with permission.

Miodentosaurus : *Miodentosaurus brevis* Cheng et al. 2007

Range: Late Triassic (Carnian) of China.

Phylogeny: Askeptosauridae **:** *Askeptosaurus* +*

Horizon: Upper Triassic Wayao Member of the Falang Formation, Guanling area, Guizhou Province

Comments: Differs from *Askeptosaurus* in having a much shorter rostrum and fewer teeth.

Links: Miodentosaurus brevis (thalattosaurian) - Chinese academy of sciences, photo, note how short the skull is; David Peters - Reptile Evolution; Wikipedia

---

Endennasaurus

Range: Late Triassic of Tethys Europe.

Phylogeny: Askeptosauroidea **:** Askeptosauridae + *

Comments: a specialised, toothless form, similar to Askeptosaurus, but with a longer toothless jaws.

Link: Wikipedia, David Peters - Reptile Evolution

Thalattosauroidea

Range: Middle to Late Triassic.

Phylogeny: Thalattosauriformes **:** Askeptosauridae + * : (*Nectosaurus* + *Xinpusaurus*) + Thalattosauridae

Characters: *Clarazia* and *Thalattosaurus* have a relatively short rostrum distinct from the elongate Askeptosaurid condition, with convergent lateral margins and that terminates in a pointed tip, supratemporal contacts frontal bone, heavy postorbital bar, diastema separates the premaxillary from the maxillary teeth, deep lower jaw (Rieppel, 1987; Rieppel et al 2005)

Comments: One of the two major clades of thalattosaurs, the other being the Askeptosauroidea. Specialised forms tend towards a durophageous (feeding on molluscs or other hard-shelled animals) condition, convergent with placodonts and omphalosaurs. (MAK101003) The Thalattosauroidea are easily distingusihed by the distinctive downturned snouts. In *Clarazia* and Thalattosaurus, the snouts taper to a narrow tip, with the premaxillae (the front jaw bones) at the tip are downturned. *Xinpusaurus* also has downturned premaxillae, but the end of the maxillae are sharply upturned, forming a notch in the skull. In *Hescheleria*, *Nectosaurus*, and *Paralonectes*, the premaxillae are abruptly downturned at the end of the snout, forming nearly a right angle with the rest of the jaw. In these forms, the end of the snout is a toothy hook separated from the rest of the jaw by a space (a diastema) (from Wikipedia)

Nectosaurus *Nectosaurus halius*

Range: Carnian of California.

Phylogeny: Thalattosauroidea **:** Thalattosauridae + (*Xinpusaurus* + *)

Characters: Highly derived rostral structure: maxilla is short with an anteriorly truncated (vertical) margin, a narrow but high ascending process, and a dorsally curving medial flange that is in natural articulation with the ventrally deflected vomer. nearly vertically placed premaxilla. Rieppel et al 2005

Link: Wikipedia MAK101003

Xinpusaurus *Xinpusaurus suni*

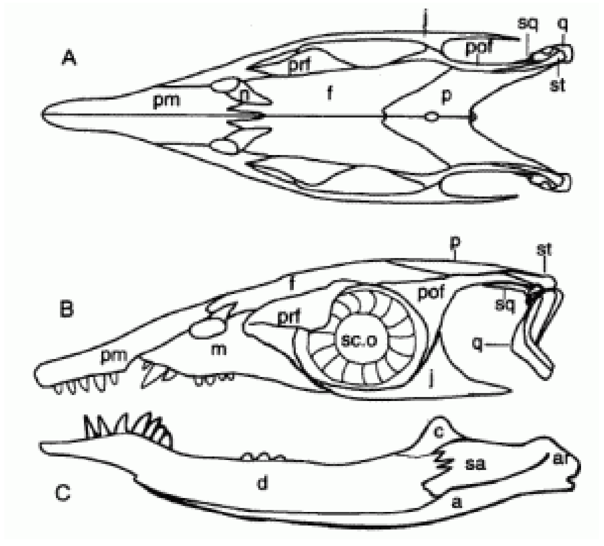
Range: Carnian of China.

Phylogeny: Thalattosauroidea **:** Thalattosauridae + (*Nectosaurus* + *)

Characters: Small size, short snout with weak ventral bend

Comments: Originally described as a Cymbospondyline ichthyosaur. David Peters - Reptile Evolution gives a different-looking skull, with a swordfish/euhrinosaurus-like extended upper mandible. Controversially interprets *Xinpusaurus* as a basal Thalattosauriforme, related to the mesosaur *Stereosternum*, *Hupehsuchus*, and the basal ichthyopterygian *Utatsusaurus*

Reference: Liu & Rieppel 2001 MAK101003



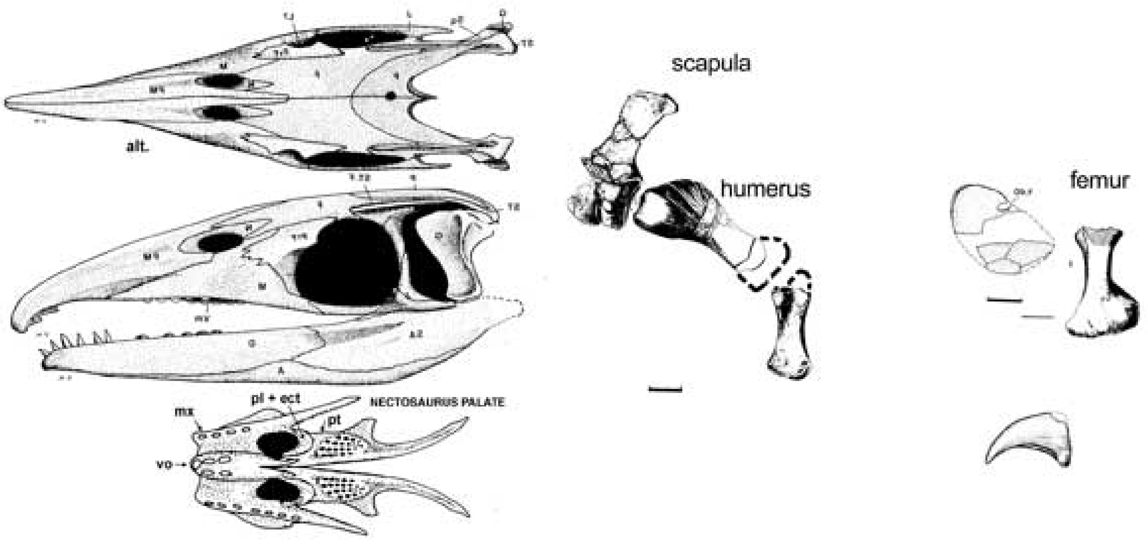
Reconstructed skull of the small Thalattosaur *Xinpusaurus* c.f. *suni* from the Carnian of China, length 14 cm. This genus is very close to *Nectosaurus*, a contemporary form from California, showing the global distribution of these animals. Diagram from Liu & Rieppel 2001 p.83

Thalattosauridae : *Agkistrognathus*, *Clarazia*, *Hescheleria*, *Paralonectes*, *Thalattosaurus*

Range: Middle to Late Triassic.

Phylogeny: Thalattosauroidea **:** (*Nectosaurus* + *Xinpusaurus*) + * **:** *Thalattosaurus* + Claraziidae

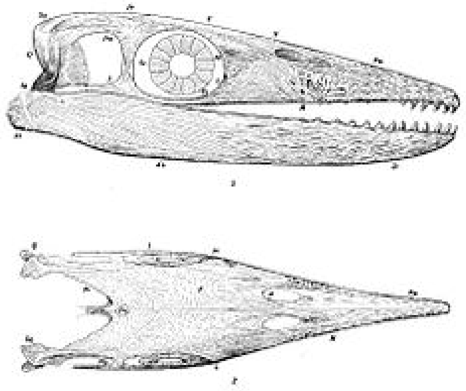
Characters: see under Thalattosauroidea



Reconstruction of skull and limbs of *Thalattosaurus alexandrae* , from the Carnian of California. The original animal is estimated at about two meters long. Drawing copyright © David Peters - Reptile Evolution - original url, reproduced with permission.

Thalattosaurus *Thalattosaurus alexandrae* Merriam 1904

Range: Early/middle (Olenekian/Anisian) to Late (Carnian) Triassic.



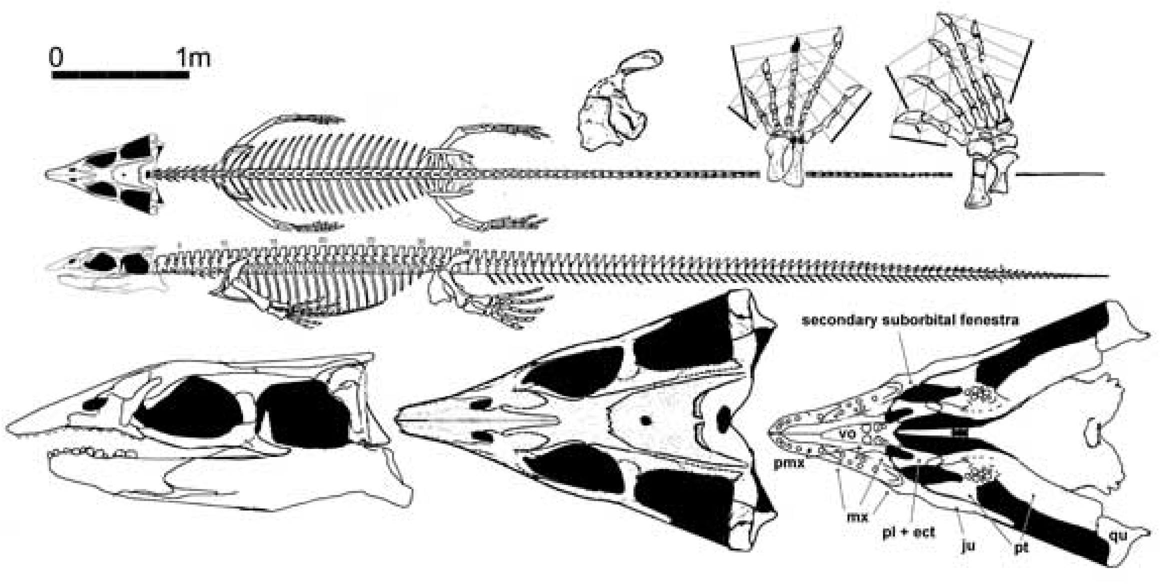
Thalattosaurus alexandrae , reconstructed by John C. Merriam, incorrectly showing a straight rostrum. This image is reproduced a number of times, e.g. Zittel and Eastman's Textbook of paleontology - Wikipedia, pubic domain. Reference: Merriam 1905

Phylogeny: Thalattosauridae **:** Claraziidae + *

Characters: elongate snout, limbs paddle like, upto 2.5 meters (Benton, 1985 p.152), thecodont dentition (also in Tanystrophid prolcertiformes) (Rieppel, 1987 p.128)

Comments: The post-crania is poorly known, but the humerus and femur appear short and robust (Peters). Merriam's reconstruction of the skull (left) incorrectly shows a simple, straight snout and jaws, Peters shows a down-curved rostrum like that of *Clarazia* and *Xinpusaurus*, or even for that matter *Chasmatosaurus* or *Dilophosaurus*. *Thalattosaurus alexandrae* (UCMP-9084) was named by Merriam in 1904 in honor of Annie Alexander, an amateur paleontologist and patron to the University of California Museum of Paleontology (Hilton 2003 p.80)

Links: David Peters - Reptile Evolution, Wikipedia



Reconstruction of skull and skeleton of *Clarazia schinzi*. The original animal was about a meter long. Drawing copyright © David Peters - Reptile Evolution - original url, reproduced with permission.

Claraziidae : *Clarazia*, *Hescheleria*

Range: Middle Triassic of Switzerland.

Phylogeny: Thalattosauridae **:** *Thalattosaurus* + *

Characters: about a meter long, acrodont dentition, general lepidosaur skeleton, heavy jaws, duraphagous (shellfish-eating) dentition, overhanging premaxilla (convergent with Archosauriformes) , 30-32 presacral (neck and back) vertebrae, long deep tail about 60% of overall length, reduced limbs, large paddle-like hands and feet, cruciform interclavical (convergent with lepidosaurs) (Benton, 1985 p.151; Rieppel, 1987)

Comments: . Considered Diapsida *incertae sedis* by Benton, 1985, shown to be Thalattosaurs by Rieppel, 1987 who placed them alongside Thalattosauridae, later revisions by Rieppel and others make the Claraziidae a daughter clade of Thalattosauridae. So perhaps should be renamed Claraziinae. MAK101003

Links: David Peters - Reptile Evolution

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Diapsida: Saurosphargidae

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
       |
       `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
               |=="Younginiformes"
               `--+--Claudiosaurus
                   |--Weigeltisauridae
                    `--+--+--+?--Thalattosauria
                        |   |   `?-
-Saurosphargidae
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Hupehsuchia
                        `--Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

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Hupehsuchia

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Diapsida: Overview

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
       |
       `--DIAPSIDA
         |==Araeoscelida
         `--Neodiapsida
            |=="Younginiformes"
            `--+--Claudiosaurus
                `--+--Weigeltisauridae
                    `--+--+--Thalattosauria
                        |    `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Saurosphargidae
                        |?--Hupehsuchia
                        |    |--Hupehsuchus
                        |    |--Nanchangosaurus
                        |    |--Unnamed species
(SSTM 5025)
                        |    `--Unnamed species
(V4070)
                        `--Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

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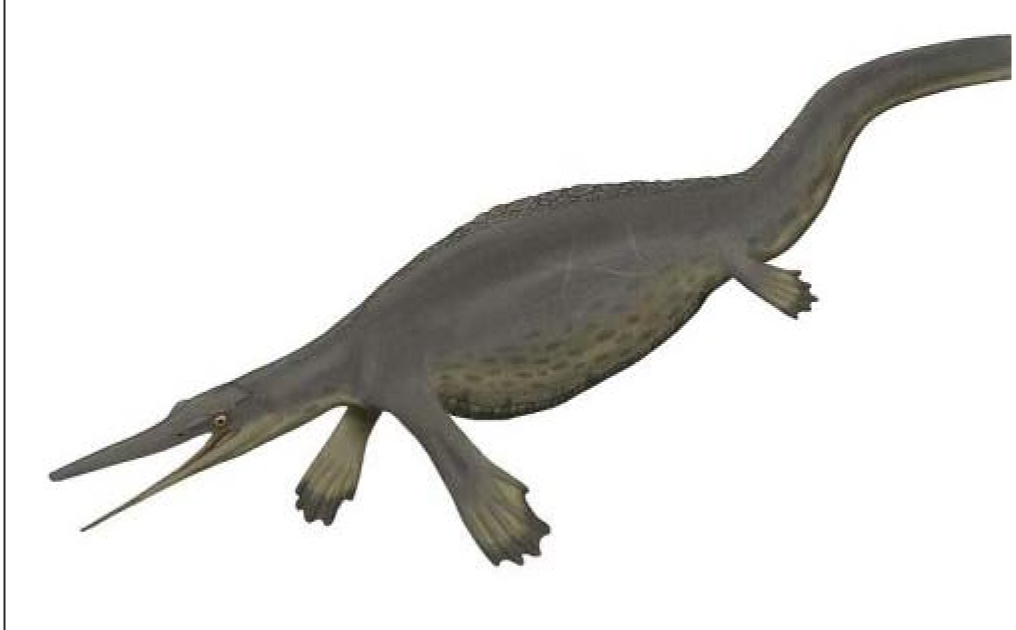
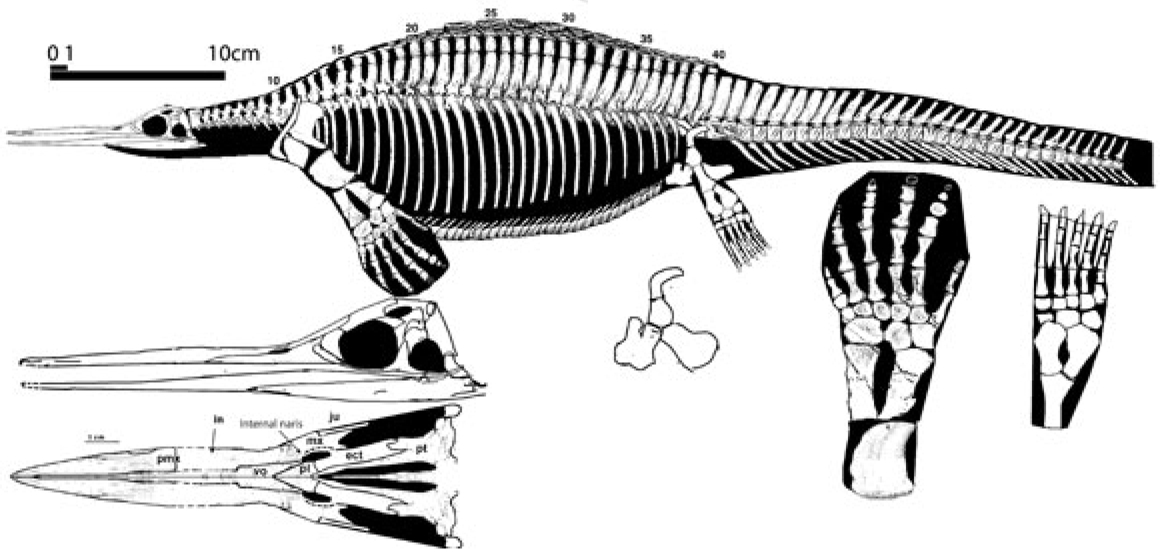
4. Unnamed species (SSTM 5025) X
5. Unnamed species (V4070) X



Life restoration of *Hupehsuchus nanchangensis*. illustration by Smokeybjb (Wikipedia)

Introduction

During the Early Triassic there was an enormous radiation of diapsid reptiles after the end Permian mass-extinction. These included a number of distinct lines of near-shore marine forms, most of which suddenly appear during the Olenekian. As with many highly specialised taxa, their actual position on the evolution tree remains ambiguous, and it is quite likely that many were not even related, or only very distantly so. However, pending better understanding of their evolutionary relationships, I have grouped them together in a series of small units, beginning with the Hupehsuchia, creatures that, because of their armour plates, were previously thought to be an intermediate stage between ichthyosaurs and archosaurs, but are now perhaps better understood as ichthyosaur mimics. Yet despite being in some respects more ichthyosaur-like than actual early Triassic ichthyosaurs (toothless jaws, flippers with extra digits), these strange animals do not seem to have spread beyond the late Early or Early Middle Triassic of China. MAK110923



Skull, skeleton, and flippers of *Hupehsuchus nanchangensis* Early Triassic of China. The original animal was about a meter in length. Drawing copyright © David Peters Reptile Evolution.

Introduction

The Hupehsuchia are a group of near-shore marine diapsid reptiles known only from a handful of species (some of them not even named) the late Olenekian (or possibly Early Anisian) of China. They represent one of a number of short-lived Triassic reptiles that appeared and briefly radiated after the end Permian mass-extinction. It is assumed that they they died out through competition with the more successful ichthyosaurs, which they resemble and with which they may be related to. But as with many highly specialised taxa, their actual position on the evolution tree remains ambiguous. They may be basal Neodiapsids, basal Saurians, or early offshoots of the Lepidosauromorphs or Archosauromorphs. Or they may not be. The tendency seems to be to portray them as the sister taxon of Ichthyopterygia (see e.g. passing references in discussion at Vertebrate Zoology and Wkipedia dendrogram), although these can simply be convergences from a common terrestrial neodiapsid / eosuchian ancestor. MAK100928, 111116

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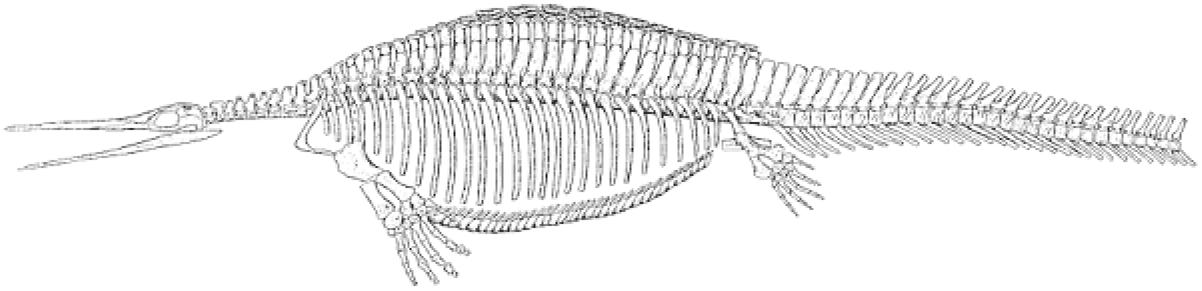
Taxonomy and phylogenetics

Hupehsuchia was first defined as a suborder of "Thecodonta" in 1972 when it was first thought to be a group of early archosaurs (Young & Dong 1972). It was also thought to be related to several other groups of Triassic reptiles previously thought to be clearly distinct. The presence of the supposed antorbital fenestra described above was seen as evidence for grouping hupesuchians within Archosauria, but the antorbital fenestra characteristic of archosaurs is surrounded by the maxilla and lacrimal, not the nasal and prefrontal. The dermal plates were also seen as evidence for terrestrial archosaur ancestors and comparisons were made with some early armored forms. However, a later study in 1976 could find no similarities between the dermal plates of hupehsuchians and the armor of early archosaurs.(Charig et al 1976) It is more likely that the ancestors of hupehsuchians were earlier, more basal terrestrial diapsids, as suggested by several synapomorphies they share with such primitive ancestors. In 1991 Hupehsuchia was recognized as a distinct order after better methods of specimen preparation allowed new features to be revealed that distinguished Hupehsuchia from all other diapsid orders.(Carrol & Dong, 1991)

The assumed position of the naris in hupehsuchians as explained above can be taken as evidence for possible ichthyosaurian affinities, as it is in the same general area as those of ichthyosaurs. Hupehsuchians do resemble earlier ichthyosaurs in outward appearance with slightly fusiform bodies and long, straight, non-lunate tails. Other features shared with ichtyosaurs include a supraoccipital similar to what is seen in early forms, a relatively long antorbital region, and a short transverse process for the ribs. Many more differences exist between hupehsuchians and ichthyosaurs, however. In hupehsuchians, the surfaces of the vertebral centra that articulate with one another are distinctively flat, or acelous, while in ichthyosaurs they are noticeably heterocelous (it is also important to note that the surfaces of centra in the possible early diapsid ancestors of hupehsuchians were amphicelous). Yet there were some early ichthyosaurs and ichthyosaur relatives such as *Chaohusaurus* and *Utatsusaurus* that possessed vertebrae that were not deeply heterocoelus and more closely resembled those of hupehsuchians. (Young & Dong 1972; Shikama et al 1978) Unlike more derived ichthyosaurs, the centra of these two genera are about as long as they are high. In hupehsuchians, where the neural arches dominate the vertebral column, the height of the centra is reduced and the height to length ratio of the centra is smaller, meaning that they are also about as long as they are high. This may suggest that hupehsuchians may have evolved from an ichthyosaur relative. It has also been suggested that hupehsuchians were related to or members of Sauropterygia. Indeed, *Nanchangosaurus* was classified as a sauropterygian upon its initial description.

Many of the features seen in known hupehsuchian specimens that are comparable to those of more well



Hupehsuchus, drawing of skeleton. From Planetopia - Evolution of Ichthyopterygia (original source unknown)

known diapsids may not necessarily be evidence of ancestry or relationship. The lower jaw and rostrum of hupehsuchians have been compared to many other secondarily aquatic tetrapods such as plesiosaurs, whales, and the early marine bird *Hesperornis*, all of which have developed a similar morphology independently in response to the need for adaptation to a marine environment.

Classification of Hupehsuchia remains difficult because most of the derived characters exhibited in the clade that can be helpful in phylogenetic analyses are also present in other unrelated groups of secondarily aquatic reptiles, and the overall record of diapsids during the Late Permian-Early Triassic is relatively poor, making it difficult to find any closely related or ancestral taxa. Even higher level classification is difficult because many of the plesiomorphies that characterize such groups are absent in the highly derived, marine adapted hupehsuchians. For example, several characteristics suggest that Hupehsuchia belongs within Neodiapsida, but most of the derived characteristics that define the clade are absent or hard to distinguish in hupehsuchians, even though their ancestors may have possessed these characteristics at one point. Three derived characteristics of Neodiapsida are a reduced number of teeth on the pterygoid, an absence of teeth on the parasphenoid, and a lack of caniniform mixillary teeth, but none of these apply to hupehsuchians because they lack teeth altogether (Benton 1985). Many derived characteristics that define neodiapsids regard the limbs and girdles, but these characteristics are not seen in marine reptiles because the limbs and girdles are too highly modified. Many characteristics of the skull cannot be seen in hupehsuchians due to poor preservation of remains. Therefore, any placement of Hupehsuchia within Neodiapsida remains tentative until more specimens are found.

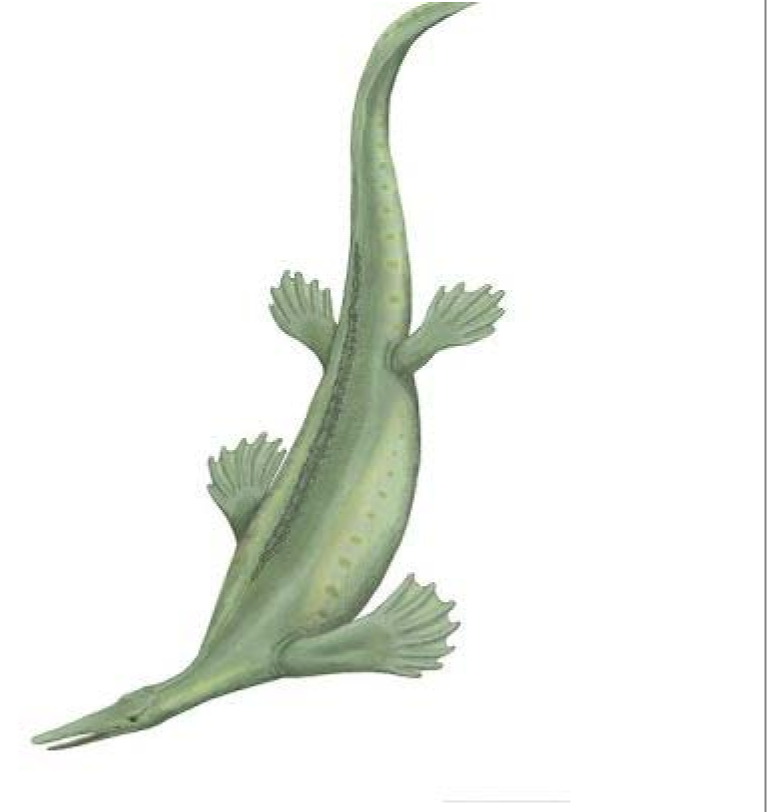
Due to the great number of derived characteristics in hupehsuchians that are a result of convergence, computational phylogenetic analyses using computer programs based on the method of maximum parsimony do not produce cladograms that can accurately establish a relationship between Hupehsuchians and other diapsids. Such programs do not recognize situations where sister group relations are not justified (Carrol & Dong, 1991).

Only two named genera are known to belong to the order, and both are members of the same family, Nanchangosauridae. They are likely sister taxa. Both have been found from the Jialingjiang Formation in Hubei Province, China. Originally this formation was dated to the Anisian stage of the Middle Triassic but it is now thought to have formed slightly earlier during the late Olenekian stage of the Early Triassic.

Paleobiology

Hupehsuchians were clearly well adapted to marine life, as they possessed limbs that were paddle-like in shape and had fusiform bodies. It is likely that the characteristically elongated neural spines were associated with well developed epaxial muscles (muscles lying above the transverse process of the vertebrae) that facilitated lateral undulation in an axial subundulatory mode.(Massare 1988) The pattern of articulation in the vertebrae suggest that such undulation was concentrated posteriorly near the pelvic girdle and tail. It is likely that *Hupehsuchus* was better equipped for lateral undulation as a means of locomotion than *Nanchangosaurus* was. This is evidenced by the assumed greater degree of lateral compression in the body of the former genus as well as generally more elongate neural spines.

The presence of polydactyly in SSTM 5025 may have been an adaptation to moving across underwater substrates in a similar manner to some early tetrapods of the Devonian such as *Acanthostega*.(Coates & Clack 1990)



Life restoration of a polydactylous hupehsuchian based on SSTM 5025. This type of polydactlyly is characteristic of fish-like amphibians (stem tertapods) such as *Acanthostega*. Subsequent tetrapods had only five or less digits, apart from a few latipinnate (broad finned) ichthyosaurs. This is a very rare instance of stem tertapod-like polydactly in a higher tetrapod. Illustration by Smokeybjb (Wikipedia)

The flat, toothless rostrum may have supported an avian-like bill, or perhaps rows of baleen as seen in cetaceans of the suborder Mysticeti. It seems that hupehsuchians were adapted to continuous ram feeding, a form of mobile suspension feeding.(Sanderson & Wassersug 1990) The large skull and lack of a fixed symphysis with the lower jaw is indicative of such a feeding method, but the narrowness of the rostrum and the existence of marine vertebrates with larger skulls that were not completely edentulous (e. g. ichtyosaurs) seem to point against it. The long necks of hupehsuchians would seem to inhibit continuous ram feeding at high speeds through the water, so it is more likely that they practiced intermittent ram feeding at slower speeds.

The purpose of the dorsal dermal plates of hupehsuchians is unknown. These plates as well as the ventral gastralia and the tendency for pachyostosis would have added considerable weight to hupehsuchians, allowing them to have neutral buoyancy. However, the position of the dorsal plates are high above the center of gravity, and it seems that this would have made the bodies of hupehsuchians unstable. Hupehsuchians were among the largest marine animals of their time, so there would be no need for dorsal plates as a protective measure. The tendency for the dorsal plates to be more developed anteriorly may have allowed the anterior portion of the vertebral column to remain relatively rigid while the posterior portion could freely undulate.

It is unsure whether the plates were acquired subsequent to an adaptation to the marine environment or were inherited from a terrestrial ancestor, in which such plates would have given rigidity to the spine and protection from predators. In any case, if *Nanchangosaurus* is seen as representative of an ancestral morphological pattern that led to the more derived *Hupehsuchus*, then the plates seem to have experienced further development in hupehsuchians and must have had some advantage.

The general shape of hupehsuchians seems to have made any locomotion on land nearly impossible, and, although there is no direct evidence seen in known specimens, these animals were probably viviparous, giving live birth at sea rather than laying eggs on land.(Carrol & Dong, 1991) Vivipary is also seen in ichthyosaurs.

Smokeybjb 20090801

Hupehsuchia / Nanchangosauridae: *Hupehsuchus, Nanchangosaurus*

Range: Late Early/Early Middle Triassic (late Olenekian or Anisian) of China. (The order gets its name from Hubei Province, China, from which many specimens have been found.)

Phylogeny: Neodiapsida **:::** ?Ichthyopterygia + * **:** *Hupehsuchus* + *Nanchangosaurus* + Unnamed species (SSTM_5025) + Unnamed species (V4070).

Characters: Hupehsuchians display an unusual combination of characteristics. The overall shape of the body is fusiform, with a long tail and large, paddle like limbs. The skull is elongate and the jaws are edentulous. The rostrum is flatteded with the premaxilla thought to form most of the dorsal and lateral surface while the maxilla is mostly restricted to the ventral surface beyond the base of the rostrum. An opening between the nasal and the prefrontal in one hupehsuchian specimen (known as IVPP V3232) was initially interpreted as an antorbital fenestra but is now thought to be an artifact caused by the damage of the surrounding bones during preservation. Its position is not indicative of a narial opening either. More likely the naris lies between the nasal and the maxilla in an area anterior to that of the supposed antorbital fenestra, although the preservation of this area in known specimens is too poor to prove definitively that it is the external naris and not an artifact of preservation as is the case for the fenestra. (Carrol & Dong, 1991)

The neck is relatively elongated and the cervical ribs are short. An unusual feature of the neural spines of the trunk region, from the 11 vertebra to the first caudal, is that each is divided into two distinct units by a suture line. One is proximinal to the rest of the vertebra and the other is distal to it. There is some anteroposterior displacement of these two units along the vertebral column, suggesting that they are not ossified to one another. In vertebrae 8-14, the distal ends of the distal portions of the neural spines are expanded posteriorly. An additional anterior expansion of the neural spine is seen in all vertebrae after the 14th. These expanded distal regions exhibit some sculpturing, and may have penetrated the dermis. Another unusual characteristic of hupehsuchians is the presence of dermal plates over the neural spines of the approximately 34 presacral vertebrae. A small dermal bone overlies each space between the posterior expansion of one distal neural spine and the anterior expansion of the one behind it. Above these dermal bones lie even larger dermal plates that directly overly even numbered neural spines. Gastralia are present in some specimens that form a type of ventral armor from the pectoral to the pelvic girdle. The medial row cosists of large, overlapping, V-shaped elements, and lateral rows consist of smaller, cylindrical bones that are widely spaced. Smokeybjb 20090801 (Wikipedia)

Links: Enigmatic Triassic Hellasaur Friday - Hupehsuchus redux (very useful posting at microecos blog); Wikipedia

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Nanchangosaurus

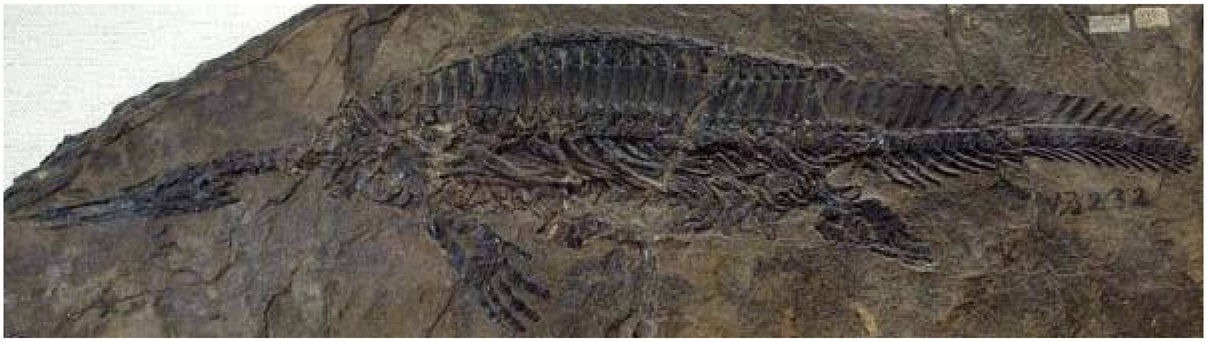
Range: Late Early/Early Middle Triassic (late Olenekian or Anisian) of China.

Phylogeny: Hupehsuchia **:** *.

Characters: *Nanchangosaurus* possesses a frontal that participates in the orbital margin and is quite long, more similar to what is seen in basal diapsids. Additionally, the dorsal plates lack sculpturing.

Comments: The first Hupehsuchian to be described, named in 1959.(Wang, 1959) Known from a single specimen from the Daye Limestone in the Hsunjian District of Hubei Province. Smaller in size than *Hupehsuchus*, and although several characteristics of the single representative specimen suggest it belonged to a juvenile individual, other differences between the two genera are clearly non-ontogeneic and dispel the possibility that the single specimen of *Nanchangosaurus* could be from an immature *Hupehsuchus*. Different means of preservation can also be taken as evidence for different body forms in the two genera. It is important to note that all specimens of *Hupehsuchus* are preserved in lateral view while the single specimen of *Nanchangosaurus* is preserved in dorsal view (except for the neural spines, which were probably too long to be preserved in this manner). It is possible that *Hupehsuchus* had a more laterally compressed body than *Nanchangosaurus*, which, as a result, would favor preservation in lateral view. Smokeybjb 20090801

Hupehsuchus



Mounted specimen of *Hupehsuchus nanchangensis* on display at the Paleozoological Museum of China. Photo (c) Captmondo, Wikipedia

Range: Late Early/Early Middle Triassic (late Olenekian or Anisian) of China.

Phylogeny: Hupehsuchia : *.

Characters: zygapophyses of the trunk region are more modified, while those of *Nanchangosaurus* resemble those of more primitive terrestrial reptiles.

Comments: named in 1972 from a locality in the Xunjian Commune of Nanzhang County. Similar to *Nanchangosaurus*. Smokeybjb 20090801

Links: Illustration; Hupehsuchus (Yahoo egroups post); David Peters - Reptile Evolution (argues for sister relationship with Utatsusaurus and hence with , a basal ichthyosaurs) MAK110923

V4070 (Unnamed genus)

Range: Late Early/Early Middle Triassic (late Olenekian or Anisian) of China.

Phylogeny: Hupehsuchia : *.

Comments: found from the same locality as *Hupehsuchus* and is representative of a different, unnamed genus.(Carrol & Dong, 1991) The pectoral girdle, neck, and base of the skull are present but are all badly weathered, with impressions present in the underlying matrix of the area that provide little more detail. An impression has been made by much of the postcranial skeleton but that too has experienced much weathering. V4070 is proportionally quite similar to *Hupehsuchus*, with the tail being around 93% the length of that of *Hupehsuchus*, but studies of the fore and hindlimbs reveal many differences between the two genera, with carpal and tarsal configuration differing greatly. The overall form of the limbs is more paddle-like than what is seen in *Hupehsuchus*, although the phalanges still retain a cylindrical configuration. Additional differences include shorter neural spines and neural and haemal arches in the dorsal and caudal vertebrae in V4070, although the cervical neural spines seem to be longer than those of *Hupehsuchus*. The dermal plates seem to extend down to the caudal vertebrae, unlike specimens of *Hupehsuchus* in which the dermal plates are absent from the caudal vertebrae. It is possible that caudal dermal plates were present in *Hupehsuchus* but have been lost during preservation. Smokeybjb 20090801 (Wikipedia)

SSTM 5025 (Unnamed genus)

Range: Late Early/Early Middle Triassic (late Olenekian or Anisian) of China.

Phylogeny: Hupehsuchia : *.

Comments: In late 2003, a new specimen of hupehsuchian called SSTM 5025, found from the same area as *Hupehsuchus* and V4070, was briefly mentioned in the journal *Nature*.(Wu et al 2003) It is most notable for exhibiting polydactyly, in which there more than the usual maximum of five digits per limb as seen in most advanced tetrapods. Polydactyly is also seen in ichthyosaurs. However, in ichthyosaurs, this condition occurs as either bilateral polydactyly in the case of ophthalmosaurids (extra digits anterior to digit I and posterior to digit V) or interdigital or postaxial phalangeal bifurcation as in non-ophthalmosaurids.(Motani 1999) Preaxial polydactyly occurs in SSTM 5025, where extra digits only develop anteriorly to digit I. This condition is seen in earlier stem tetrapods from the

Devonian period such as *Ichthyostega* and *Acanthostega*.(Coates & Clack 1990) SSTM 5025 possessed seven digits on the forelimbs and six on the hindlimbs. The wide manus and pes of the specimen resemble the limb-like fins of extant frogfishes (Clack, 2002; Edwards 1989) Smokeybjb 20090801 (Wikipedia)

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Omphalosauria

Diapsida: Overview

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
      `--o DIAPSIDA
         |==Araeoscelida
         `--o Neodiapsida
            |=="Younginiformes"
            `--+--Claudiosaurus
                `--+--Weigeltisauridae
                    `--+--+--Thalattosauria
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Saurosphargidae
                        |?--Hupehsuchia
                        `--o Sauria
                            |?--CHORISTODERA
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

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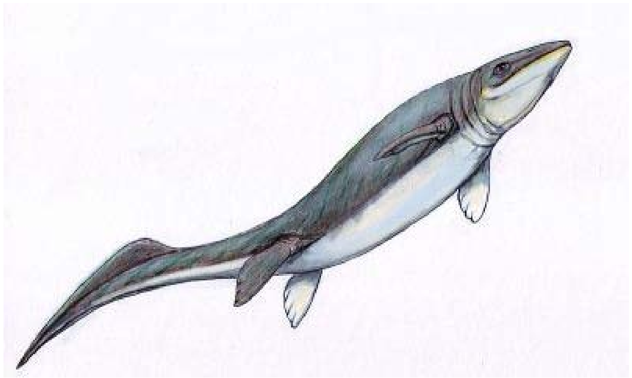
1. *Omphalosaurus* X

Life reconstruction of *Omphalosaurus nevadianus*. Artwork copyright © Dmitry Bogdanov - deviant art

Introduction

The Omphalosaurs are another lineage of those strange Early Triassic marine reptiles that were evolving alongside each other, and often resembled each other, either because they actually were related, or they weren't, but converged (parallel evolution, or homoplasy to give the technical term) with others of similar lifestyle . The Omphalosaurs were quite successful animals; their massive pavement-like teeth (used for feeding on hard shelled animals like molluscs) being known from the Triassic of Nevada, Austria, Spitzbergen, and Spain. Like the Hupehsuchia they resemble ichthyosaurs, with which they may, or may not, be related (we have tentatively placed them as sister group (close cousins) to primitive Ichthyosaurs. Because little is known of the complete animal, the above life reconstruction is inevitably tentative. MAK110923



Speculative reconstruction of *Omphalosaurus* - From Middle Triassic (Asinian-Ladinian) of Nevada and Germany. About 3 m long. Artwork by Dmitry Bogdanov - Wikipedia. Compare with this and this Japanese reconstruction.

Omphalosaurus is a type of marine reptile known from the latest Early Triassic to the Middle Triassic, distinguished by its characteristic pavement or button-like teeth, which were clearly used to feed on hard-shelled prey. It is widely distribution in the northern hemisphere, occurring in the eastern Pacific realm, in Spitsbergen, and in the western Tethys, but remains poorly known (Sander & Faber 2003). It was considered as non-ichthyopterygian by Merriam, who disocovered it, a view supported by some, although others assigned it to the Ichthyopterygia (Motani 2000 p.295). Using thecladistic approach it has been argued that *Omphalosaurus* either is not (Motani 2000), or is (Sander & Faber 2003), an Ichthyopterygian. This question remains unresolved, and its exact position in the diapsid tree is currently unknown.

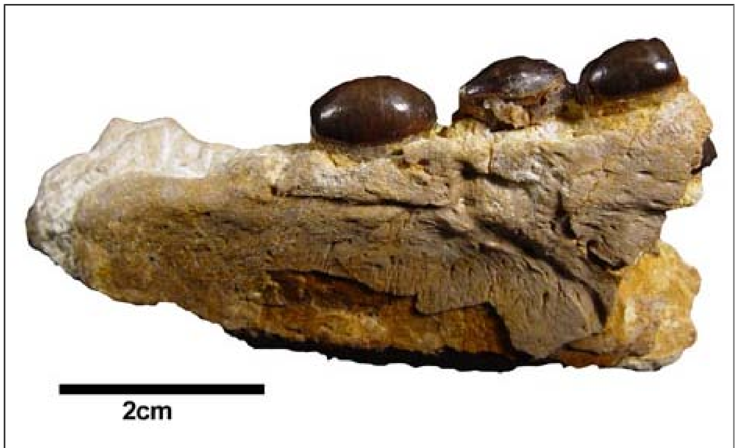
Description

Omphalosaurus :*O. nettarhynchus, O. nevadanus, O. nisseri.* (teeth only), *O. wolfi*.

Range: Early Triassic of Spitsbergen, Middle Triassic of Nevada and Germany.

Phylogeny: Neodiapsida **:::** Thalattosauria + (Ichthyopterygia + *)

Characters: rather elongate snout with crushing dentition placed anteriorly; button-like teeth concentrated along the skull midline, forming a convex upper and concave lower pavement of , set in the premaxillae and the dentaries, respectively (Sander & Faber 2003) vertebrae are of the ichthyosaurian type (Sander & Faber 1998)



Teeth and mandible of *Omphalosaurus*, © Universität Bremen, original url.

Comments: A durophagous (mollusc-eating) form, or opossiblya herbivore like *Placodus*, feeding on seaweed. Originally considered a very primitive ichthyosaur. Cladistic analysis by Motani (2000) showed that similarities with ichthyopterygia are either shared primitive characteristics (symplesiomorphies) or convergences, and that the genus also possesses characters that do not exist in any ichthyopterygians, such as a splenial jaw symphysis. This interpretation was rejected by Sander & Faber 2003, who on the basis of a recently discovered partial skeleton from the earliest Ladinian German Alps argue that *Omphalosaurus* possesses four synapomorphies placing it within the ichthyosaurs and five characters suggestive of ichthyosaurian affinities. Pending resolution of these conflicting claims, I have in the dendrograms tentatively placed *Omphalosaurus* near the stem of the ichthyopterygian line, but outside the Ichthyopterygia itself. Alternatively, Omphalosaurs may be related to Sauropterygia or Archosauromorphs (Motani 2000 pp.299-300)

Links: Dinosaurs about com Omphalosaurus wolfi (fossil), Sea saurian (in German); Wikipedia, speculative reconstruction - Japanese website, speculative reconstruction and text (in Japanese)

Systematic paleontology:

Order Omphalosauria Huene, 1922 (sometimes suborder)
Family Omphalosauridae Merriam, 1906
Genus *Omphalosaurus* Merriam, 1906
Type species: *Omphalosaurus nevadanus* Merriam, 1906, Middle Triassic, Nevada.
Further species:

> *Omphalosaurus nettarhynchus* Mazin & Bucher, 1987, Middle Triassic, Nevada
> *Omphalosaurus peyeri* Maisch & Lehmann, 2002, Middle Triassic, Germany; (= *Pessopteryx nisseri* Wiman, 1910 (*partim*) chimera, postcrania belong to true ichthyosaur)
> *Omphalosaurus wolfi* Tichy, 1995, Middle Triassic, Germany. (= *O. nevadanus*?)
> *Omphalosaurus merriami* Maisch, 2010, Middelhook, Isfjord, Svalbard. Sticky Keep Formation, Lower Triassic.

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Diapsida: Classification

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
       |
       `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
               |=="Younginiformes"
               `--+--Claudiosaurus
                   |--Weigeltisauridae
                    `--+--+--+?--Thalattosauria
                        |   |   `?-
-Saurosphargidae
                        |   `--ICHTHYOSAURIA
                        |?--Omphalosaurus
                        |?--Hupehsuchia
                        `--Sauria
                            |--LEPIDOSAUROMORPHA
                            `--ARCHOSAUROMORPHA
```

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Diapsida: Dendrogram

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `==EUREPTILIA
        |
        `--DIAPSIDA
           |==Araeoscelida
           `--Neodiapsida
               |=="Younginiformes"
               `--+--Ichthyosauria
                  `--Sauria
                     |--LEPIDOSAUROMORPHA
                     `--ARCHOSAUROMORPHA
```

Contents

The following is an unfortunately rather uninformative dendrogram. On the one hand, little phylogenetic work has been done with groups like the Hupehsuchia who are shown with a flattened bush arrangement that one gets from simply translating a low-phylo information Linnaean taxonomy to a cladistically-based dendrogram without adding any new input. On the other hand, the extreme specialisations of some of these early taxa, and lack of widely applicable synapomorphies, render any actual cladistic analysis dubious to the extreme. Hence the placement of even higher grade taxa like the ichthyosaurs on this tree should be taken as tentative and provisional MAK111116

```
REPTILOMORPHA
|--SYNAPSIDA
`--+--ANAPSIDA
   `--+==EUREPTILIA
      `--o DIAPSIDA MH, ToL
          |==Araeoscelida (probably paraphyletic, i.e. Aeroscelida = Diapsida))
          |  |-- Spinoaequalis
          |  `--+-- Petrolacosaurus
          |     `-- Araeoscelis
          `--o Neodiapsida MH
             |--Orovenator
             `--+--Lanthanolania
                |--Youngina           " Younginiformes" (paraphyletic)
                |--Thadeosaurus
                `--+--o Tangasaurinae
```

```
|   |--Tangasaurus
|   `--+--Hovasaurus
|       `-- Acerosodontosaurus
`--+--Claudiosaurus
    `--+--o Weigeltisauridae
        |   |--Weigeltisaurus
        |   `--Coelurosauravus
        `--+--+--+--+--o Thalattosauria/Thalattosauriformes
            |   |   |   |--Askeptosauroidea
            |   |   |   |   |--Endennasaurus
            |   |   |   |   `--Askeptosauridae
            |   |   |   `--Thalattosauroidea
            |   |   |      |--+--Nectosaurus
            |   |   |      |  `--Xinpusaurus
            |   |   |      `--Thalattosauridae
            |   |   |         `--+--Thalattosaurus
            |   |   |            `--Claraziidae
            |   |   `?--o Saurosphargidae
            |   |        |--Saurosphargis
            |   |        `--Sinosaurosphargis
            |   `--ICHTHYOSAURIA
            |?--Omphalosaurus
            |?--o Hupehsuchia
            |     |--Hupehsuchus
            |     |--Nanchangosaurus
            |     |--Unnamed species (SSTM 5025)
            |     `--Unnamed species (V4070)
            `--o Sauria  MH
               |?--CHORISTODERA
               |--LEPIDOSAUROMORPHA
               `--ARCHOSAUROMORPHA
```

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Diapsida: References

Abbreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--SAUROPSIDA
   |--ANAPSIDA
   `--EUREPTILIA
            `--o DIAPSIDA
               |==Araeoscelida
               `--o Neodiapsida
                  |=="Younginiformes"
                  `--+?--Ichthyosauria (in
Sauria?)
                     `--o Sauria
                        |--LEPIDOSAUROMORPHA
                        `--ARCHOSAUROMORPHA
```

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Thalattosaurs

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Hupehsuchia

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Eureptilia: Overview

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
          |   `--Captorhinidae
          |     |--Concordia
          |     `--+--Romeria
          |        `--+--Captorhinus
          |            `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

Contents

The Eureptilia ("true reptiles") are one of the groups that emerged through cladistic studies of amniote evolution. In linnaean taxonomy reference would be made to Captorhinomorpha, a paraphyletic taxon that nevertheless is useful in reference to the earliest and most basal forms. In addition to these primitive Permo-Carboniferous reptiles, Eureptilia includes that very diverse group of reptiles, the Diapsids, the early members of which are considered in a later unit.

Captorhinomorphs were small, lizard-like forms, that doubtless scurried through the Permo-Carboniferous undergrowth in search of insects and other small invertebrates. Others became early herbivore sor omnivores, and some specialised later types, belonging to the clade Moradisaurinae, grew to quite a reasonable size. MAK120313

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Eureptilia

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
          |   `--Captorhinidae
          |      |--Concordia
          |      `--+--Romeria
          |         `--+--Captorhinus
          |             `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                   `--+--Protorothyrididae
                      `--DIAPSIDA
```

Contents

Taxa on this Page

1. *Coelostegus* X
2. Eureptilia
3. *Thuringothyris* X

During the Middle Carboniferous, the amniote radiation gave rise to three primary clades, the Eureptiles, the Anapsids, and the Synapsids (four if the diadectomorphs were apomorphic, as opposed to crown group) amniotes). In this unit we are concerned with the early Eureptilia (or "Romeriida"), which in earlier books and linnaean taxonomy were called Captorhinomorpha (in a linnaean-cladistic synthesis this would become Paraorder Captorhinomorpha). These were vaguely lizard-like terrestrial forms, characterised by very primitive features, showing that they had only just diverged from their reptiliomorph ancestors.

The evolutionary systematic perspective (e.g. Carroll 1988) presents these early reptiles as the ancestral stem group from which all other reptiles (and from there birds and mammals) evolved, represented as the bubble at the base of the romerogram. But the new cladistic paardigm showed them to be the sister group of the anapsida, the two together constituting the Sauropsida.

The problem with the cladistic model is statigraphic incongruence; the fact that supposedly more basal types don't appear until many millions of years after the more advanced forms. In this case. No anapsid is known prior to the

Permian, whilst derived protorythyrids are found in the middle Carboniferous. Frustratingly, no stratocladistic analysis has ever been performed on early amniotes, so we don't know how stratigraphic sequence would constrain phylogeny. As a result are left with a reliance on two selective and less than complete uses of all posisble data, and hence two systems with both persuasive arguments and major shortcomings. Evolutionary systematics requires numerous, far from parsimony, reversals, cladistics a number of ghost lineages and long periods of cryptic evolution.

Hence in understanding these very early and primitive reptiles we are currently limited to a choice between a stratigraphy and phenetics only (no synapomorphies), or a morphology only (no stratiigraphic sequence), approach, the two methodologiesnot unexpectedly resulting in toally different phylogenies. In this unit we have most followed the current cladistic paradigm as far as phylogeny goes, although as a compromise to stratigraphic sequence we are considering Eureptilia, or Paraorder Captorhinomorpha, before Anapsida. MAK120317

Descriptions

Eureptilia: defined as turtle doves > turtles (diapsids > anapsids)

Range: from the Late Carboniferous

Phylogeny: Sauropsida **:** Anapsida + *: Captorhinidae + (Protorothyrididae + Diapsida).

Characters: premaxilla without ventral curvature [MR05]; supratemporal small; parietal & squamosal broadly in contact, so that postorbital does not reach supratemporal; tabular not contact opisthotic; jugal anterior process sharply pointed [MR05]; jugal without medial process [MR05]; jugal with distinct anterior and posterior ventral margins [MR05]; stapes short [MR05]; parasphenoid denticulate [MR05]; lower jaw with dorsal ridge [MR05]; retroarticular process absent [MR05]; caniniforms absent [MR05].

Links: link (Tree of Life); Reptile Phylogeny 1; PhyloCode Discussion - Message 2001-06-0004- Re- Nomina Conversa (problem with the definition); Biology 356 (nice discussion); 6SULQJHU (another problem).

References: Müller & Reisz (2005) [MR05]. ATW051015.

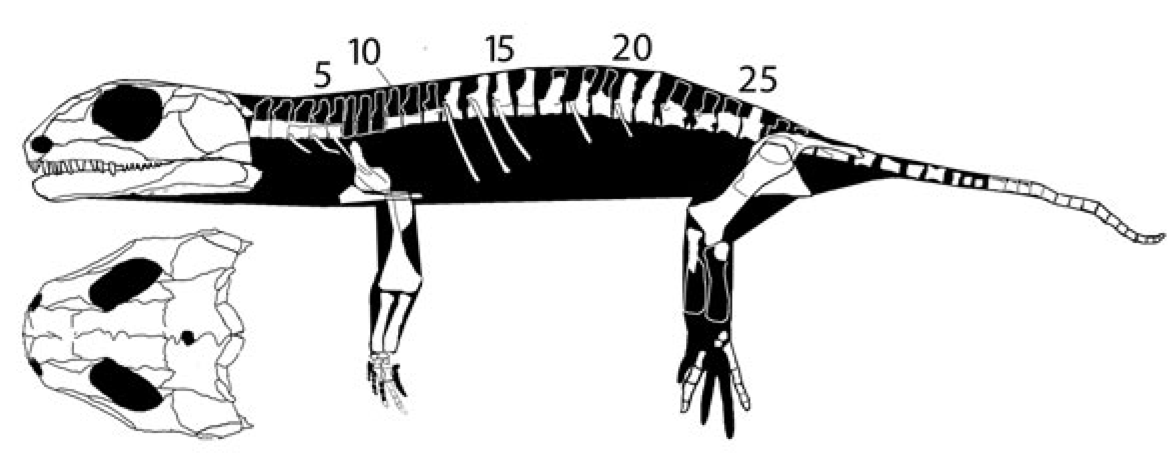
Coelostegus prothales

Range: Late Carboniferous of Nyr'any, Czech Republic.

Phylogeny: Eureptilia **:** ((Captorhinidae + *Thuringothyris*) + (Protorothyrididae + Diapsida)) + *.

Comments: Most basal Eureptilian, according to Müller & Reisz 2006.

Thuringothyris mahlendorffae Müller J et al. 2006



Range: Early Permian of Germany.

Phylogeny: Eureptilia **:** *Coelostegus* + ((Protorothyrididae + Diapsida)) + (Captorhinidae + *).

Comments: Originally interpreted as a protorothyridid, cladistic analysis shows it to be a stem captorhinid (Müller & Reisz 2006). This tiny anoimal had a snout-vent length of only 10cm, plaing it in the size range of the earliest amniotes,

Image: illustration copyright David Peters, reproduced with permission

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Eureptilia

Captorhinidae

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         `--+--Captorhinidae
            |  `--Concordia
            |     |--Concordia
            |     `--+--Romeria
            |        `--+--Captorhinus
            |            `--Moradisaurinae
            `--+--Brouffia
               `--Romeriida
                 |--Paleothyris
                 `--+--Hylonomus
                    `--+--Protorothyrididae
                       `--DIAPSIDA
```

Contents

Taxa on this Page

1. Captorhinidae X
2. *Concordia* X

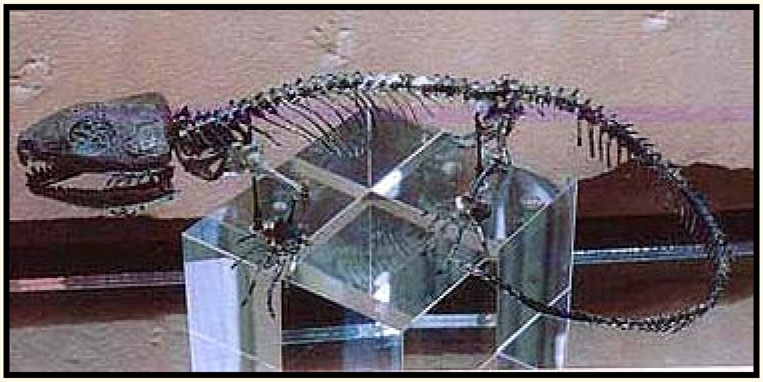
The Captorhinidae (in former times considered as 'stem reptiles') were one of the earliest and most primitive reptiles. They first occured in the Late Carboniferous of North America. In Upper Permian times they spread throughout the world but dissapeared from the North American fossil record, and finally they became extinct by the end of the Permian. Captorhinid fossils today are known from all continents with the exception of Antarctica and Australia. Captorhinids have an anapsid skull which is triangular in dorsal view and more or less heavily ornamented with a honeycomb-like pattern of ridges and pits, similar to that of numerous Late Paleozoic amphibians or, to a certain degree, modern crocodiles. Their body size ranges from that of a modern lizard up to that of a medium-sized modern alligator or the large Komodo Island monitor.

It has been mistakenly said that multiple tooth rows are a characteristic trait of captorhinids. This is not true and related to the fact that *Captorhinus aguti*, a representative with multiple rows of teeth, is the by far most common captorhinid. In reality captorhinids are divided into basal, rather small, lightly built forms with single rows of teeth, and into derived, larger forms with multiple rows of teeth. The most derived multiple-tooth-rowed forms form a clade referred to as subfamily Moradisaurinae. Cladistic analyses reveal that the evolution of multiple tooth rows took place at least three times independently within captorhinids: in *Captorhinus*, *Captorhinikos* and within the moradisaurines.

There is little doubt that the basal single-tooth-rowed forms were most likely feeding on insects and/or small vertebrates. The more robust built multiple-tooth-rowed forms seem to have fed on fibrous plants but an omnivorous diet or a diet consisting of hard-shelled invertebrates, such as clams or crabs, cannot be ruled out. Zidane080425 (from Palaeos org)

Descriptions

Captorhinidae **:** *Captorhinus*.



Range: Permian of North America, Europe & East Africa.

Phylogeny: Eureptilia **:::** (Protorothyrididae + Diapsida) + (*Thuringothyris* + * **:** *Concordia* + (*Romeria* + (*Protocaptorhinus* + (*Rhiodenticulatus* + (*Saurorictus* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae))))))))

Characters: Robust skull; premaxilla downturned, with massive ventral base [MR05]; maxilla with narrow lateral exposure [MR05]; lacrimal suture with nasal usually mucg shorter than frontal suture [MR05]; lacrimal suture with nasal as long as frontal suture [MR05]; prefrontal usually wedged into posterior section of nasal [MR05]; pineal foramen on anterior part of parietals [MR05$]; supratemporals reduced or absent; tabular absent [MR05$]; jugal anterior process broad & blunt [MR05]; jugal with medial process [MR05]; large medial process of the jugal; single (lower) temporal fenestra; braincase supported by supraoccipital process; middle ear region open at least laterally and ventrally; ectopterygoid absent [MR05$]; external surface of lower jaw usually ornamented [MR05]; flat teeth; most have multiple rows of marginal teeth; number of maxillary teeth <25 [MR05$].

Links: Phylogeny and Classification of Amniotes; CAPTORHINIDA; Paleopedia - Cotylosaurs Palaeocritti - Eureptilia.

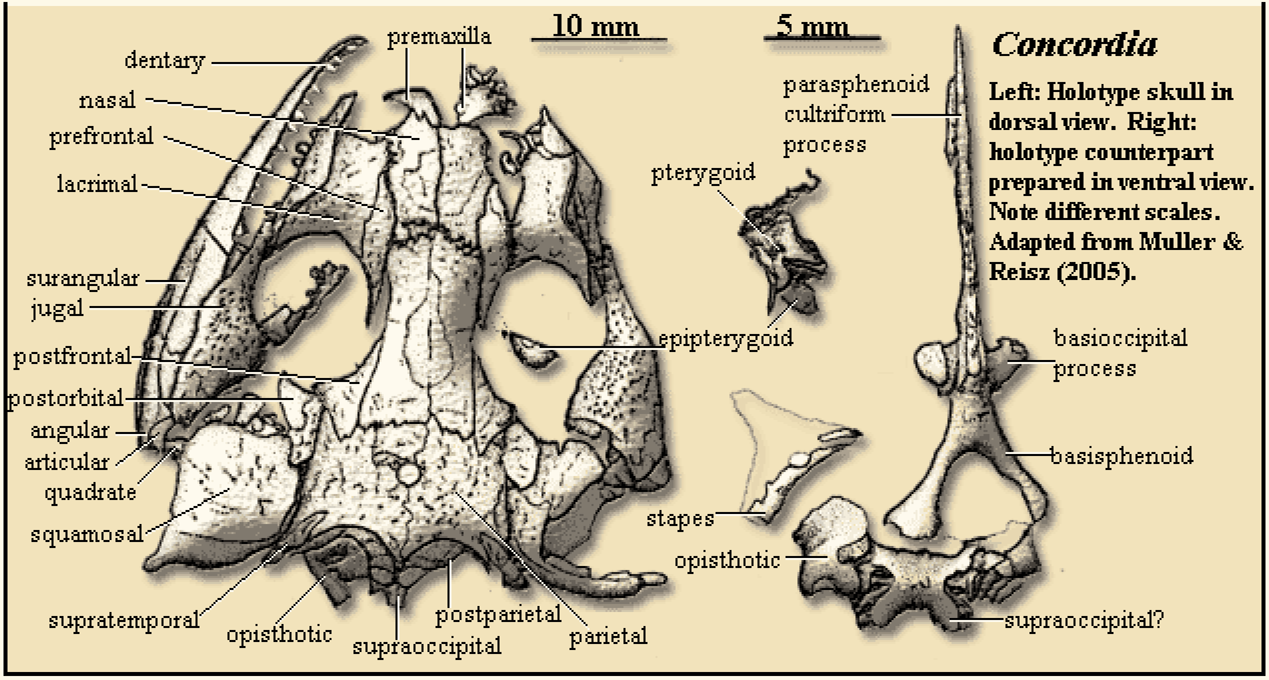
Image: *Captorhinus aguti* © 2000 Friends of the Geology Museum (Univ. of Wisconsin -- Madison), reproduced by permission. ATW010208.

References: Müller & Reisz (2005) [MR05]. ATW051015.

Concordia cunninghami Müller & Reisz, 2005.

Range: Pennsylvanian (Gzhelian) of Kansas, USA. Known from two skulls.

Phylogeny: Captorhinidae **:**



Concordia

Left: Holotype skull in dorsal view. Right: holotype counterpart prepared in ventral view. Note different scales. Adapted from Muller & Reisz (2005).

(*Romeria* + (*Protocaptorhinus* + (*Rhiodenticulatus* + (*Saurorictus* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae))))))) + *.

Characters: premaxilla short, not overlapping lower jaw [MR05]; premaxilla without ventral curvature [MR05!]; premaxilla with 2-pronged nasal suture [MR05]; *Type B septomaxilla*, close to posterior border of naris [MR05]; maxilla slender & elongate [MR05]; maxilla dorsal lamina slight [MR05]; maxilla forming ventral border of naris, not extending to orbit [MR05**$**]; maxilla with well-developed horizontal lamina, expanded anteromedially [MR05]; nasals long, plate-like, rectangular, with slight expansion posteriorly [MR05]; lacrimal quite large, forming most of anterior & half of ventral orbital margin [MR05]; lacrimal dorsally expanded [MR05**$**]; dorsal & ventral lacrimal duct foramina on lacrimal in orbital margin [MR05]; lacrimal strongly interdigitating nasal suture [MR05]; lacrimal elongate contact with jugal [MR05]; prefrontal posteriorly elongate, almost reaching postfrontal & forming much of orbit dorsal margin [MR05]; prefrontal wide anterior to orbit, with sharp anterior tip wedged between nasal & lacrimal [MR05]; lacrimal suture with nasal as long as frontal suture [MR05]; prefrontal ventral lamina partially covered by lacrimal [MR05]; frontals rectangular, forming most of skull table above orbits [MR05]; frontals slightly expanded posteriorly, with serrated suture to parietals [MR05]; postfrontal triradiate, with sharp anterior point, and forming posterodorsdal orbit [MR05] **[1]**; postfrontal with posterior point inserted into parietal [MR05]; parietals short, much broader than frontals, & posteriorly embayed, creating 1 median and 2 lateral posterior processes [MR05!]; posterolateral process of parietal with slot for small, superficial supratemporal [MR05]; anterior of supratemporal on skull table, with ornament, but posterior occipital and unornamented [MR05]; parietal with extended occipital flange underlying paired, adjacent, semilunar postparietals on occiput [MR05]; tabulars absent [MR05]; jugal large, forming most of suborbital skull, with long preorbital process, short dorsal postorbital process, and flat temporal lamina [MR05]; jugal anterior tapers to a point [!] & inserts between maxilla & lacrimal [MR05] **[2]**; jugal dorsal process supports postorbital [MR05]; jugal temporal lamina extend below squamosal & probably contact quadratojugal [MR05]; jugal medial process absent [MR05]; jugal with distinct anterior and posterior ventral margins [MR05]; squamosal large, covering most of temporal region, bearing distinct occipital flange separated by vertical ridge [MR05]; quadrate broad in lateral view, with tall dorsal process [MR05]; basioccipital longer than broad, with anterolateral basal tubera [MR05]; basioccipital forming part of occipital condyle [MR05]; spraoccipital with well and "almost equally developed dorsolateral and ventrolateral processes surrounded by prominent, dorsally directed flanges. The semicircular canals are situated between the two projections." [MR05: 564] **[3]**; opisthotic stout and compact, with paroccipital process absent **[4]**; stapes short, with poorly developed shaft & large stapedial foramen [MR05!]; alar (posterior) basisphenoid projections probably contacted basisphenoid tubera [MR05]; parasphenoid completely fused to basisphenoid [MR05]; basipterygoid processes stout & directed anterolaterally [MR05]; parasphenoid cultriform process denticulate [MR05!]; vomer small [MR05]; pterygoids terminating anteriorly on midline between vomers [MR05]; interpterygoid vacuity present posteriorly [MR05]; pterygoid quadrate ramus with separate dorsal flange extending from basicranial articulation to dorsal process of quadrate, supporting elongate epipterygoid [MR05]; lower jaw largely unornamented [MR05]; lower jaw with long dorsal ridge for external jaw adductor [MR05!]; dentary quite straight, with abrupt curvature to symphysis [MR05]; long splenial present, not contributing to symphysis [MR05]; dentary makes up 75% length of jaw [MR05]; retroarticular process absent [MR05!]; articular small and lens-like [MR05]; teeth generally small, homodont, pointed & recurved distally [MR05];

5 small, pointed, premaxillary teeth [MR05]; caniniforms absent, but 4 anterior maxillary teeth somewhat elongate, others shortening posteriorly [MR05!]; single maxillary tooth row with 18 teeth [MR05]; probably 17 dentary teeth [MR05]; 2 vomerine tooth rows, with medial row continuing pterygoid denticles [MR05]; vomerine lateral denticles autapomorphic [MR05**$**].

Notes: "!" indicates feature unique among captorhinids, but likely plesiomorphic for Eureptilia. **[1]** The postfrontal in the referred specimen has a different shape. It is probably simply broken, but the bone labelled "postorbital" in the referred specimen has the correct shape for the postfrontal, and might have been dislodged by a fragment (labelled "postfrontal"), which could, in turn, be a piece of the thoroughly splintered epipterygoid. These skulls were both recovered from split shales. The fossil side was then embeded in resin and apparantly prepared from the opposite (rock) side. This, the authors note, created some difficulties in identifying pieces deeply embedded in the resin, such as the circumorbital bones of the referred specimen. **[2]** One problem with getting too artistic is that it can obscure details. Our attempts to gussy up the figure from [MR05] obscure this insertion, which is quite clear in the original image. **[3]** Note that the semicircular canals, *i.e.* normally the guts of the otic capsule, are described as lying dorsal to the supraoccipital. Ummm. We have concerns about this reconstruction of the occiput and posterior braincase. After struggling with it for some hours, we've decided that we lack sufficient expertise to make any comments at all, beyond this vaguely dissatisfied grunting noise. We therefore grunt, and readers may make of that what they will. **[4]** The paroccipital process is said to be absent. However, observe the opisthotic illustrated on the left side of the holotype (dorsal view) image here. It shows an unprecedented *ventromedially* directed process. Ummm. See footnote 3 for explanation of grunting noise. ATW051016

Comments: *Concordia cunninghami* is the oldest known and most basal captorhinid so far and the only recognized species of the genus. It is known from two almost complete skulls coming from Upper Pennsylvanian rocks of the famous Hamilton Quarry in Greenwood County, Kansas.

C. cunninghami not surprisingly shows many features that are typical for basal eureptiles but are not present in more derived captorhinids. The premaxilla is small and seems not to have formed a down-curved "beak" as it is seen in almost all of the remainder of the captorhinids. The lacrimal is dorsoventrally expanded and forms the main portion of the lateral wall of the snout which is similar to the condition in Rhiodenticulatus. The skull table lacks the tabular bone, a feature considered as synapomorphy among captorhinids. The supratemporal is small as well and points, in dorsal view, anteromedially into the posterolateral corner of the parietal as seen in another basalmost captorhinid, Romeria, or in the "Protorothyridid" Protorothyris. The same applies for the posterior margin of the skull roof which is embayed bilaterally in contrast to the pattern present in more derived captorhinids where this margin posesses a single median embayment. Like in Romeria and Protocaptorhinus the parietal foramen is very large compared to the overall size of the skull.

Maxilla and dentary are lined with a single row of as much as 18 small, pointed teeth. The palatal bones and the basisphenoid (a ventral element of the braincase) are covered with numerous denticles. A unique feature of C. cunninghami is that the vomer not only exhibits medial rows of denticles but, in addition, has also lateral ones. An important captorhinid apomorphy, the reduction of the ectopterygoid and replacement of that bone by the adjacent ones, seems to be present in C. cunninghami where it is obviously replaced by the transverse process of the pterygoid. In Captorhinus, however, it is rather a medial process of the jugal that occupies the position of the ectopterygoid. A remarkable occipital feature is that the opisthotic seems not to have the lateral projection which usually contacts the cheek bones, known as paroccipital process. This process is a characteristic trait in all basal amniotes as well as in more modern reptiles, such as squamates.

The oldest known eureptile and one of the closest relatives of captorhinids is the "Protorothyridid" *Hylonomus* from the Upper Pennsylvanian of Nova Scotia. Thus, although still geologically younger, the discovery of *C. cunninghami* considerably shortens the ghost lineage of the captorhinids.

Some Facts

Family: Captorhinidae

Etymology of genus: "unity, agreement, harmony", refers to the fact that the occurrence of a captorhinid in Upper Pennsylvanian strata confirms the long-held assumption that captorhinids must have existed as early as in Late Carboniferous times

Etymology of species: named after the paleontologist Christopher R. Cunningham

Paleography: Cherokee Basin, northwestern Pangaea

Locality: Greenwood County, Kansas, USA

Horizon: Calhouns Shale (Shawnee Group)

Stratigraphic Range: Upper Pennsylvanian (Late Carboniferous): Virgilian

Zidane 080526 (Palaeos org)

References: Müller & Reisz (2005) [MR05].

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checked ATW050509

Eureptilia

Captorhinidae (2)

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         |   `--Captorhinidae
         |     |--Concordia
         |     `--+--Romeria
         |        `--+--Protocaptorhinus
         |           `--+--Rhiodenticulatus
         |              `--+--Saurorictus
         |                  |?- Acrodenta
         |                  |?- Baeotherates
         |                 `--+--Captorhinus
         |                     `--Moradisaurinae
         `--Romeriida
            |--Paleothyris
            `--+--Protorothyrididae
               `--DIAPSIDA
```

Contents

Taxa on this Page

1. *Acrodenta* X
2. *Baeotherates* X
3. *Protocaptorhinus* X
4. *Rhiodenticulatus* X
5. *Romeria* X
6. *Saurorictus* X

Descriptions

Romeria *R. texana*, *R. prima*

Phylogeny: Captorhinidae **:** *Concordia* + (*Protocaptorhinus* + (*Rhiodenticulatus* + (*Saurorictus* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae)))))) + * **:** *Romeria texana* + *Romeria prima*)

Comments: ***Romeria*** is a genus of small single-tooth-rowed captorhinids. Two species are currently recognized: *R. texana*, known from two partial skulls and one poorly preserved postcranial skeleton, and *R. prima* known from one skull with associated forelimbs, all of which come from the Lower Permian red beds of North Texas.

Facsimile of type specimen of *R. texana* in oblique lateral view.

Contents

Scientific History: The type species *R. texana* was discovered during field collections of the Museum of Comparative Zoology in the in the second half of the 1930s. Its description was published in 1937 and is based on one single cranium whithout braincase. In 1973 a juvenile individual, collected together with material of the microsaur *Pantylus*, was attributed to that species.

The circumstances of discovery of the second species, *R. prima*, are not documented. *R. prima* was first described in 1973 on the basis of one single, almost complete skull and a few postcranial bones. Since 1973 no newmaterial of *Romeria* has been found by scientific collectors.

Characteristics of the genus: *Romeria* is caracterized by a unique composition of features that are present in other basal eureptiles rather than by distinct apomorhies. Its pineal foramen, the opening in the center of the skull table, is very large, relative to skull size, as seen in *Protocaptorhinus* and *Concordia*. In other respects the skull of *Romeria* is quite similar to that of more basal eureptile taxa such as *Protorothyris* or *Concordia*: it is rather lightly built, has large orbitae compared to skull size, numerous denticles on the palatal bones, a bilaterally embayed posterior margin of the skull roof, and supratemporals that, in dorsal view, project anteromedially into the posterolateral corners of the parietals. However *Romeria* shows the typical captorhinid traits such as the lost of the tabular bone, the down-curved premaxilla, or the absence of large teeth on the transverse flange of the pterygoid.

Romeria texana

Facsimile of type specimen of *R. texana* in posterodorsal view.

The structure of the skull corresponds primarily to the characteristics of the genus. Therfore only description of the dentition is given here. All teeth have the shape of simple cones. The anteriormost premaxillary teeth are the largest in these bones. Posteriorly they decrease in size rapidly. The anteriormost maxillary teeth are similar in size to the posterior premaxillary teeth but become larger posteriorly to reach maximum size at the 6th position. Posterior to that postiton they become successively smaller again. Unfortunately the juvenile postcranial skeleton mentioned above is enclosed in a nodule of ironstone, being very resistant to efforts of preparation. Therefore

nothing is known about the postcranium of *R. texana*.

Romeria prima: *R. prima* differs from *R. texana* in having a much shorter anterior process of the prefrontal bone. The dentition resembles that of *R. texana* with the exception of that *R. prima* has two less premaxillary teeth and that the teeth are generally more gracile. Besides those differences the skull structure of both species of *Romeria* is nearly identical. Unfortunately little is known about the palate of *R. prima*. However, is seems quite plausible that it closely resembles that of *R. texana* including the shagreen dentition.

In contrast to *R. texana* also the forelimbs of *R. prima* are known. Admittedly, these bones are rather poorly preserved. As far as one can judge they show no major differences to that of other basal generalized amniotes.

Validity of the genus: Recently reasonable doubts are casted on the validity of the genus since no unequivocal apomorphies are included in its definition. There is possibility that such apomorphies could be discovered by further examination of the postcranial type material of *R. prima*. Because such new findings might not be made in the type species *R. texana* probably both names will have to be declared nomina dubia and a new genus will have to be erected on the basis of the type material of *R. prima* subsequently.

Some facts:

</tr>

***Romeria* Price 1937**	
Species Recognized	**Data**
- *R. texana* Price 1937	**Family:** Captorhinidae **Etymology of genus:** named after the famous paleontologist Alfred S. Romer **Etymology of species:** self-explaining **Paleogeography:** "Eastern Shelf" of Midland Basin, northwestern Pangaea **Locality:** Archer County, Texas, USA **Horizon:** Putnam Formation (Wichita Group)
- *R. prima* Clark & Carroll 1973	**Etymology of species:** "the first", refers to the lower stratigraphic level of the type locality implying older geological age **Paleogeography:** same as in *R. texana* **Locality:** same as in *R. texana* **Horizon:** Moran Formation (Wichita Group)

	Synonyms: the authors originally applied the wrong gender to the species name ("*Romeria primus*")
Stratigraphic Range: Lower Permian **:** Wolfcampian	

References: CLARK, J. and CARROLL, R.L. (1973): Romeriid Reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology* 144 (5): 353-408

MODESTO, S.P. (1998): New information on the skull of the Early Permian reptile *Captorhinus aguti*. *PaleoBios* 18 (2/3): 21-35

PRICE, L.I. (1937): Two new cotylosaurs from the Permian of Texas. *Proceedings of the New England ZoÃ¶logical Club* 16: 97-102

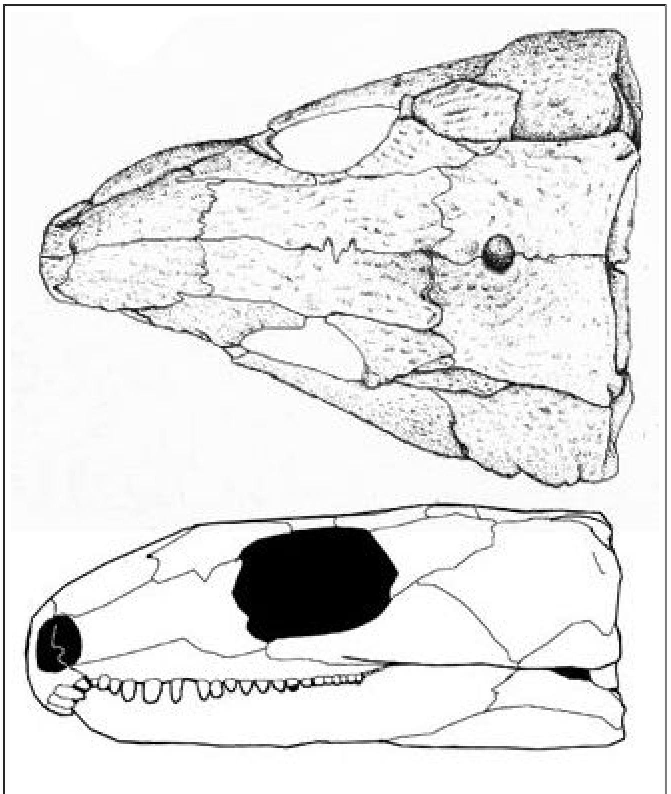
Credits: Zidane 25 May 2008

Protocaptorhinus pricei

Phylogeny: Captorhinidae **:** *Concordia* + (*Romeria* + ((*Rhiodenticulatus* + (*Sauroricts* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae))))) + *))

Comments: ***Protocaptorhinus pricei*** is a small single tooth-rowed captorhinid from the Lower Permian red beds of North Texas and Central Oklahoma.
It is the only recognized member of the genus *Protocaptorhinus*.

Within captorhinids it is an "intermediate" form showing basal traits in skull structure such as a large pineal foramen in relation to skull size, single tooth-rows, small denticles on the bones of the palate, or a small, slender supratemporal that is excluded from contribution to the skull table. However *P. pricei* is derived in having a single median embayment of the posterior margin of the skull table, a trait shared by all "higher" captorhinids, up to and including the moradisaurines. In *Romeria* and *Protorothyris*, however, this margin is embayed bilaterally, i.e. on both sides of the median suture of the skull roof. The supratemporal in *P. pricei* lies transversely at the posteromedial margin of the squamosal as seen in *Captorhinus*, whereas in *Romeria* and *Protorothyris* it projects, in dorsal view, into the posterolateral corner of the parietal.



Protocaptorhinus pricei Clark & Carroll Artinskian, Early Permian, ~25 mm skull length, Illustration copyright David Peters, reproduced with permission

Two partial skulls of *Protocaptorhinus* have been reported from Upper Permian deposits of Zimbabwe implying that this genus spread from northwestern Pangaea into the southeastern regions of the supercontinent and survived from the Early to the Late Permian. Given both the large temporal and the large spatial distance it seems, however, quite unlikely that no divergence on a generic level should have taken place between the North American and the southern African "protocaptorhinus-like" forms and thus occurrence of *Protocaptorhinus* in Upper Permian strata of Zimbabwe is rather questionable. The state of knowledge on the Zimbabwean captorhinid does not allow an unequivocal assignment to *Protocaptorhinus* or another known or new genus so far. Thus these fossils are currently considered as Captorhinidae *incertae sedis*. Nevertheless it is remarkable that basal "protocaptorhinus-like" forms apparently survived through to Late Permian times.

Protocaptorhinus pricei **Clark & Carroll 1973**
Some Facts

Family: Captorhinidae

Etymology of genus: self-explaining

Etymology of species: species named after the Brazilian paleontologist Llewelyn Ivor Price

Paleogeography: "Eastern Shelf" of Midland Basin, Anadarko Basin

Localities: Archer County, Texas, USA

Logan County, Oklahoma, USA

Horizons: Admiral Formation, Petrolia Formation (both Wichita Group), Wellington Formation

Synonyms: *Pleuristion brachycoelus* Case 1902

Stratigraphic Range: Lower Permian **:** Wolfcampian

References: CASE, E. C. (1902): On some vertebrate fossils from the Permian beds of Oklahoma, pp. 62-68. in A. H. VAN FLEET, Second Biennial Report, Dept. of Geol. Nat. Hist., Territory of Oklahoma

CLARK, J. and CARROLL, R.L. (1973): Romeriid Reptiles from the Lower Permian. Bull. Mus. Comp. Zool., 144(5), pp. 353-408

GAFFNEY, E.S. and MCKENNA, M.C. (1979): A Late Permian Captorhinid from Rhodesia. Amer. Mus. Novit., vol. 2688. American Museum of Natural History, New York, 15 p.

MODESTO, S. P. (1996). A basal captorhinid from the Fort Sill fissures, Lower Permian of Oklahoma. Oklah. Geol. Notes, 56, pp. 4-14.

OLSON, E.C. (1984): The Taxonomic Status and Morphology of *Pleuristion brachycoelus* Case; Referred to *Protocaptorhinus pricei* Clark and Carroll (Reptilia: Captorhinomorpha). J. Paleontol., 58(5), pp. 1282-1295

Credits: Zidane 25 May 2008

Rhiodenticulatus heatoni

Phylogeny: Captorhinidae **:** *Concordia* + (*Romeria* + (*Protocaptorhinus* + ((*Saurorictus* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae)))) + *)))

Comments: ***Rhiodenticulatus heatoni***, the only recognized species of the genus, is a small, single-tooth-rowed captorhinid.

Although generally primitive it shows some remarkable features in its skull structure: the lacrimal, a bone of the anterior side wall of the skull, is very high dorsoventrally, hence the snout has, in contrast to other captorhinids, a somewhat domed appearance. One of the middle upper jaw teeth has a base diameter about as twice the base diameter of the adjacent teeth but exceeds them only little in height. The premaxillary teeth are homodont whereas in most other captorhinids the first tooth is the largest and the following teeth are succesively smaller. Besides the skull also some postcranial bones are known, showing, however, no significant differences to that of other captorhinids. *R. heatoni* is the only representative of the, compared to other Permian taxa, poor captorhinid fossil record of the terrestrial Permian deposits of New Mexico.

Rhiodenticulatus heatoni **Berman & Reisz 1986**

Some Facts

Family: Captorhinidae

Etymology of genus: "nose with small teeth"

Etymology of species: named after the paleontologist Malcolm J. Heaton

Paleogeography: southern margin of Ancestral Rocky Mountains, northwestern Pangaea

Locality: Rio Arriba County, New Mexico, USA

Horizon: Cutler Formation

Stratigraphic Range: Lower Permian **:** Wolfcampian

References: BERMAN, D.S. and REISZ, R.R. (1986): Captorhinid reptiles from the Early Permian of New Mexico, with description of a new genus and species. Ann. Carnegie Mus., 55, pp. 1-28

Credits: Zidane 25 May 2008

Saurorictus australis

Phylogeny: Captorhinidae **:** *Concordia* + (*Romeria* + (*Protocaptorhinus* + (*Rhiodenticulatus* + (*Saurorictus* + (*Captorhinus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae))) + *))))

Comments: ***Saurorictus australis*** is a small single-tooth-rowed captorhinid from Upper Permian terrestrial deposits of the Karoo Basin, South Africa. Its fossil record comprises one single however almost complete, moderately deformed skull and a few scrappy postcranial elements. It is the only recognized species of the genus.

Although coming from Upper Permian strata *S. australis* strikingly resembles the basal single-tooth-rowed captorhinids from the Lower Permian of North America. What distinguishes *S. australis* from those Lower Permian representatives is the presence of a foramen on the anteriormost portion of the maxillary bone. This foramen opens anterodorsally and thus seems not to be one of the supralabial foramina that commonly line the alveolar margins of maxillary or dentary. Another difference in the skull structure of *S. australis* to that of other basal captorhinids is the full reduction of the supratemporal bone whose position is occupied by the anterolateral portion of the parietal. Moreover its posterior margin of the skull roof is rather straight or even pointed posteriorly instead of being embayed as seen in other captorhinids.

S. australis seems to be the most derived basal captorhinid and its presence in Upper Permian deposits implies, accompanied with its placement within captorhinid phylogeny, a ghost lineage leading back to the Early Permian for this taxon. A close relationship of *S. australis* to another southern African captorhinid formerly referred to Protocaptorhinus seems obvious but is as yet not confirmed.

***Saurorictus australis* Modesto & Smith 2001**

Some Facts

Family: Captorhinidae

Etymology of genus: "lizard-smile"

Etymology of species: "southern", refers to the fact that it is the southernmost discovery of a captorhinid so far

Paleography: Karoo Basin, southern Pangaea

Locality: Beaufort West District, Western Cape Province, South Africa

Horizon: *Tropidostoma*-Assemblage Zone, Teekloof Formation* (Beaufort Group)

Stratigraphic Range: Upper Permian **:** Tatarian

*information on lithostratigraphic subdivision of Beaufort Group from Catuneanu et al. (2005)

References: CATUNEANU, O., WOPFNER, H., ERIKSSON, P.G., CAIRNCROSS, B., RUBIDGE, B.S., SMITH, R.M.H. and HANCOX, P.J. (2005): The Karoo basins of south-central Africa. J. Afr. Earth Sci., 43(1-3), pp. 211-253

MODESTO, S.P. and SMITH, R.H.M. (2001): A new Late Permian captorhinid reptile: a first record from the South African Karoo. J. Vert. Paleont., 21(3), pp. 405-409

Credits Zidane 25 May 2008; Retrieved from Palaeos org

Acrodenta irerhi

Comments: ***Acrodenta irerhi*** is a poorly known multiple tooth-rowed captorhinid from terrestrial Upper Permian deposits of central Morocco. Its remains solely include one fragment of upper jaw bone bearing three rows of conical teeth. Because the rocks in which *A. irerhi* was found have been considerd to be Triassic in age the fossil was originally described as a rhynchocephalian. *A. irerhi* is the only recognized species of the genus.

Acrodenta irerhi Dutuit 1976

Some Facts

Family: Captorhinidae

Etymology of genus: "the sharp-toothed" (the name refers to the adjective "acrodont" due to the author's assumption the animal described was a rhynchocephalian)

Etymology of species: the species is named after the type locality, the small moroccoan village Irerhi

Paleogeography: close to or within Mauretanides fold belt of Hercynian System, central Pangaea

Locality: 1 km southwest of Irerhi, halfway between the cities of Argana and Timezgadouine, central Morocco

Horizon: Ikakern Formation (former "Lower Series" of Argana Formation) of Argana Basin

Synonyms: in the more recent work on *Acrodenta* it is called "Acrodonta". This name, however, is preoccupied by a group of squamates erected as early as 1864 by E. D. Cope.

Stratigraphic Range: Upper Permian **:** Tatarian*

*information on correlation of Ikakern Formation with global stratigraphy from Jalil & Janvier (2005)

References: DUTUIT, J.-M. (1976): Il est probable que les RhynchocÃ©phales sont reprÃ©sentÃ©s dans la faune du Trias marocain. C. R. Acad. Sc. Paris D, 283, pp. 483-486

JALIL, N.-E. and DUTUIT, J.-M. (1996): Permian Captorhinid Reptiles from the Argana Formation, Morocco. Palaeontology, 39(4), pp. 907-918

JALIL, N.-E. and JANVIER, P. (2005): Les pareiasaures (Amniota, Parareptilia) du Permien supÃ©rieur du Bassin

dâ€™Argana, Maroc. Geodiversitas, 27(1), pp. 35-132

Comparative Toxicogenomics Database

Credits: Zidane 25 May 2008

Baeotherates fortsillensis

Comments: ***Baeotherates fortsillensis*** is a small multiple-tooth-rowed captorhinid. It is known from one tiny lower jaw fragment coming from the Lower Permian Fort Sill fissure fills of Oklahoma. It is the only recognized species of the genus.

The lower jaw fragment measures only 1.3 cm in length, bears 15 teeth and shows some unique features. The articulation surface of the symphysis (symphysial pad) is enlarged antero-posteriorly and not bipartite. In most captorhinids the symphysial pad is much narrower antero-posteriorly, somewhat sinuous and consists of an upper buttress (usually formed by the dentary) and a lower buttress (usually formed by the splenial). Moreover the Meckelian canal usually contributes to the symphysis in the shape of a horizontal notch that points anteriorly from half the height of the lingual margin of the symphysial pad. In *B. fortsillensis* both splenial and Meckelian canal are completely excluded from contribution to the symphysial pad. Above all the lateral surface of the dentary is only weakly sculptured.

The single tooth row comprises no caniniform teeth, i.e. there are no teeth in the anterior portion of the jaw that are significantly higher than the more posterior or most anterior teeth. Such caniniforms are widely observed in captorhinids and also in "protorothyridids". The anterior teeth are conical and have recurved tips. The posteriormost teeth are similar to those in *Captorhinus aguti* and the intermediate teeth are transitional in shape. On the posteriormost portion of the jaw fragment a second tooth row, consisting only of two teeth is present.

Although quite similar to them it is not fully clear whether *B. fortsillensis* is truly a representative of the captorhinids since it also shows close affinities to the microsaur *Cardiocephalus*, which occurs in the Fort Sill fissure fills as well but has no multiple tooth rows. For example, in both *B. fortsillensis* and *Cardiocephalus* the splenial appears to reach the dorsal dentary-coronoid suture, whereas in *Captorhinus* it only reaches the ventral edge of the coronoid. Moreover *B. fortsillensis* shares the expanded symphysial pad of the dentary with *Cardiocephalus*. However, these structures are subject to intergeneric variation in both microsaurs and captorhinids. Finally, assignment of *B. fortsillensis* to the family Captorhinide is solely based on the presence of multiple tooth rows, a feature not known from microsaurs.

The small size, accompanied with the less developed sculpturing on the lateral surface of the mandible, suggests immaturity of the specimen. Because the ontogeny of *Captorhinus aguti* is well documented by hundreds of fossils of juvenile specimens this species can be ruled out. Furthermore the presence of a second tooth row makes it unlikely that *B. fortsillensis* represents an early developmental stage of *C. laticeps* or *C. magnus*. Nevertheless the dentition seen in *B. fortsillensis* is more similar to that in the members of the genus *Captorhinus* than to that in more basal captorhinids. If it truly is a captorhinid, *B. fortsillensis* may represent a taxon close to that genus.

Baeotherates fortsillensis **May & Cifelli 1998**
Some Facts
Family: Captorhinidae **Etymology of genus:** "small hunter" **Etymology of species:** named after the military base Fort Sill near the type locality, the famous Dolese Brothers quarry in Richards Spur **Paleography:** Wichita Uplift, northwestern Pangaea **Locality:** Comanche County, Oklahoma, USA **Horizon:** Garber Formation (Sumner Group)

Stratigraphic Range: Lower Permian **:** Leonardian

References: MAY, W.J. and CIFELLI, R.L. (1998): *Baeotherates fortsillensis*, a new captorhinid reptile from the Fort Sill fissures, Lower Permian of Oklahoma. *Oklahoma Geology Notes* 58: 128-137

MODESTO, S.P. (1998): New information on the skull of the Early Permian reptile Captorhinus aguti. *PaleoBios* 18 (2/3): 21-35

Weblinks: | www.permiantetrapods.net (photographs of specimens found in the Dolese Bros. quarry)

Credits Zidane 29 May 2008

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Eureptilia

Captorhinidae (3)

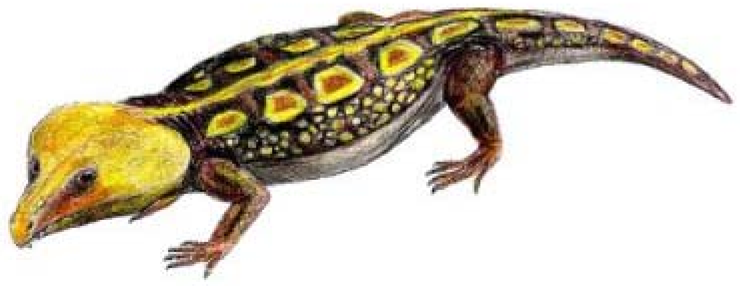
Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         |  `--Captorhinidae
         |     |--Concordia
         |     `--+--Romeria
         |        `--+--Captorhinus
         |           `--+--Captorhinikos
         |              `--+--Labidosaurus
         |                 `--Moradisaurinae
         `--Romeriida
            |--Paleothyris
            `--+--Protorothyrididae
               `--DIAPSIDA
```

Contents

Taxa on this Page

1. *Captorhinikos* X
2. *Captorhinus* X
3. *Labidosaurus* X



Life restoration of *Labidosaurus hamatus*, illustration by Smokeybjb (Wikipedia)

Descriptions

Captorhinus

Phylogeny: Captorhinidae : *Concordia* + (*Romeria* + (*Protocaptorhinus* + (*Rhiodenticulatus* + (*Sauroictus* + (*Captorhinikos* + (*Labidosaurus* + Moradisaurinae))))) + *))

Comments: *Captorhinus* is the type genus of the family Captorhinidae. This genus comprises the single-tooth-rowed species *C. laticeps* and *C. magnus* as well as the multiple-tooth-rowed *C. aguti*. All members of the genus are exclusively known from Lower Permian terrestrial deposits of Texas and Oklahoma.

Contents

Scientific History: Captorhinus is the longest-known genus of the family and its scientific record dates back to the 1880s. In 1882 E. D. Cope described *Ectocynodon aguti* and later assigned it to his genus *Pariotichus* leading to the new combination *P. aguti*. In 1909 S. W. Williston described the species *P. laticeps*.

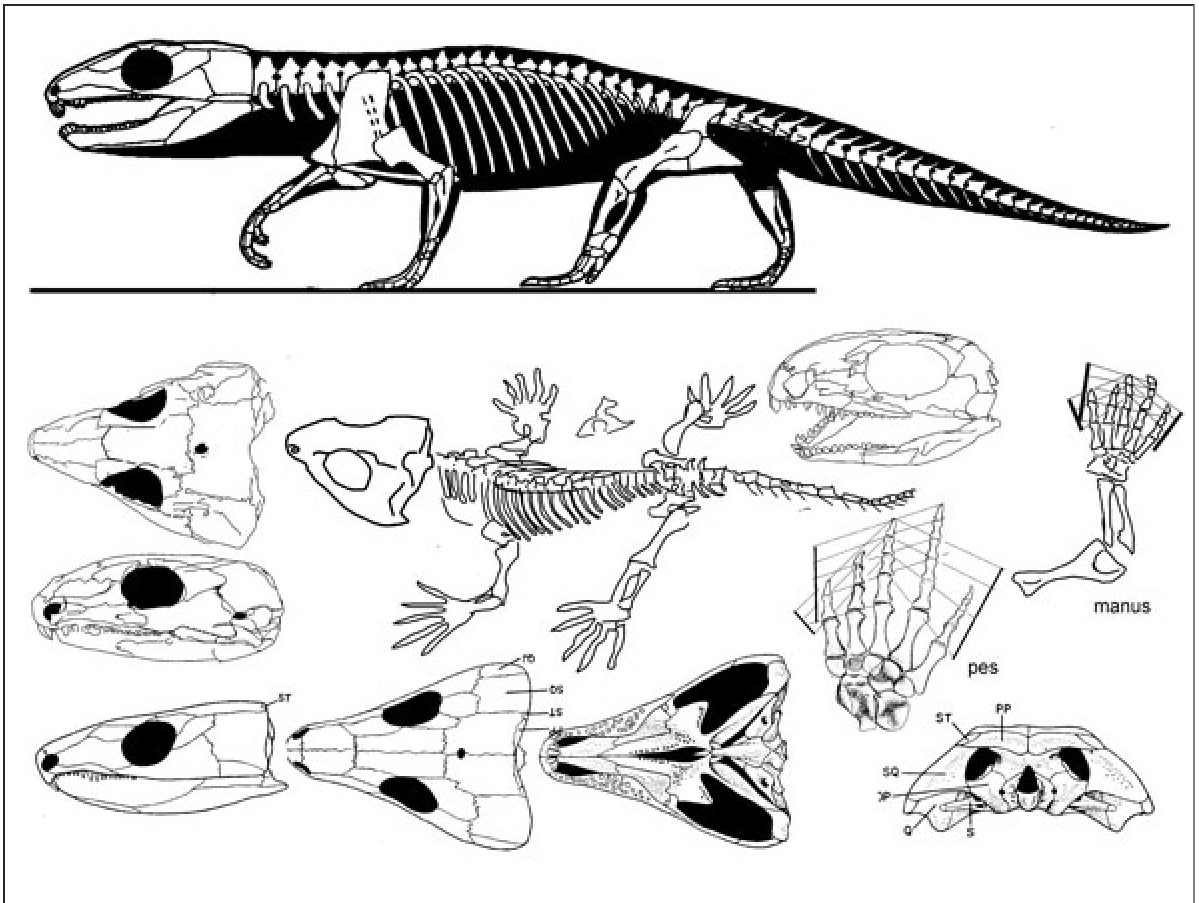
A first revision of these "cotylosaurs" by E. C. Case in 1911 revealed that most of the representatives of *Pariotichus* belong to another genus erected by Cope in 1895: *Captorhinus*. Case identified four species of *Captorhinus*: *C. aguti*, *C. angusticeps*, *C. isolomus*, and *C. aduncus*. In that course *P. laticeps* was synonymized with *C. isolomus*. Moreover Case de facto declared *Ectocynodon* a nomen dubium due to the bad state of preservation of its type material. Strictly speaking the state of preservation of the holotype of*Captorhinus* is not much better, however, Case deemed it diagnostic at that time. Seen that *Ectocynodon* is thus the senior synonym proper it provides a good example for a nomen oblitum, because it has never been used in captorhinid taxonomy since 1911.

In 1959 a second revision of the captorhinid fossils by R. J. Seltin lead to the recognition of only one species of *Captorhinus*: *C. aguti*. Oddly Seltin (1959) erected the new species *Labidosaurus oklahomensis* on the basis of a small single-tooth-rowed skull with *Captorhinus*-like appearance. Later doubts were casted on the assignment of the material formerly referred to *P. laticeps* to *C. aguti* because of the presence of a single tooth row, unlike to all other remains of *C. aguti* which show multiple tooth rows in at least one branch of the lower or upper jaw. In 1979 M. J. Heaton thus erected the genus *Eocaptorhinus* for these exclusively single-tooth-rowed remains leading to the new combination *E. laticeps*. In addition Heaton assigned Seltin's *L. oklahomensis* to this species. Finally *E. laticeps* was reassigned to *Captorhinus* by several authors because of its general similarity to *C. aguti* (see below), but this time retained its status as distinct species.

In 2001 the scientifically youngest species of *Captorhinus* was reported by Kissel et al. and subsequently, in 2002, was given the name *C. magnus*.

Characteristics of the genus: *Captorhinus* is characterized by a series of cranial traits that occur in other basal captorhinids as well, e.g. relatively large eye openings, shagreen dentiton on palatal bones, a distinctive sculptural pattern on the bones of the dermal skull roof and on the bones of the external surface of the mandible, and a down-curved, hook-like premaxilla. However within the genus one species existst that has multiple tooth rows, a feature not known from other basal captorhinids, such as *Romeria* or *Protocaptorhinus*. In addition the posterior teeth of the maxillary are not simple cones as in more basal captorhinids but are either chisel-shaped or ogival. Also the posterior part of the skull is clearly more expanded laterally, being reminiscent rather to the moradisaurines than to the basal members of the family. A unique feature of *Captorhinus* may be the retroarticular process of the lower jaw being conspiciously longer than broad, since this is as yet not seen in any other captorhinid taxon.

***Captorhinus aguti*:** *C. aguti* is the type species of the genus. It is without doubt the by far best known captorhinid species. Hundreds of well preserved, articulated skulls and skull fragments are collected at the famous Dolese Brothers quarry near Fort Sill in Oklahoma.



Captorhinus aguti (Cope 1882) Artinskian, Early Permian, ~40 cm in length, studies of skull and skeleton. Illustration copyright David Peters, reproduced with permission

C. aguti is distinguished primarily from *C. laticeps* and *C. magnus* in having multiple rows of teeth on the maxillary and dentary bones. These rows are, in contrast to the tooth rows seen in moradisaurines, not oriented parallel to the lateral margins of the jaws but are oriented obliquely to that margins, in a way that each row is followed posterolaterally by the next one. Thus, up to eight rows are observed in *C aguti* without the dentigerous bones forming the strongly medially expanded tooth plates which characterize the jaws of the moradisaurines. Nevertheless the toothed areas of maxillary and dentary are broader mediolaterally than in the single-tooth-rowed captorhinids.

***Captorhinus laticeps*:** *C. laticeps* is distinguished form *C. aguti* in lacking multiple tooth rows in all four branches of the jaws. In almost all other respects it is very similar to *C. aguti*. *C. laticeps* differs from *C. magnus* in being considerably smaller and in having chisel-shaped instead of ogival teeth on the posterior portion of maxillary and dentary.

***Eocaptorhinus* :** *Eocaptorhinus* is considered a synonym of *Captorhinus*. The genus was erected by Malcolm J. Heaton in 1979 including fossils hitherto referred to *Pariotichus laticeps* Williston leading to the new combination *Eocaptorhinus laticeps*. Heaton chose this name meaning "early *Captorhinus* because the remains of this animal are striking similar to *Captorhinus aguti*, with the exception of lacking the characteristic multiple tooth rows, but come from an geologically older horizon. Disregarding the principles of cladistics Heaton made an stratophenetic approach in elucidating the evolution of captorhinids, postulating an anagenetic *Romeria* -> *Protocaptorhinus* -> *Eocaptorhinus* -> *Captorhinus* model.

More recent examinations of *Eocaptorhinus* and *Captorhinus aguti* revealed that they share such a great number of non-dentitional traits that distinction on a generic level became obsolete. Moreover in one locality (Ft. Sill, Oklahoma) captorhinid remains with both, single tooth rows and multiple tooth rows are present without any possibility of stratigraphic differentiation of the fossils found at that time. In addition it has been shown that in *C. aguti* some specimen have a single tooth row on one and a double tooth row on the other branch of the jaw. Thus, despite minor differences in postcranial body structure, it has been ambiguous wether *C. laticeps* and *C. aguti* are truly distinct species and if not in which way both forms are related: as sympatric subspecies, as males and females, or afterall as distinct ontogenetic stages of one single species.

Then a significant difference in the shape of the teeth of both forms was recognized: *C. aguti* was discovered to have teeth that resemble rather a pointed arch (also called ogive) whereas *C. laticeps* has teeth that are rather chisel-shaped. However this seemed not sufficient to legitimate the "two-species-concept".

The discovery of a new species, *Captorhinus magnus*, throwed light on this obscure relationship in a cladistical way. *C. magnus* is approximately as twice as large as *C. aguti* and its jaws are equipped with only one single row of, however ogival, teeth. Most important is the fact that *C. magnus* is unequivocally distinct from *C. aguti* in having an concave articulation surface at the distal end of the femur whereas in *C. aguti* this articulation surface is convex, a feature hardly relatable to ontogeny. Sexual dimorphism could also be excluded because further collections at the Ft. Sill site obtained that specimen of *C. magnus* are more abundant in the lower parts of the section whereas *C. aguti* is more abundant in the higher part. In case of sexual dimorphism a by far more regular distribution would be expected. Finally, inclusion of the new taxon in the phylogenetic analyses yielded that *C. laticeps* and *C. aguti* are no longer sister clades but *C. aguti* is sister to *C. magnus*. Thus, any conspecific or closer relationship of *C. laticeps* and *C. aguti* can be ruled out due to the close relationship of *C. aguti* to another, species of *Captorhinus* that is clearly not conspecific with *C. aguti*.

***Captorhinus magnus*:** *C. magnus* differs from *C. aguti* in having only one single row of teeth on dentary and maxillary. From *C. laticeps* it is distinct in being twice as large and in having ogival teeth in the posterior portion of maxillary and dentary. Moreover the distal articulation surface of the femur is concave whereas in *C. aguti* and *C. laticeps* it is convex.

Phylogeny: *Captorhinus* comprises rather derived representatives of basal captorhinids. The dentition, accompanied with the laterally widened posterior portion of the skull, shows a certain degree of specialization compared to the more basal forms.

Some facts:

</tr>

<table>
<tr><th colspan="2"><i>Captorhinus</i> Cope 1895</th></tr>
<tr><th>Species Recognized</th><th>Data</th></tr>
<tr><td><i>C. aguti</i> Cope 1882</td><td>Family: Captorhinidae
Etymology of genus: "capture-nose", refers to the assumption that the hook-like premaxilla was used to capture prey animals
Etymology of species: name is derived from the extant</td></tr>
</table>

	rodent agouti (*Dasyprocta*) since Cope had the impression that the skull on which he based the species *Ectocynodon aguti* (see synonyms list) would be similar in shape to the skull of this animal **Paleogeography:** Wichita Uplift, northwestern Pangaea **Locality:** Comanche County, Oklahoma, USA **Horizon:** Garber Formation (Sumner Group) **Synonyms:** *Ectocynodon aguti* Cope 1882, *Ectocynodon incisivus* Cope 1888, *Pariotichus aguti* Cope 1882 (Cope 1895, new comb.), *Pariotichus incisivus* Cope 1882 (Cope 1895, new comb.), *Captorhinus angusticeps* Cope 1895, *Pariotichus isolomus* Cope 1895, *Pariotichus angusticeps* Cope 1895 (Broom 1910, ? *lapsus calami*), *Captorhinus isolomus* Cope 1895 (Case 1911, new comb.)
- *C. laticeps* Williston 1909	**Etymology of species:** "broad-headed" **Paleogeography:** "Eastern Shelf" of Midland Basin, Anadarko Basin, northwestern Pangaea **Locality:** Baylor, Wilbarger, and Wichita Counties, Texas, USA Kay County, Oklahoma, USA **Horizon:** Clyde Formation, Admiral Formation, Belle Plains Formation (all Wichita Group), Wellington Formation (Sumner Group) **Synonyms:** *Pariotichus laticeps* Williston 1909, *Captorhinus isolomus* Cope 1895 (Case 1911, new comb.), *Captorhinus aguti* Cope 1895 (Case 1911, new comb.) (Seltin, 1959), *Labidosaurus oklahomensis* Seltin 1959, *Labidosaurus stovalli* (Olson, 1962a, b)*, *Eocaptorhinus laticeps* Williston 1909 (Heaton 1979, new comb.)
- *C. magnus* Kissel et al. 2002	**Etymology of species:** "large" **Paleogeography:** same as in *C. aguti* **Locality:** same as in *C. aguti* **Horizon:** same as in *C. aguti*
Stratigraphic Range: Lower Permian **:** Leonardian	

*Olson (1962a, b) for unknown reasons used this name with reference to Seltin's (1959) species *Labidosaurus oklahomensis*

References: BROOM, R. (1910): A comparison of the Permian reptiles of North America with those of South Africa. *Bulletin of the American Museum of Natural History* 28: 197-234

CASE, E.C. (1911): A revision of the Cotylosauria of North America. *Carnegie Institution of Washington Publication* vol. 145, Washington, D.C., 122 p.

COPE, E.D. (1895): The Reptilian Order Cotylosauria. *Proceedings of the American Philosophical Society* 34 (149):

436-457

DODICK, J.T. and MODESTO, S.P. (1995): The Cranial Anatomy of the Captorhinid Reptile*Labidosaurikos meachami* from the Lower Permian of Oklahoma. *Palaeontology* 38 (3): 687-711

HEATON, M.J. (1979): Cranial Anatomy of Primitive Captorhinid Reptiles from the Late Pennsylvanian and Early Permian, Oklahoma and Texas. *Oklahoma Geological Survey*, *Bulletin* vol. 127. The University of Oklahoma, Norman, 83 p.

KISSEL, R.A., DILKES, D.W. and REISZ, R.R. (2002): *Captorhinus magnus*, a new captorhinid (Amniota: Eureptilia) from the Lower Permian of Oklahoma, with new evidence on the homology of the astragalus. Canadian Journal of Earth Science, 39 (9): 1363-1372

MODESTO, S.P. (1998): New information on the skull of the Early Permian reptile *Captorhinus aguti*. *PaleoBios* 18 (2/3): 21-35

SELTIN, R.J. (1959): A review of the family Captorhinidae. *Fieldiana Geology* 10 (34):461-509

OLSON, E.C. (1962a): Late Permian Terrestrial Vertebrates, U.S.A. and U.S.S.R. *Transactions of the Philosophical Society of America, New Series* 52 (2): 1-224

OLSON, E.C. (1962b): Part II. - The Osteology of *Captorhinikos chozaensis* Olson. pp. 49-68 in: Permian Vertebrates from Oklahoma and Texas. *Oklahoma Geological Survey, Circular* vol. 59. The University of Oklahoma, Norman

Weblinks: | photographs of specimen of *Captorhinus aguti* from the Richards Spur (Ft. Sill) locality

| photographs of specimen of *Captorhinus magnus* from the Richards Spur (Ft. Sill) locality

Credits: Zidane 2 June 2008

Captorhinikos valensis Olson 1954

Phylogeny: Captorhinidae ::: *Captorhinus* + ((*Labidosaurus* + Moradisaurinae) + *)

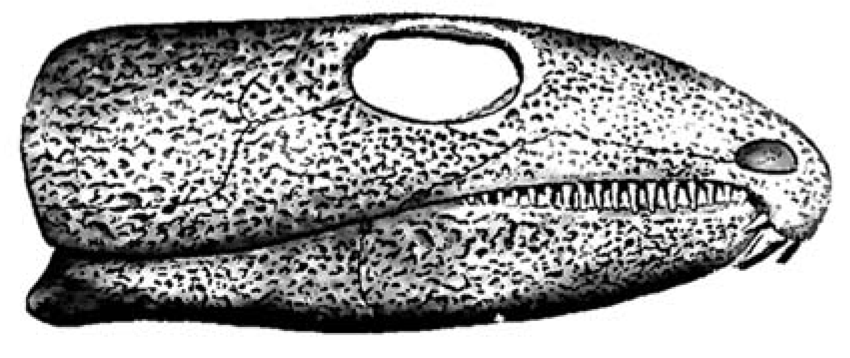
Horizon: Upper Vale Fmormation (Kungurian) of Texas.

Reference: E. C. Olson. 1954. Fauna of the Vale and Choza: 9. Captorhinomorpha. Fieldiana: Geology 10(19):211-218

Link: Paleobiology Database

Labidosaurus hamatus

Phylogeny: Captorhinidae ::: *Captorhinus* + (*Captorhinikos* + (Moradisaurinae + *))



Drawing of a skull of *Labidosaurus hamatus* (modified from Case, 1911)

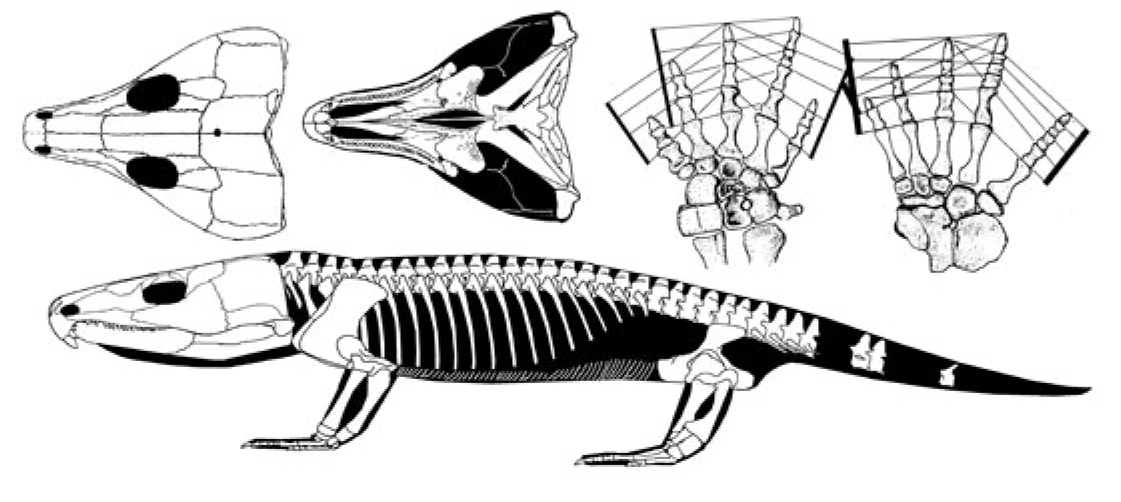
Comments: ***Labidosaurus hamatus*** is the largest among the single-rowed captorhinids and is known from a few skulls and numerous postcranial remains coming from the Lower Permian red beds of North Texas. It is currently the only recognized species of the genus *Labidosaurus*

Its skull measures about 20 cm in length. Given that the trunk length in *Captorhinus* is approximately 3.6-fold the skull length, the

This reconstruction is somewhat outdated but shows well the characteristics of the species.
The heavy ornamentation of the skull bones, a typical trait in larger captorhinids, is nicely depicted.

overall body length in *L. hamatus* was more than 90 cm. Another particularity concerning the skull is the large hook-like tip of the snout, formed by the premaxillary bone. Most of the captorhinids have such a down-curved premaxillary but in *L. hamatus* this feature is much more pronounced. Use and function of this toothed "beak" is as yet unclear. Some authors suggested it served as a tool for digging, but absence of characteristic scratch marks on the anterior teeth does not support this hypothesis.

The skull morphology places *Labidosaurus* close to the large multiple tooth-rowed captorhinids, the moradisaurines. Because herbivory is assumed for the latter the diet of *L. hamatus* may have included plants but its single rows of sharp conical teeth, rather suitable for piercing animal prey, suggests that it was most likely an omnivore.



Labidosaurus hamatus Cope 1895 Artinskian, Early Permian, ~75 cm in length, studies of skull, hand, and skeleton. Illustration copyright David Peters, reproduced with permission

The vertebral column of *L. hamatus* consists of 25 trunk vertebrae and at least 33 caudal vertebrae. There are two temporally and spatially coexisting morphotypes present in the vertebral column of *Labidosaurus*: one that has vertebrae with short neural spines and long such spines alternating and another that has exclusively vertebrae with short neural spines.

L. hamatus is one of the historically longest-known members of the family and was described as early as 1895 by one of the trailblazers of US-american vertebrate paleontology Edward D. Cope (albeit under a different name of genus). Some captorhinid fossils formerly referred to *Labidosaurus* are today assigned either to other captorhinid genera or to *L. hamatus*.

***Labidosaurus hamatus* Cope 1895**
Some Facts
Family: Captorhinidae **Etymology of genus:** "lipped reptile" **Etymology of species:** "hooked" **Paleogeography:** "Eastern Shelf" of Midland Basin, northwestern Pangaea **Locality:** Baylor County, Texas, USA **Horizon:** deepest part of Clear Fork Group (former "Arroyo Formation") **Synonyms:** *Pariotichus hamatus* Cope 1895, *Labidosaurus broilii* Case 1911

Stratigraphic Range: Lower Permian **:** Leonardian

References: CASE, E.C. (1911): A revision of the Cotylosauria of North America. Carnegie Institution of Washington Publication, vol. 145, Washington, D.C., 122 pp.

COPE, E.D. (1895): The Reptilian Order Cotylosauria. Proc. Am. Phil. Soc., 34(149), pp. 436-457

COPE, E.D. (1896): Second contribution to the history of the Cotylosauria. Proc. Am. Phil. Soc., 35(151), pp. 122-139

MODESTO, S.P., SCOTT, D.M., BERMAN, D.S., MÃœLLER, J. and REISZ, R.R. (2007): The skull and the paleoecological significance of *Labidosaurus hamatus*, a captorhinid reptile from the Lower Permian of Texas. Zool. J. Linn. Soc., 149(2), pp. 237-262

SUMIDA, S.S. (1987): Two Different Vertebral Forms in the Axial Column of *Labidosaurus* (Captorhinomorpha: Captorhinidae). J. Paleontol., 61(1), pp. 155-167

Credits Zidane 25 May 2008

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Eureptilia: *Romeria texana*

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         |  `--Captorhinidae
         |     |--Concordia
         |     `--+--Romeria
         |        `--+--Captorhinus
         |           `--Moradisaurinae
         |
         `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

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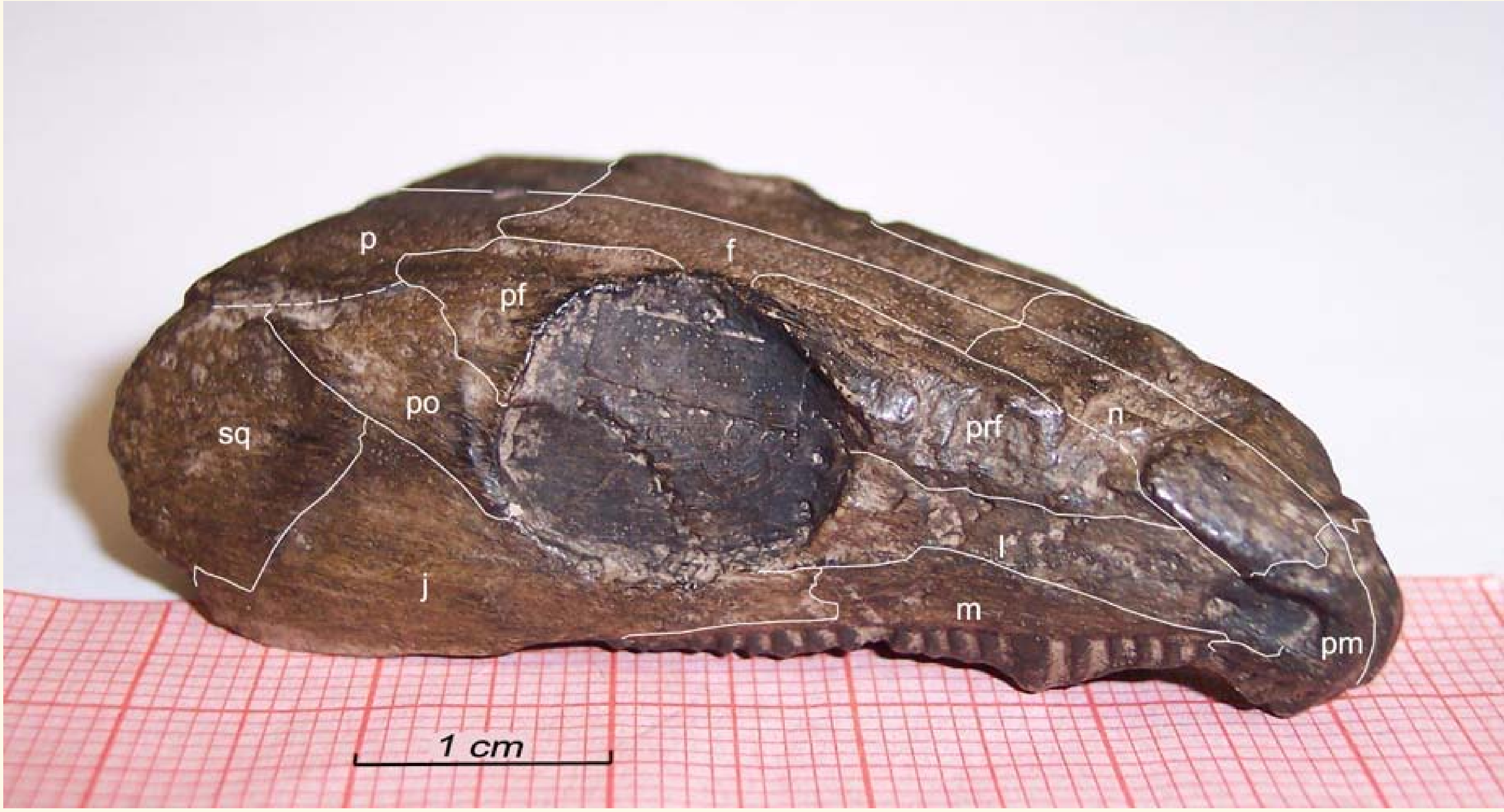


Facsimile of the type specimen of *Romeria texana* (MCZ 1480). The smoothness of the dermal bones is due to preparation. Originally these bones were sculptured in a typical captorhinid manner.

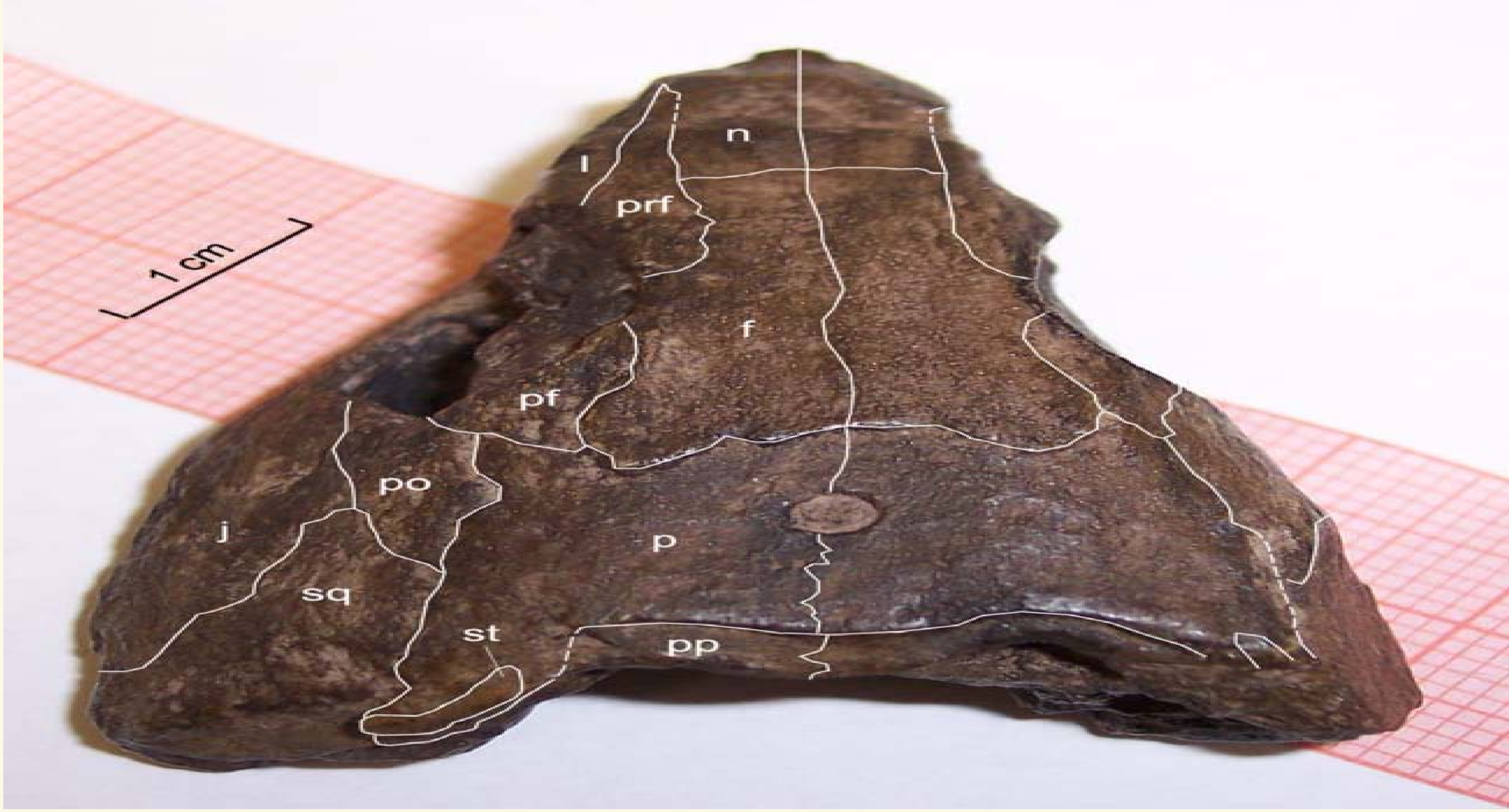
Abbreviations: **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxillary; **n**, nasal; **p**, parietal; **pf**, postfrontal; **pm**, premaxillary; **prf**, prefrontal; **po**, postorbital; **sq**, squamosal.

Eureptilia: *Romeria texana* (2)

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
          |   `--Captorhinidae
          |     |--Concordia
          |     `--+--Romeria
          |        `--+--Captorhinus
          |            `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

Contents



Facsimile of the type specimen of *Romeria texana* (MCZ 1480). Well visible is the bilateral embayment of the posterior skull table. The smoothness of the bones is due to preparation. Originally these bones were sculptured in a typical captorhinid manner.

Abbreviations: **f**, frontal; **j**, jugal; **l**, lacrimal; **n**, nasal; **p**, parietal; **pf**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **po**, postorbital; **sq**, squamosal, **st**, supratemporal.

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text content Zidane; page MAK120316

Eureptilia

Captorhinidae: Moradisaurinae

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         |   `--Captorhinidae
         |     |--Concordia
         |     `--+--Romeria
         |        `--+--Captorhinus
         |           `--Moradisaurinae
         |              |--Labidosaurikos
         |              `--+--Gecatogomphius
         |                 |--Kahneria
         |                 |?- Rothianiscus
         |                 `--Moradisaurus
         `--Romeriida
            |--Paleothyris
            `--+--Protorothyrididae
               `--DIAPSIDA
```

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1. *Gecatogomphius* X
2. *Kahneria* X
3. Moradisaurinae X
4. *Labidosaurikos* X
5. *Moradisaurus* X

The subfamily **Moradisaurinae** comprises the most derived captorhinids and forms a monophyletic group. They are opposed to the "Captorhininae", the more basal, mainly single-tooth-rowed forms which closely resemble other generalized amniotes, such as *Protorothyris* or *Hylonomus*. The "captorhinines" are a paraphyletic group and therefore this term is only used for comparative purposes.

All moradisaurines are characterized by having multiple rows of teeth in their jaws which virtually form whole tooth batteries. The teeth are positioned on medially extended tooth plates formed by the maxillary and dentary bones. From this follows that these teeth are homologous to the teeth of the single tooth row seen in more basal captorhinids. However dentition on palatal bones, a common trait of basal amniotes, is greatly reduced or even entirely absent in moradisaurines. It has been speculated whether the medial margins of the upper tooth plates were connected to each other by a layer of soft tissue and formed a secondary palate in the living animal.

Because multiple tooth rows, however not in that great extent, also occur in captorhinids that fell outside the moradisaurine clade (e.g. in *Captorhinus aguti*) it seems that multiple tooth rows have evolved several times within captorhinids.

The teeth itself often show a distinct wear pattern. Wear facets occur just below the tip on both sides of the crown and sometimes reach down to the half of te crown's height. This quite regular wear pattern differs from the more irregular pattern observed in *Captorhinus aguti* and most likely was generated by the occlusion of opposing teeth of the upper and lower jaw in a way that one tooth row of the upper jaw fitted between two tooth rows of the lower jaw, and vice versa. This, in turn, is suggestive of changes in feeding behavior in the moradisaurines compared to their more generalized "captorhinine" ancestors (however, it is important to note that *C. aguti* is quite specialized already).

Most conclusive is to assume a herbivorous diet for the moradisaurines. However in most genera no postcranial elements are preserved which could provide evidence for that assumption, such as an expanded, barrel-shaped rib cage, appropriate for carrying an enlarged intestinal tract which would be required for digestion of plant material. Solely in *Moradisaurus*, the type genus of the subfamily, there are signs for modifications of the postcranial skeleton due to adaptation to herbivory. Its hindlimb is much more massive built than those of the "captorhinines". It resembles strongly that of an edaphosaur or a pareiasaur, both of which are Late Paleozoic, unequivocally herbivorous amniotes, hence this massiveness may not result from allometric scaling anlone. Alternative models of moradisaurine feeding behavior include omnivory or durophagy, the latter meaning that they used their tooth batteries to crush hard shelled invertebrates, such as clams or crabs, to achieve their meat. - Zidane080528

Descriptions

Moradisaurinae

Phylogeny: Captorhinidae **:::** *Captorhinus* + (*Labidosaurus* + * **:** *Labidosaurikos* + (*Gecatogomphius* + (*Kahneria* + *Moradisaurus*)))

Range: Mid to Late Permian of N Am, EEur, & Afr.

Comments: See description above

Labidosaurikos meachami

Phylogeny: Moradisaurinae **:** (*Gecatogomphius* + (*Kahneria* + *Moradisaurus*)) + *

Comments: ***Labidosaurikos meachami*** is a large, multiple-tooth-rowed captorhinid. It is the basalmost member of the subfamily Moradisaurinae. It is known from one single, however almost complete and virtually perfectly preserved skull coming from Lower Permian terrestrial deposits of central Oklahoma.

In vivo reconstruction of *L. meachami*

Contents

Scientific History: *L. meachami* has been discovered as early as in 1939 but has not been named and introduced to paleontology until 1950. Finally a detailed description of the skull has been published in 1995.

Skull: The heavily ornamented skull of *L. meachami* measures about 28 cm in length. Given that the trunk length in *Captorhinus* is approximately 3.6-fold the skull length, the overall body length in *L. meachami* was as much as 1.3 m. *L. meachami* shows almost the whole range of features which define the moradisaurines. Its snout is, compared to the posterior part of the skull, very narrow. Its dentigerous bones form wide tooth plates equipped with batteries of relatively small subconical teeth. The supratemporal is comparativley large and sculptured. The postparietal is not entirely overlapped dorsally by the parietal and its exposed portion is sculptured as well. Both supratemporal and postparietal contribute to the skull table in a way that the parietal is excluded from the posterior rim of that table. *L. meachami*, however, differs from the other well known moradisaurine *Moradisaurus* in retaining a band of small denticles on the posterior egde of the transverse flange ("wing") of the pterygoid. Another difference to *Moradisaurus* is the lateral wall of the mandible being only modestly bulged, however this bulge is still much more pronounced than in smaller moradisaurines such as *Kahneria* or *Gecatogomphius*.

Teeth: The only premaxillary tooth preserved is the largest tooth of the upper jaw and slightly recurved. The anteriormost dentary tooth is the largest of the lower jaw, however, only its base is preserved. The teeth of the maxillary and dentary tooth plates are arranged in six and five, respectively, longitudinal rows in which the teeth of two adjacent rows each alternate resulting in a chessboard-like pattern. Most of these teeth show distinctive wear facets. The teeth of the most labial row are exclusively worn on the lingual side whereas wear in the most lingual row is restricted to the labial side. Almost all teeth of the median rows are worn on both labial and lingual sides. This wear pattern is apparently the result of interdigitation of the tooth rows of upper and lower jaw. Thus it is very likely that the teeth were used for grinding fibrous plants.

A second species ?: A second species of *Labidosaurikos*, *L. barkeri*, has been described from the deepest part of the "Choza Formation" (upper part of Clear Fork Group) of North Texas in 1954 but has been questioned as early as 1959. It differs from *L. meachami* in having one less row of teeth in both maxillary and dentary. The material, however, is fragmentary. Given that the Texas specimens seem to be immature the number of tooth rows could be related to age. Because no further unequivocal difference between *L. meachami* and *L. barkeri* is as yet reported a revisional examination of the Texas fossils is needed to verify the validity of *L. barkeri*.

Some facts

Labidosaurikos meachami **Stovall 1950**

Family: Captorhinidae

Etymology of genus: name refers to the its similarity to *Labidosaurus* (note that at that time no other moradisaurine was known)

Etymology of species: named after E. D. Meacham, dean of the College of Arts and Sciences of the University of Oklahoma at that time

Paleogeography: Anadarko Basin, "Eastern Shelf" of Midland Basin*, northwestern Pangaea

Locality: Logan County, Oklahoma, USA; Foard County, Texas, USA*

Horizon: Hennessey Formation (Sumner Group)

upper part of Clear Fork Group (formerly referred to as "Choza Formation")*

Synonyms: ? *Labidosaurikos barkeri* Olson 1954

Stratigraphic Range: Lower Permian **:** Leonardian

refers to data on *L. barkeri

References: DODICK, J.T. and MODESTO, S.P. (1995): The Cranial Anatomy of the Captorhinid Reptile *Labidosaurikos meachami* from the Lower Permian of Oklahoma. *Palaeontology* 38 (3): 687-711

OLSON, E.C. (1954): Fauna of the Vale and Choza: 9 Captorhinomorpha. *Fieldiana Geology* 10 (19): 211-218

SELTIN, R.J. (1959): A review of the family Captorhinidae. *Fieldiana Geology* 10 (34):461-509

STOVALL, J.W. (1950): A New Cotylosaur from North Central Oklahoma. *American Journal of Science* 248 (1): 46-54

Credits: Zidane 26 May 2008

Gecatogomphius kavejevi

Phylogeny: Moradisaurinae : *Labidosaurikos* + ((*Kahneria* + *Moradisaurus*) + *)

Comments: *Gecatogomphius kavejevi* is a multiple-tooth-rowed, moradisaurine captorhinid from the western forelands of the Ural Mountains in Russia. It is as yet the best known captorhinid from eurasia and the only recognized species of the genus.

Contents

Scientific History: *G. kavejevi* was discovered in 1955 by the Soviet geologist M. S. Kaveev who found a fragment of a lower jaw at the bank of the Vjatka River in Kirov District. Subsequently this bone was sent to the Academy of Science of the USSR. In 1957 it has been named and published. Since then only one further remain of *G. kavejevi*, a single fragmentary maxillary tooth plate, came to light.

Description: The dentary is about 8 cm in length. Its lateral wall is sculptured with an irregular pattern of long and deep groves as seen in many other captorhinids. Medially it is widened to form the typical moradisaurine tooth plate. In its anteriormost portion the dentary shows tree caniniform teeth being as twice as large than the teeth of the tooth plate. An alveola at the tip of the bone indicates the former presence of a fourth caniniform. The tooth plate bears more than 40 bulbous teeth arranged in five rows. Similar to *Labidosaurikos* the teeth of two adjacent rows each alternate and show more or less pronounced wear facets below the apex. An important particularity in *G. kavejevi* is that the jaw bears signs of resorption pits which is the only occurence of such a feature in moradisaurines so far.

The fragment of the maxillary tooth plate also bears five rows of teeth, showing a wear pattern similar to that of the teeth on the dentary.

Phylogeny: Despite the sparseness of the material preserved *G. kavejevi* is clearly a moradisaurine, i.e. a member of the most derived clade of the family. A close relationship to the North American representative *Kahneria seltina* has been postulated, however, since the establishment of modern cladistic methods the latter never was included in relevant analyses.

Some facts

Gecatogomphius kavejevi Vjushkov & Chudinov 1957

Family: Captorhinidae

Etymology of genus: "hundreds of cheek teeth"

Etymology of species: named after the Soviet geologist M.S. Kaveev

Paleogeography: Foreland Basin of the Urals, northeastern Pangaea

Locality: banks of Vyatka River, Kirov District, western Russia

Horizon: Belebei Formation

Synonyms: Everett C. Olson (1962) used the western transcription *Hecatogomphius* in his translation of Vjushkov & Chudinov's (1957) original description of this species. Since then this genus name was used numerous times by non-russian authors.

Stratigraphic Range: Upper Permian **:** Kazanian*

Ivakhnenko (1990) assigned the horizon of provenance of *Gecatogomphius* to the Ocher assemblage, a unit of russian non-marine vertebrate biostratigraphy. In Lucas (2006) this assamblage is correlated with the Kazanian stage of global stratigraphy.

References: DODICK, J.T. and MODESTO, S.P. (1995): The Cranial Anatomy of the Captorhinid Reptile *Labidosaurikos meachami* from the Lower Permian of Oklahoma. *Palaeontology* 38 (3): 687-711

IVAKHNENKO, M.F. (1990): Early Permian Elements of Faunal Assemblages of Tetrapods from Eastern Europe [Ðàííåïåðìñêèå ýëåìåíòû ôàóíèñòè÷åñêèõ êîìïëåêñîâ òåòðàïîä Âîñòî÷íîé Åâðîïû]. *Paleontologicheskii Zhurnal* 1990 (2): 102-111 [russian]

LUCAS, S.G. (2006): Global Permian tetrapod biostratigraphy and biochronology. pp. 65-93 in SPENCER G. LUCAS et al. (eds.): *Non-Marine Permian Biostratigraphy and Biochronology*. Geological Society, London, Special Publications, vol. 265. The Geological Society, London

OLSON, E.C. (1962): Late Permian Terrestrial Vertebrates, U.S.A. and U.S.S.R. *Transactions of the American Philosophical Society, ns* 52 (2): 1-224

VJUSHKOV, B.P. and CHUDINOV, P.K. (1957): Discovery of a Captorhinid in the Upper Permian of the USSR [Îòêðûòèå Kaïòîðèíèäà â âåðõíåé Ïåðìè CCCP]. *Doklady Akadademii Nauk SSSR* 112 (3): 523-526 [russian]

Credits Zidane 25 May 2008 (PDT)

Kahneria seltina

Phylogeny: Moradisaurinae : *Labidosaurikos* + (*Gecatogomphius* + (*Moradisaurus* + *))

Comments: *Kahneria seltina* is an average-sized poorly known representative of the multiple tooth-rowed captorhinids. It is known from tooth plates of lower and upper jaws, skull fragments and few scrappy postcranial material coming from terrestrial red beds of the Middle Permian of North Texas. The tooth plates bear five rows of more or less conical teeth. *K. seltina* is, without much doubt, a member of the moradisaurines.

***Kahneria seltina* Olson 1962**
Some Facts
Family: Captorhinidae **Etymology of genus:** named after the discoverer of the type locality (today called Kahn Quarry), Jack Kahn, staff member of the University of Chicago and one of E.C. Olson's collaborators at that time **Etymology of species:** named after the paleontologist Richard J. Seltin **Paleography:** "Eastern Shelf" of Midland Basin, northwestern Pangaea **Locality:** Knox County, Texas, USA **Horizon:** San Angelo Formation (Pease River Group)
Stratigraphic Range: Middle Permian **:** Upper Leonardian or Lower Guadalupian*

*** The problem of exact stratigraphic position of San Angelo Formation has still not entirely been solved. In official geological maps of the USGS or the Texas Bureau of Economic Geology the San Angelo Formation is assigned to the Guadalupian series.**

References: OLSON, E.C. (1962): Late Permian Terrestrial Vertebrates, U.S.A. and U.S.S.R. Trans. Amer. Philos. Soc., ns, 52(2), pp. 1-224

Credits Zidane 25 May 2008

Moradisaurus grandis

Phylogeny: Moradisaurinae : *Labidosaurikos* + (*Gecatogomphius* + (*Kahneria* + *))

Comments: *Moradisaurus grandis* is the largest and most derived known multiple tooth-rowed captorhinid so far. *Moradisaurus* is type genus of the subfamily Moradisaurinae and *M. grandis* is the only species currently referred to that genus. It is known from both skull and postcranial remains.

Its skull measures more than 40 cm in length and width, and is covered with a heavy ridgeand pit sculpture. Compared with the ratio of skull/trunk length in *Captorhinus* its overall body length might have been about 1.8 m. The wide tooth plates of its jaws are equipped with 11 rows of relatively small, subconical teeth and the side walls of the massive mandible are strongly laterally bulged. The posterior portion of the skull is very wide and the flanges of the pterygoid have a large surface providing space for the attachment of the jaw musculature.

Unfortunately the state of preservation in the skull found seems not to allow the determination of the exact shape and relationships of the bones in both skull roof and palate. Nevertheless there is hope that further investigations and collections will fill this gap of knowledge.

Besides the skull also the hindlimb of *M. grandis* has been described in detail. Leg and foot are, in contrast to other multiple tooth-rowed forms, very massive and built in a way suggesting that *M. grandis* was not a fast runner. The femur resembles more that of an edaphosaur or a pareiasaur both of which are large herbivores of the Late Paleozoic. Granted that *M. grandis* was a herbivore too, and that is what is assumed for the large multiple tooth-rowed captorhinids, the changes in limb proportions seem quite plausible and related to adaptation to herbivory.

***M. grandis* lived on a river plain in the central region of the supercontinent Pangaea. This plain was periodically affected by pyroclastic flows, which, accompanied with stream-action, apparently played a significant role in burial and preservation of the fossils found in the region today.**

Moradisaurus grandis Taquet 1969

Some Facts

Family: Captorhinidae

Etymology of genus: "reptile of Moradi"

Etymology of species: "large"

Paleogeography: Iullemmeden Basin, central Pangaea

Locality: near Tchimozenog, Agadez District, northern Republic of Niger

Horizon: Moradi Formation (IzÃ©gouandane Group)

Stratigraphic Range: Upper Permian

References: O'KEEFE, F.R., SIDOR, C.A., LARSSON, H.C.E., MAGA, A. and IDE, O. (2005): The Vertebrate Fauna of the Upper Permian of Niger - III, Morphology and Ontogeny of the Hindlimb of *Moradisaurus grandis* (Reptilia, Captorhinidae). Journal of Vertebrate Paleontology, 25(2), pp. 309-319

RICQLES, A.de and TAQUET, P. (1982): La Faune de VertÃ©brÃ©s du Permien SupÃ©rieur du Niger I. Le Captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria) - Le Crane. Ann. PalÃ©ont., 68(1), pp. 33-106

TAQUET, P. (1969): Première découverte en Afrique d'un Reptile Captorhinomorphe (Cotylosaurien). C. R. Acad. Sc. Paris D, 268(1), pp. 779-781

Credits: Zidane 10:57, 25 May 2008

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Eureptilia: Protorothyrididae

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   `--Eureptilia
      |-- Captorhinidae
      `--+--Brouffia      "Protorothyrididae"
         `--o Romeriida
            `--+--Paleothyris
               `--+--Hylonomus
                  `--+--+--Anthracodromeus
                     |  |--Cephalerpeton
                     |  `--Protorothyris
                     `--o DIAPSIDA
```

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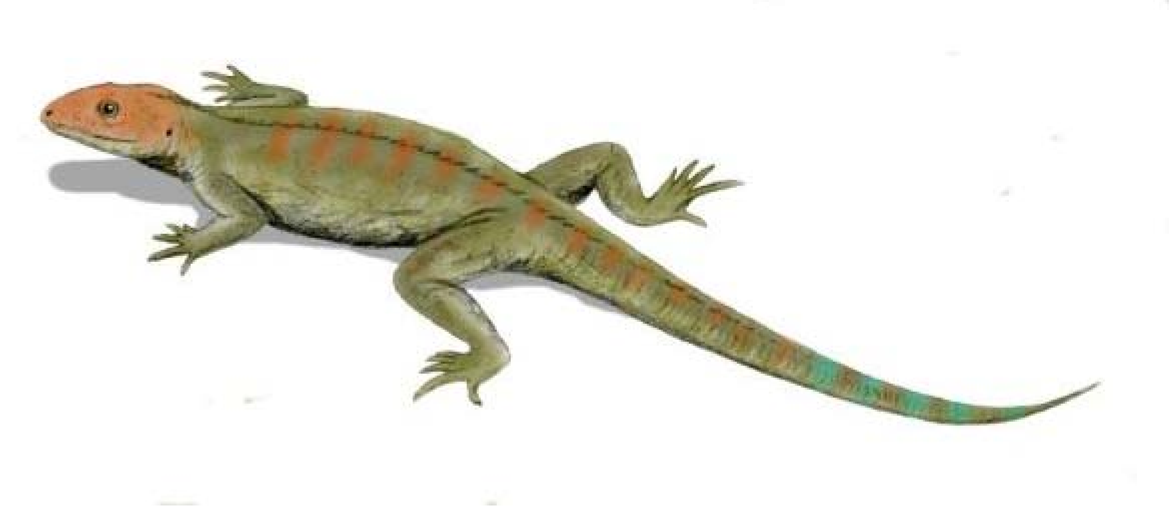
1. *Brouffia* X
2. *Hylonomus* X
3. "Protorothyrididae" X
4. *Protorothyris* X
5. Romeriida

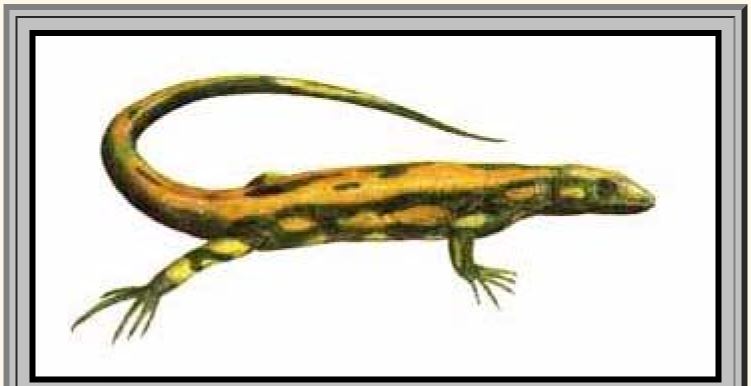


Hylonomus lyelli, an early reptile from the Late Carboniferous of Nova Scotia, Canada, illustration by Nobu

Tamura (Wikipedia)

The "Protorothyrididae" (or "Protorothyridae") are a basal group of terrestrial eureptiles. Although not that closely related to them, they were similar to modern lizards in appearance and were generalized, small, insectivorous animals. Most of them are known from the Late Carboniferous of North America and Europe. According to recent studies, they form a paraphyletic group, which means that not all descendants of the last common ancestor of this group are included. In case of the protorothyridids, the diapsids (the sister clade of *Anthracodromeus* + *Cephalerpeton* + *Protorothyris)* are traditionally excluded. If the Early Permian genus *Thuringothyris* is also considered a protorothyridid the group even becomes polyphyletic because *Thuringothyris* is more closely related to the Captorhinidae while all other protorothyridids are closer to the Diapsida. The para- or polyphyly of a group is indicated by using its name enclosed in quotation marks. Zidane 080421 Palaeos org

Protorothyrididae: Small, short legged, lizard-like insectivores. Carroll & others place as early amniote stem group. *Hylonomus*



***Hylonomus lyelli*, a protorothyrid from the Late Carboniferous of Nova Scotia. Image from Cox *et al*. (1988).**

Range: Middle Carboniferous to Early Permian of North America & ?Europe.

Phylogeny: Eureptilia:: Diapsida + *. Unfenestrated skull?

Comments: In evolutionary systematics, the Protorothyrididae are the stem-lineage from which all other amniotes evolved, and hence are more basal than in cladistics. In the cladistic analysis of Müller & Reisz 2006 they are a paraphyletic grade rather than clade, and the stem lineage from which the Diapsida evolved (cladistics). MAK120317

Links: Protorothyrididae; reptiles; Dinosaurier Album 2 (OK, so the grass is anachronistic. I still love this page); H-Paleontology and Geology Glossary- H (entry on *Hylonomus*). ATW030210. Paeobiology database,

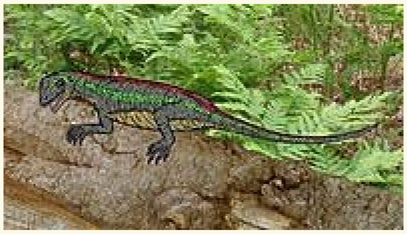
Brouffia Brouffia orientalis

Range: Late Carboniferous of Nyr'any, Czech Republic.

Phylogeny: Eureptilia **:** Romeriida + *.

Comments: More basal than *Paleothyris* , according to Müller & Reisz 2006. MAK101001

Romeriida *Paleothyris* + Diapsids



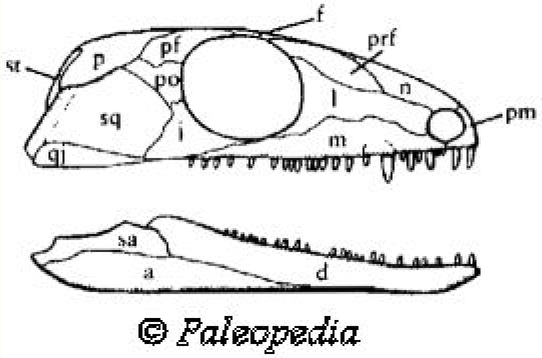
Range: Late Carboniferous to Recent.

Phylogeny: Eureptilia **:** Captorhinidae + * **:** *Paleothyris* + Diapsida.

Characters: separation of the tabular bone from the opisthotic bone, ventrally keeled anterior pleurocentra, long and slender carpi and tarsi, and overlapping metapodials.

Comments: Phylogenetically defined by Laurin & Reisz 1995 as the last common ancestor of *Paleothyris* and diapsids, and all its descendants.. It is named after Alfred Sherwood Romer. Protorothyridids were once placed in the family Romeriidae along with the captorhinid *Romeria*. Because *Romeria* is now considered to be a captorhinid, and Captorhinidae is placed outside of Romeriida, the genus is excluded from the clade. Recent studies have proposed that

Protorothyrididae is a paraphyletic taxon (Müller & Reisz 2006). Therefore, it is possible that many protorothyridids do not lay within the clade Romeriida. Smokeybjb 091231 (text and image from Wikipedia)



Paleothyris *Paleothyris acadiana* Carroll 1969

Range: Middle Pennsylvanianof Nova Scotia.

Phylogeny: Romeriida **:** Diapsida + *.

Characters: Postorbital far from occiput, Parasphenoid teeth present, Trunk neural arches narrow Humerus long and slender (Laurin & Reisz 1995 p.203) (generic protorothyrid characteristics) Increase in the strength of the jaws when compared with basal tetrapods. Pterygoideus supplements the adductors in pulling the jaw up and forward Palatal teeth small, perhaps role was to to hold food, tongue may have been toughened on the upper surface to work against palatal teeth. Stapes heavy as in basal tetrapods, so hearing probably limited to low frequency vibrations. There was no otic notch and hence no tympanium. (all these features were typical no doubt for protorothyrids and basal eureptiles as a whole) (Benton, 2000, pp.104-5)

Comments: Skull better known than that of *Hylonomus* (Benton, 2000, p.104). May have been nocturnal. Laurin & Reisz 1995 used *Paleothyris* instead of Protorothyrididae because the latter is poorly defined and paraphyletic.

Links: Wikipedia, Paleothyris - Prehistoric Land Reptiles MAK101001

Image from Paleopedia - Cotylosaurs

Hylonomus Hylonomus lyelli

Range: Early Pennsylvanian epoch in Nova Scotia.

Phylogeny: Romeriida **:::** (*Protorothyris* + Diapsida) + *.

Comments: Earliest known Sauropsid, but not the most primitive reptile. This implies that reptilian evolution had already been underway several millions of years.

Links: Paeobiology database, Wikipedia MAK101001

Protorothyris: *Protorothyris archeri*, *Protorothyris morani*

Range: Early Permian of Texas and West Virginia.

Phylogeny: Romeriida **:::** Diapsida + *.

Characters: tabular (which has been lost in *Captorhinus*, this would have had no effect on the adductor muscles from inside the skull roof) limited to the occiput and rested without sutural attachment upon the squamosal. In early works this is part of the morphological sequence, *Protorothyris—Romeria—Captorhinus* (Fox, 1964), in cladistic analysies the sequence goes the other way, with Captorhinids more basal. (Laurin & Reisz 1995; Muller & Reisz 2006.

Links: Paeobiology database, Wikipedia MAK101001

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Eureptilia: Captorhinomorpha: Classification

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
          |   `--Captorhinidae
          |     |--Concordia
          |     `--+--Romeria
          |        `--+--Captorhinus
          |            `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

Contents

The following rather hasty classification scheme uses Linnean taxonomy and is modified from Carroll 1988, For the cladistic equivalent, see the dendrogram page MAK120317

Subclass Anapsida Osborn, 1903 (= Anapsida Williston, 1917) [1]
 Order Captorhinomorpha Carroll & Baird, 1972 [2] primitive, lizard-like Permo-Carboniferous reptiles
  Family Protorothyrididae Price, 1937 primitive persistantly conservative lizard-like types, Mid Carb to Early Perm, Eur & N Am
   Family Captorhinidae Case, 1911 small to large insectivorous to herbivourous forms with triangular heads and downturned premaxillae, Late Carb to Late Perm of N Am, EEur, Afr, EAs
    Subfamily "Captorhininae" paraphyletic assemblage of small, primitive, mainly single-tooth-rowed forms which resemble other generalized amniotes, Late Carb to Late Perm of N Am, EEur, Afr
    Subfamily Moradisaurinae Ricql�s and Taquet 1982 large, highly derived, herbivorous forms, Mid to Late Perm of N Am, EEur, Afr, EAs

---

Notes

[1] as paraphyletic stem taxon sensu Carroll, not a monophyletic clade sensu Gauthier, Resiz, etc. Replaces the "Cotylosauria" of Romer, Colbert, etc

[2] Carroll's doubly paraphyletic Captorhinida is here rejected; and the families Bolosauridae and Acleistorhinidae previously included under the Captorhinomorpha are included under the Anapsida proper

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Eureptilia: Dendrogram

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
          |    `--Captorhinidae
          |       |--Concordia
          |       `--+--Romeria
          |          `--+--Captorhinus
          |             `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

Contents

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   `--o Eureptilia
      |--Coelostegus
      `--+--+--Thuringothyris
         |  `--o  Captorhinidae MH
         |     |--Concordia
         |     `--+--Romeria
         |        `--+--Protocaptorhinus
         |           `--+--Rhiodenticulatus
         |              `--+--Saurorictus
         |                 |?- Acrodenta
         |                 |?- Baeotherates
         |                 `--+--o Captorhinus
         |                    `--+--Captorhinikos
         |                       `--+--Labidosaurus
         |                          `--o Moradisaurinae
         |                             |--Labidosaurikos
         |                             `--+--Gecatogomphius
         |                                |--Kahneria
         |                                |?- Rothianiscus
         |                                `--Moradisaurus
         `--+--Brouffia
            `--o Romeriida
               `--+--Paleothyris
                  `--+--Hylonomus
                     `--+--Protorothyrididae MH
                        |  |--Anthracodromeus
                        |  |--Cephalerpeton
                        |  `--Protorothyris
                        `--DIAPSIDA MH, ToL
```

---

checked ATW050512

Eureptilia: References

Abreviated Dendrogram

```
AMNIOTA
|--SYNAPSIDA
`--+--ANAPSIDA
   |
   `--EUREPTILIA
      |--Coelostegus
      `--+--+--Thuringothyris
         |  `--Captorhinidae
          |     |--Concordia
          |     `--+--Romeria
          |        `--+--Captorhinus
          |            `--Moradisaurinae
          `--+--Brouffia
            `--Romeriida
               |--Paleothyris
               `--+--Hylonomus
                  `--+--Protorothyrididae
                     `--DIAPSIDA
```

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- Eureptilia
- Captorhinidae
- Protorothyrididae
- Classification
- Dendrogram
- References

Benton, M.J. 2000. *Vertebrate palaeontology*. 2nd ed.
Protorothyris

Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. WH Freeman and Company, New York
Classification

Cox, B, RJG Savage, B Gardiner, & D Dixon (1988), **Collins Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals**. Collins Publ. Aus., 312 pp. Eureptilia

deBraga, M & O Rieppel (1997), *Reptile phylogeny and the interrelationships of turtles*, **Zool. J. Linnean Soc.** 120: 281-354. Neodiapsida.

deBraga, Michael; and Reisz, Robert R. (1995). "A new diapsid reptile from the uppermost Carboniferous (Stephanian) of Kansas". *Palaeontology* 38 (1): 199�212. pdf

Fox, R.F., 1964. The Adductor Muscles of the Jaw in Some Primitive Reptiles. University of Kansas, Lawrence. Project Gutenburg Protorothyris

Laurin, M. & Reisz, R.R. (1995) A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society* , 113: 165�223. pdf
Paleothyris, Romeriida

M�ller, J & RR Reisz (2005), *An early captorhinid reptile (Amniota: Eureptilia) from the Upper Carboniferous of Hamilton, Kansas*. **J. Vert. Paleontol.** 23: 561-568.
Captorhinidae, *Concordia*, Eureptilia.

Muller, J. & Reisz, R.R. 2006. The Phylogeny of Early Eureptiles: Comparing Parsimony and Bayesian Approaches in the Investigation of a Basal Fossil Clade. *Syst. Biol*. 55(3):503-511, html/pdf
Coelostegus, *Brouffia*, *Paleothyris*, *Thuringothyris*

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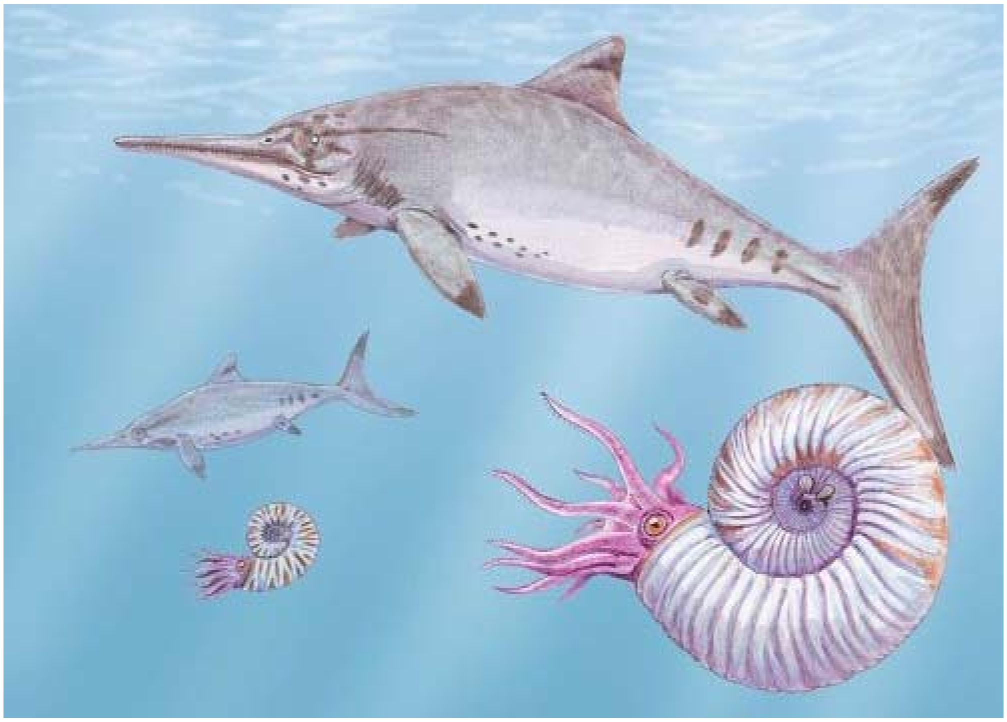
MAK101001

Ichthyosauria: Overview

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                 `--+--Parvipelvia
   |                    |--Eurhinosauria
   |                    `--+--Thunnosauria
   |                       `--Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Contents



The advanced Ichthyosaur *Ophthalmosaurus yasikovi* (with ammonites), from the Late Jurassic of Central Laurasia
Artwork by Dmitry Bogdanov (wikimedia)

Introduction

Benjamin Waterhouse Hawkins' lifesize model of *Ichthyosaurus*, one of a number of sculptures of prehistoric animals that accompanied the renovated Crystal Palace, and were made in collaboration with Richard Owen and other leading scientific figures of the time. Unveiled in 1854, these were the first ever life-sized models of extinct animals. Compare with the more realistic reconstruction above. Ironically, Hawkins' sculpture provides a not unreasonable representation of the more basal, eel- or serpent-like, early to middle Triassic Ichthyosaurs (although obviously the bony ring supporting the eyeball would not be visible in the living animal). (wikimedia).

The Ichthyosaurs ("fish lizards") were a very successful group of air-breathing Mesozoic marine reptiles that bore an uncanny resemblance to modern day (late Cenozoic) dolphins. Along with the plesiosaurs, the ichthyosaurs were among the first Mesozoic reptiles to be discovered, and the two groups of "antediluvian monsters" had a strong effect on the 19th century Victorian imagination (*right*). (Glendening, 2009)

Ichthyosaurs were very diverse early in their history (during the Triassic period), where they began as smallish (~1 m) elongate eel-like swimmers but soon evolved into the largest marine reptiles that ever lived (up to 15 to 20 meters and more - the size of whales). These Triassic ichthyosaurs were very different ecologically from their Jurassic descendants, mostly longer bodied with long, broad tails. They probably tended to be ambush predators with more generalized prey preference, as shown by the heterodonty (different tooth sizes and shapes) in many Early and Middle Triassic species. (Massare & Callaway 1990)

During the late Triassic they developed their familiar deep, streamlined bodies and lunate tails, and this morphotype continued through the Jurassic and Cretaceous. These ichthyosaurs were mainly pursuit predators, altthough transitional forms like the giant toothless *Shonisaurus* were relatively slow moving and probably fed on cephalopods (Nicholls & Makoto 2004). The late Triassic and early Jurassic were the high points of the Ichthyosaur reign. The Toarcian turnover seems to have affected them heavily and only a single clade made it through to the middle Jurassic, the very succesful Ophthalmosaurs. Although the Ichthyosaurs straggled on to the mid Cretaceous (Cenomanian age) they never regained their previous dominance, there place as top marine predator being taken by large pliosaurs. and later mosasaurs

Despite their dolphin-like form, ichthyosaurs lacked the stamina of modern marine mammals. They were sprinters, not endurance swimmers, with a typically reptilian metabolism. The reason for their decline may have been tied up with an inability to keep up with the new fast swimming Teleost fish that appeared during the Jurassic, or perhaps also faster belemnite cephalopods. The Cretaceous *Platypterygius* however seems to have been a more opportunist feeder (Kear et al 2003).

Being so fish-like in form, ichthyosaurs could not crawl up onto the land to lay their eggs. Instead, the eggs remained in the mother until they hatched. She then gave birth to live young. Skeletons of baby ichthyosaurs have been found inside the skeletons of adults. MAK991007, 100925.

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Ichthyosauria

Ancestral Ichthyosaurs

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |    `--o Ichthyopterygia / ICHTHYOSAURIA
   |        |--Utatsusaurus
   |        `--+--Grippidia
   |           `--+--Ichthyosauria
   |              `--+--Merriamosauria
   |                 `--+--Euichthyosauria
   |                    `--+--Parvipelvia
   |                       |--Eurhinosauria
   |                       `--+--Thunnosauria
   |                          `-
-Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Contents

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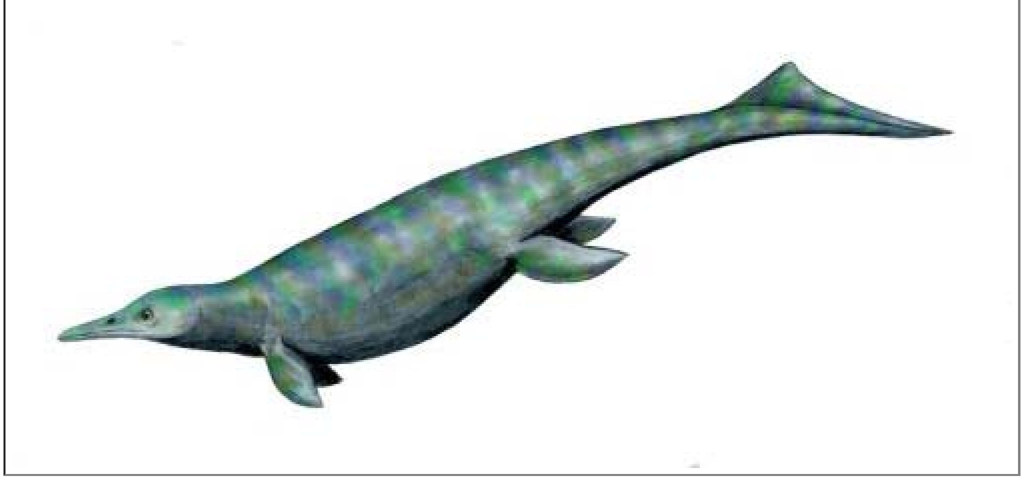
1. Grippidia X
2. Ichthyopterygia X
3. *Utatsusaurus* X



Utatsusaurus hataii, an Early Triassic Ichthyosaur from Japan
illustration by Nobu Tamura (Wikipedia)

Ancestral Ichthyosaurs

Ichthyopterygia ("fish flippers") was a designation introduced by Sir Richard Owen in 1840 to designate the Jurassic Ichthyosaurs that were known at the time, but the term is now used more often for both true Ichthyosauria and their more primitive early and middle Triassic ancestors (Motani 1997, Motani et al. 1998, Motani 1999b).

Basal Ichthyopterygians (prior to and ancestral to true Ichthyosauria) were mostly small (a meter or less in length) with elongate bodies and long spool shaped vertebrae, indicating that they swam in a sinuous eel-like manner. This allowed for quick movements and maneouverability that were an advantage in shallow-water hunting (Motani 2000). Even at this early stage they were already very specialised animals with proper flippers, and would have been incapable of movement on land.

These animals seem to have been widely distributed around the coast of the northern half of Pangea, as they are known the Late Olenekian and Early Anisian of Japan, China, Canada, and Spitsbergen (Norway). By the later part of the Middle Triassic they were extinct, having been replaced by their descendents, the true ichthyosaurs. MAK060529 (Wikipedia)

Descriptions

Ichthyopterygia:

Range: Early Triassic to Late Cretaceous

Phylogeny: Neodiapsida:::: Sauria + *: *Utatsusaurus* + (Grippidia + Ichthyosauria)

Characters: euryapsid skull; primitive tooth implantation probably subthecodont [M97]; replacement teeth outside pulp cavity [M97]; uniquely down-turned vertebral column that enters the lower lobe of its caudal fin; flippers for limb; live birth.

Links: Dinosauricon; JVP; Notes; CVA; Wikipedia, Ichthyosaurs.

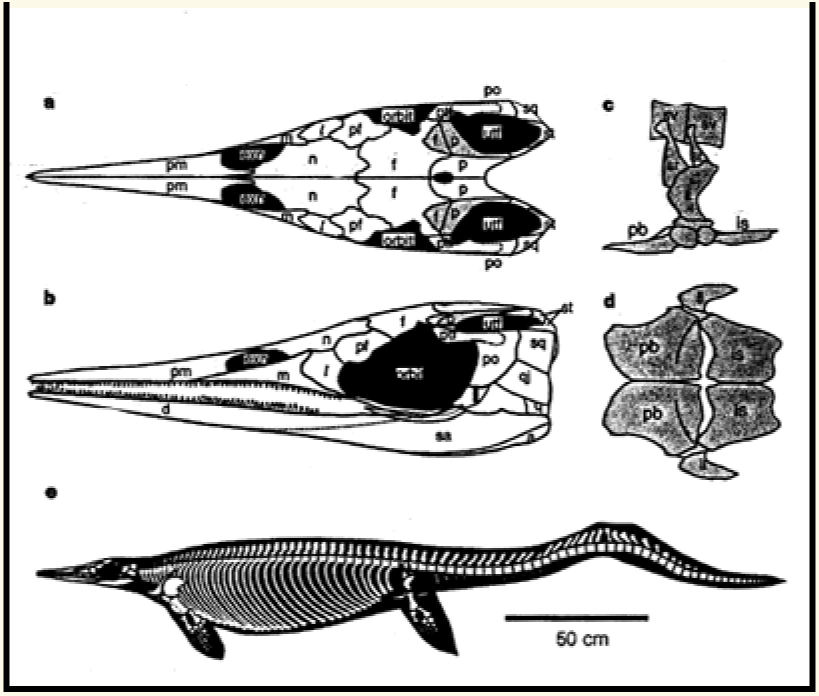


Image: *Utatsusaurus* from [M+98].

References: Motani (1997) [M97]; Motani *et al*. (1998) (M+98) (image). ATW020518.

Utatsusaurus:

Range: Early Triassic of Japan & Canada

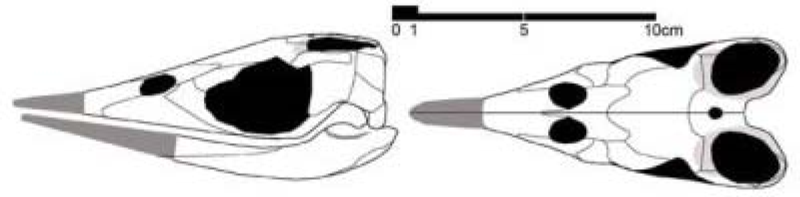
Phylogeny: Ichthyopterygia: (Grippidia + Ichthyosauria) + *.

Utatsusaurus from Fossil Gallery. Note that the forelimbs show a characteristic ichthyosaur pattern of polyphalangy, but are very small. The dorsal vertebrae are narrow and relatively long.

Characters: 1.4 - 3.0 m "lizard with flippers"; lower temporal fenestra absent [M+98]; tooth implantation pleurodont anteriorly, shifting to subthecodont [M97]; replacement teeth are lingodistal to functional tooth [M97]; tooth roots expanded [M97]; body relatively long and thin; about 40 small diameter, cylindrical vertebrae (undulatory swimming) [M+98]; 2 well-defined sacral (but transversely thin and weakly articulated with ilium) ribs with distal expansion [M+98]; sacral ribs not fused to vertebrae [M+98]; small flippers; humerus & femur of equal length [M+98]; hindlimb larger than forelimb [M+98]; restricted to continental shelf

Links: Fish-lizards; Fossil Gallery; JVP; Utatsusaurus; Utatsusaurus (Japanese); Ordnung der Ichthyosauria (German -- probably an excellent page); Tohoku MNH; Yamagata (Japanese: excellent photo); Utatsusaurus ??????? ???? (Japanese models); ??????? (Korean); 05.20.98 - UC Berkeley study establishes that extinct ... (press release); The Journal of Vertebrate Paleontology (abstract); Scientific American- Feature Article- Rulers of the Jurassic Seas ... (also in Polish); 07.15.98 - "Fish-Lizards" Turn Out to Be More Lizard than Fish (press release); The Journal of Vertebrate Paleontology (another abstract); ?? (fossil); Dan Varner Paleo-Life Art (Dan's image of *Utatsusaurus*); ???.

References: Motani (1997) [M97]; Motani *et al*. (1998) (M+98) ATW030203.



Grippidia: *Chaohusaurus* (= *Chensaurus*), *Grippia*

Range: Early Triassic of Greenland, China, etc.

Phylogeny: Ichthyopterygia:: Ichthyosauria + *.

Characters: <1 m?; lacrimal excluded from nares

[C97]; relatively large upper temporal fenestra [C97]; postorbital participates in upper temporal fenestra (primitive) [C97]; tooth implantation subthecodont [M97]; replacement teeth lingodistal [M97]; tooth roots expanded [M97]; dentition, vertebral number & form similar to *Utatsusaurus*; humerus longer than femur (as in all other ichthyopterygians) [M+98].

Image: David Peters - Reptile Evolution.

Links: Eyes; JVP; JVP.

References: Callaway (1997) [C97]; Motani (1997) [M97]; Motani *et al*. (1998) [M+98]. ATW021024

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Ichthyosauria: Mixosaurs and Cymbospondyls

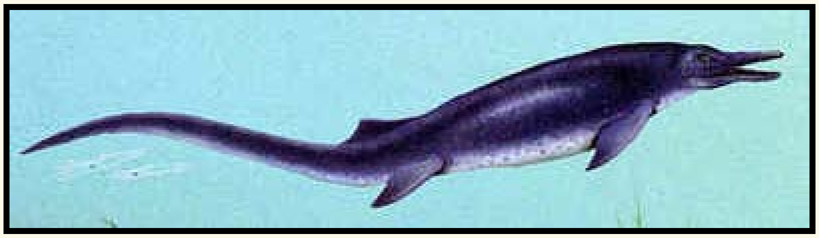
Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |            `--+--Cymbospondylus
   |               `--+--Mixosaurus
   |                  `--+--Merriamosauria
   |                     `--+--Euichthyosauria
   |                        `--+--Parvipelvia
   |                           `--Thunnosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Taxa on this Page

1. *Cymbospondylus* X
2. Ichthyosauria X
3. *Mixosaurus* X

Mixosaurs and Cymbospondyls



The most primitive forms, *Utatsusaurus* and other basal ichthyopterygians, are discussed on the previous page. Ichthyosauria, strictly speaking, are *Cymbospondylus* + *Ichthyosaurus*. ***Cymbospondylus*** is traditionally included in the Shastasauria. However, in the phylogenetic arrangement of Ryosuke Motani (adopted here) this genus is shown to be much more primitive, even more primitive than the Mixosaurs. Probably *Cymbospondylus* belongs in its own family ("Cymbospondylidae").

Cymbospondylus had a very elongate body, and the head, although large taken in isolation, was unusually small relative to the overall body. As befits its primitive status, *Cymbospondylus* lacked the familiar dorsal fin on its back and had only a very slight tail kink. It did however have the typical ichthyosaur pointed teeth in the long, beak-like jaws. MAK990620.

Mixosaurus includes several species of small creatures about a meter in length. They are among the earliest and most primitive of the Ichthyosaurs and were the sister group of the more derived merriamosaurs. *Mixosaurus* remained more reptilian than fishlike in appearance, though with flippers and a small fin on the tail. It also had a small dorsal fin on the back. *Mixosaurus* was morphologically intermediate between *Cymbospondylus* and more advanced Triassic Ichthyosaurs, such as the shastasaurs. The two lineages, the mixosaurs and *Cymbospondylus*, actually coexisted for some ten million or so years, along with other, even more basal early ichthyosaurs such as *Hupehsuchus* and *Parvenator*. MAK990620.

Descriptions

Ichthyosauria:

Range: Early Triassic to Late Cretaceous

Phylogeny: Ichthyopterygia:: Grippidia + *. *Cymbospondylus* + (*Mixosaurus* + Merriamosauria)

Characters: Spindle-shaped body, 0.7-15.0 m; lacrimal participates in nares in most forms, but perhaps not primitive for group [C97]; largest orbit of any animal (up to 26 cm); often substantial sclerotic rings [C97]; postorbital does not participate in upper temporal fenestra [C97]; reduced cheek; strong upper temporal fenestra, but lower fenestra lost except in most basal species; supratemporal probably present primitively, but lost in many derived forms [C97a]; quadratojugal present primitively [C97]; teeth in long groove without separate alveoli in later forms; vertebral centra very short & deeply amphicoelous; neural arches separated from centra and without transverse processes(?); caudal fin in J-K species; manus 1 absent, but 2 neomorphic digits in some advanced forms; polydactyly in some, polyphalangy common and very well-developed; length of phalanges reduced; forelimbs used for steering, not propulsion; pelvic girdle not attached to spine (except *Shonisaurus* of the Middle Triassic); limbs reduced to steering fins; viviparous; diet varies, but squids probably common.

Links: Ichthyosaur Page Home (English & Japanese); Ichthyopterygia -- The Dinosauricon; Introduction to the Ichthyosauria; ucmp berkeley museum ab24; Ichthyosaur- Enchanted Learning Software; order61.htm; Ichthyosaur fossil discovery at Charmouth Dorset UK. (after Ryosuke Motani's page, perhaps the most useful site); Kleiner Museumsrundgang (German); Faktasider om marine øgler (Norwegian); Senckenberg Fossile Wirbeltiere der Meere (German); Marine Reptiles (NOT Dinosaurs); ICHTHYOSAURIA; Rolex Awards for Enterprise - Laureates; Water Reptiles of the Past and Present; The Fernleaf: Karen Carr; The Fernleaf: Karen Carr; Wikipedia.

Note: Phylogenetic position still controversial. There has been a good deal of activity recently, both generally at the base of the diapsids and, specifically, in Ichthyosaur phylogeny. In particular the "Ichthyopterygia" name has been dusted off and retooled to cover *Hupehsuchus, Grippia,* and a few others.

References: Callaway (1997) [C97]; Callaway (1997a) [C97a] . ATW020515

Cymbospondylus:

Range: Middle Triassic to Late Triassic of North & South America, China & Europe.

Phylogeny: Ichthyosauria: (*Mixosaurus* + Merriamosauria) +

*.

Characters: ~10 m; small head; elongate, longirostrine jaws; relatively small orbits [C97]; tooth implantation thecodont, but with ankylosis at bottom of socket [M97]; replacement teeth lingual of functional teeth [M97]; tooth roots not expanded [M97]; rib articulations as in shastasaurs [S97]; diapophysis makes contact with the anterior margin of centrum in dorsal vertebrae [S97]; caudal "fins" absent; paddles short.

Comments: Originally included under the Shastosauridae. Cladistic analysis by Motani 1999b shows *Cymbospondylus* to be more basal not only relatrive to shastasaurs but even to mixosaurs, whereas in Sander's (2000) analysis *Cymbospondylus* is a shastasaur, and the sister-taxon to *Besanosaurus*. However, study of the braincase of the closely related Phantomosaurus shows it to be the most plesiomorphic (primitive, non-specialised) ichthyosaur braincase currently known (Maisch & Matzke 2006), which supports the primitive status of these animals.; sim9ilarities with shastasaurs being the result of convergence (large, elongate, marine animals) and shared primitive characteristics.

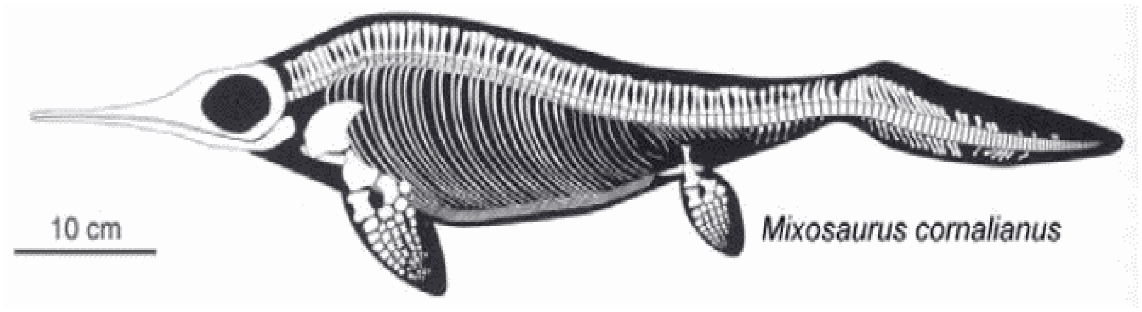
Links: Cymbospondylus; Dinosaurios; Kleiner Museumsrundgang; Dinolist; Buena Vista Museum; BBC - Sea Monsters - *Cymbospondylus*; Wikipedia.

References: Callaway (1997) [C97], Motani (1997) [M97]; Sander (1997) [S97]. ATW020515

Mixosaurus: *Mixosaurus* (= *Phalarodon*, *Sangiorgiosaurus*, *Contectopalatus* all per [C97])

Range: Middle Triassic of Europe & China (Tethys Sea), North America, New Zealand. [C97].

Phylogeny: Ichthyosauria:: Merriamosauria + *.



Mixosaurus cornalianus, Middle Triassic, Italy and Switzerland, representing the basal ichthyosaur type. Length about a meter. The kink indicates there was probably a small dorsal tail fluke. In contrast to most earlier and later ichthyosaurs, the paddles are of the short, broad "latipinnate" type (convergent with the Thunnosauria). From McGowan and Motani, 2003

Characters: ~1 m; maxilla large (primitive) [C97]; elongated preorbital skull [C97]; lacrimal excluded from nares [C97]; frontals & nasal roughly equal size (primitive) [C97]; upper temporal fenestra very small [C97]; orbit large [C97]; postorbital cheek region very short [C97]; supratemporal present [C97a]; quadratojugal retained (primitive) [C97]; pterygoid transverse process absent in some specimens [C97]; dentition ankylosed thecodont [C97], but subthecodont anteriorly [M97]; tooth roots not expanded [M97]; rib articulations uncertain [S97]; gastralia present & well-developed, forming tightly-knit plastron [C97]; dorsal fin present; caudal "fin" little developed; scapula & coracoid very similar, coracoid less symmetrical and having sickle-shaped extension [C97]; short forefin; 4+ (5?) digits on all extremities [S97]; primitive broad, plate-like pubis & ischium [C97]; ilium short & distally broad [C97]; found in deeper waters than, e.g. nothosaurs.

Links: Treasures of the Earth Ltd. Mixosaurus Page.; Buena Vista Museum Of Natural History - Ichthyosaurs In Kern County; Fossilien aus dem Muschelkalk des Kraichgaus (German. Nice life paining & photos of vertebrae); Paleontology and Geology Glossary: Mi; Dinosaurios: Mixosaurus (Spanish); Marine Reptiles: Ichthyosaur: Mixosaurus; Kleiner Museumsrundgang (German, with photo of fossil); DinoNet - Senhores dos Mares - ICTIOSSAUROS (Portuguese); ??2 -

Mixosaurus cornalianus, photo by Ghedoghedo (Wikipedia). Another specimen. This common species is the only Triassic ichthyosaur for which complete articulated skeletons are known (Motani 1999c).

Fishes2 (detailed pictures of poorly prepared specimens); Saurier aus der Mitteltrias des Monte San Giorgio (German, with very good picture of beautifully prepared specimen); forelasning7.pdf (Swedish -- I think); Ichthyosaur wars and marvellous mixosaurs (Darren Naish); Wikipedia

References: Callaway (1997) [C97]; Callaway (1997a) [C97a]; Motani (1997) [M97]; Sander (1997) [S97]. ATW020516.

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Ichthyosauria: Shastasaurs and basal Euichthyosaurs

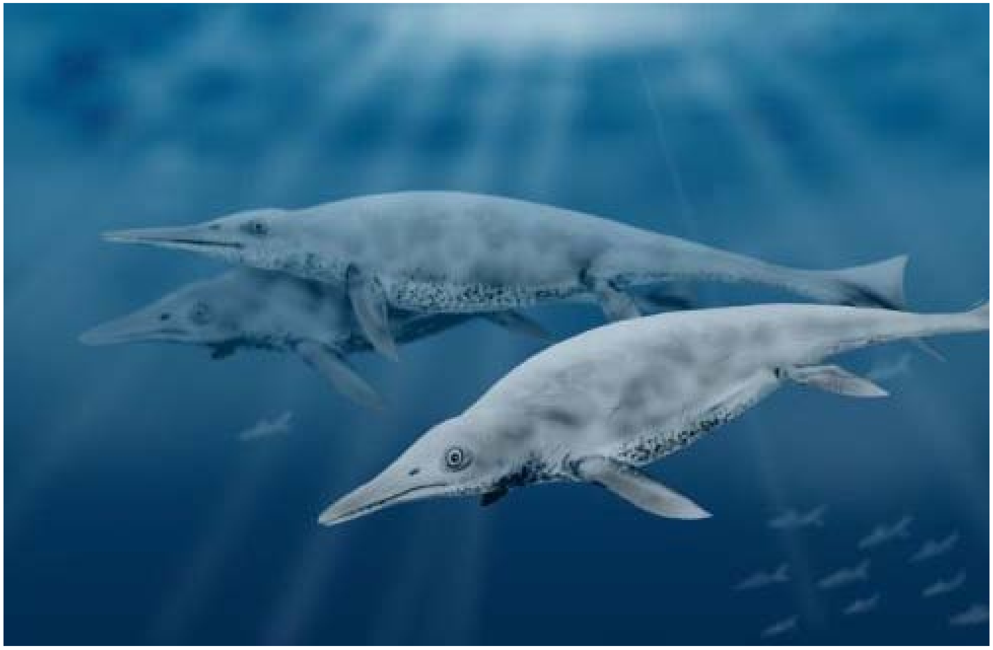
Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--Merriamosauria = Shastasauria
   |               |--Besanosaurus
   |               `--+--Shonisaurus
   |                   |--o Shastasaurus
   |                   |  |--S. sikkanniensis
   |                   |  `--+--S. liangae
   |                   |      `--S. pacificus
   |                   `-- o Euichthyosauria
   |                        `--+--Californosaurus
   |                           `--+--Callawayia /
Metashastasaurus
   |                               `--+-
-Parvipelvia
   |                                   `--
Thunnosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Overview
Ancestral Ichthyosaurs
Mixosaurs and Cymbospondyls
Shastasaurs and basal Euichthyosaurs
Temnodontosaurs and Eurhinosaurs
Thunnosaurs
Ophthalmosaurs
Dendrogram
References

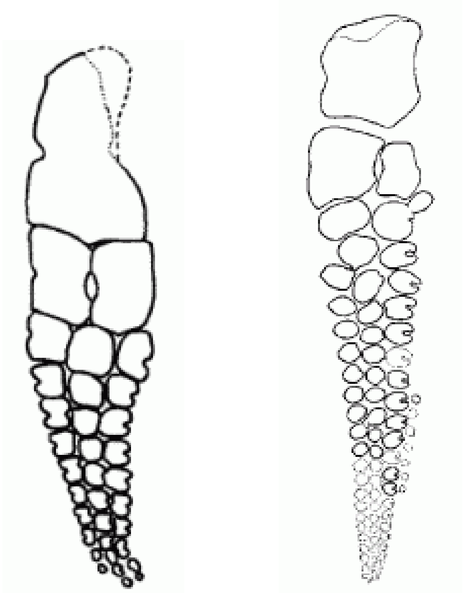
Taxa on this Page

1. *Besanosaurus* X
2. *Californosaurus* X
3. *Callawayia* / *Metashastasaurus* X
4. Euichthyosauria X
5. Merriamosauria X
6. Shastasauria X
7. *Shastasaurus* X
8. *Shastasaurus liangae* X
9. *Shastasaurus pacificus* X
10. *Shastasaurus sikanniensis* X
11. *Shonisaurus* X



Shastasaurus pacificus, an ichthyosaur from the Late Triassic of California and Mexico, illustration by Nobu Tamura (Wikipedia). Length of original animal about 7 meters. Based on related species, it is now considered that these animals had shorter snouts. Nevertheless, the above is very representative of the typical shastasaur type

Shastasaurs and basal Euichthyosaurs



Forefin of *Toretocnemus zitteli*, from Merriam 1908 (left) and *Shonisaurus popularis*, from Camp 1980 (right) (both via Maisch & Matzke 2000). In contrast to both the earlier Ichthyosaur and later Thunnosaur conditions, the flipper is very long, with only three digits/fingers (both the thumb and little finger are lost). *Californosaurus* and *Callawayia* seem to have been very similar. In more advanced ichthyosaurs (Parvipelvia and Thunnosauria, additional digits are added, broadening the fin.

Between the more primitive and elongate, serpentine-like basal ichthyosaurs of the early and middle Triassic, and the fully fish- and dolphin-like Jurassic and Cretaceous forms, are a number of intermediate types which in older books were classified as Shastasauridae, and which flourished during the later Triassic (specifically the Carnian and Norian ages). These represent an important and diverse assemblage that in the past have understandably been neglected in favour of the more famous and beautifully preserved Liassic (Early Jurassic) forms from England and Germany. But the discovery of many new Triassic forms, and cladistic analysis of both Triassic and Jurassic types, has created new interest in these earlier "fish lizards".

For the most part, these late Triassic (which all belong to the clade Merriamosauria) are intermediate in form between the sinuous and more typically reptilian early and middle Triassic species, and the fish and dolphin like latest Triassic (Rhaetian) and Jurassic and Cretaceous types. However, in contrast to their mixosaur ancestors (who had short broad fins), these late Triassic Merriamosaurs all had paddles of the elongate, "longipinnate" type (see right), usually with only three digits (fingers/toes) but each having a great many phalanges (finger/toe bones). For a long time this was used as a basis for classification ((e.g. Lydekker, 1888; von Huene 1922; McGowan 1972), and ichthyosaurs divided into latipinnate and longipinnate types, the former including Mixosaurs and most of what are now called Thunnasaurs (*Stenopterygius*, *Ichthyosaurus*, and the Ophthalmosaurs), and the latter the rest. It was thought therefore that the Triassic -Mixosaurs evolved into the broad-finned Jurassic types, and the Shatsasaurs (including

Cymbospondylus) into the narrow-finned Jurassic genera. However, this classification is no longer used, and it has been shown that *Mixosaurus* is much closer to *Cymbospondylus* (both being basal forms), whilst latipinnate and longipinnate ichthyosaurs likewise are closely related. The latipinnate Ophthalmosaurs even include a longipinnate genus, *Platypterygius*

As the following dendrograms show however, there is some disagreement over whether the Shastasaurs and basal Euichthyosaurs constitute two main clades and lines of Triassic Merriamosaur evolution, or a single series of transitional forms. In any case, the Shastasaurs did not outlive the Triassic, whilst the the Euichthyosaurs evolved into (and cladistically include) the more "typical" Jurassic ichthyosaurs. Several alternative dendrograms are given below:

```
--+--Utatsusaurus
  `--+--Grippidia
     `--+--Cymbospondylus
        `--+--Mixosaurus
           `--o Shastasauria
              |--o Merriamosauria
              |  |--Besanosaurus
              |  `--+--Shastasaurus
              |     `--Shonisaurus
              `-- o Euichthyosauria
                   `--+--Californosaurus
                      `--+-- Parvipelvia
                         `-- Thunnosauria
```

Motani 1999b (only selected genera shown)

```
--+--Utatsusaurus
  `--+--Grippidia
     `--+--Cymbospondylus
        `--+--Mixosaurus
           `--+--Besanosaurus
              `--+--Shastasaurus
                 `--+-
-Shonisaurus
                    `--+-
-Californosaurus
                       `--+-
-Callawayia (= Metashastasaurus)
                          `--+-
-Parvipelvia
                             `-
-Thunnosauria
```

Maisch & Matzke 2000 (only selected genera shown)

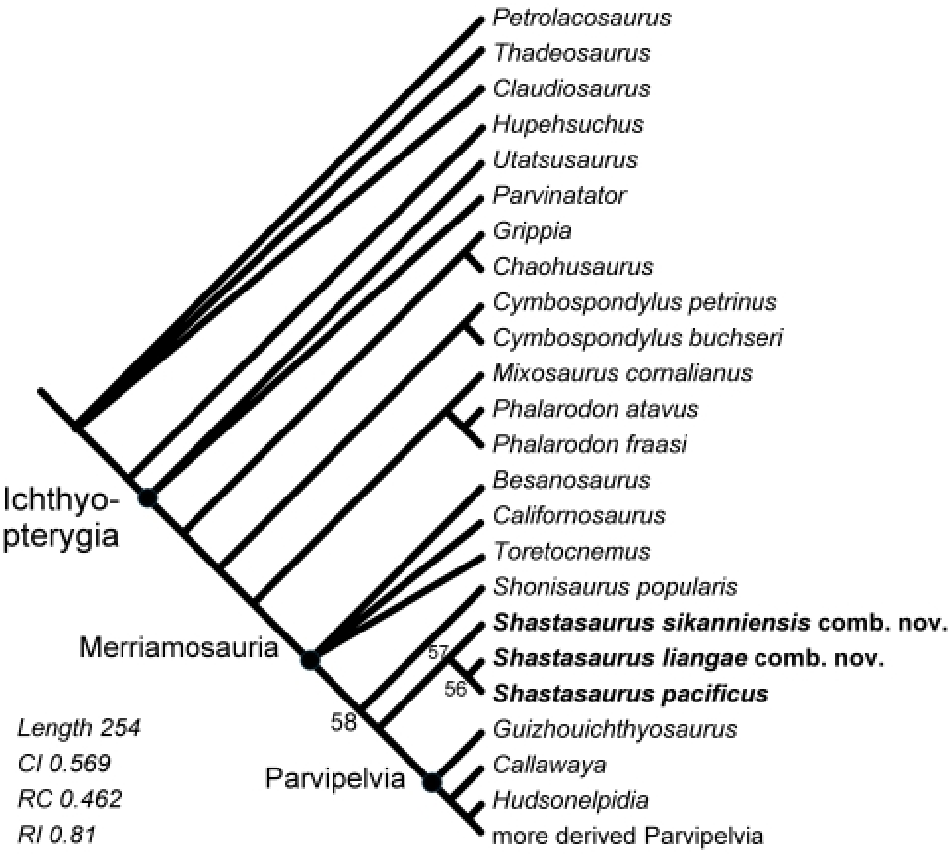
```
--+--Utatsusaurus
  `--+--+--Grippidia
     |  `--+--Mixosaurus
     |     `--+--Cymbospondylus
     |        `--+--Besanosaurus
     |           `--+--Shastasaurus
     |              `--+--Shonisaurus
     |                 `-- Metashastasaurus (= Callawayia)
     `--Parvipelvia (advanced forms)
```

Nicholls & Manabe, 2001 (only selected genera shown) found a monophyletic Shastasauridae, with *Mixosaurus* and *Cymbospondylus* as successive sister taxa to *Besanosaurus* + (*Shastasaurus* + (*Shonisaurus* + *Metashastasaurus*)). I don't have a copy of the original paper so I am not sure if *Mixosaurus* and *Cymbospondylus* are in the right position in the above cladogram.

```
--+--Utatsusauridae
  `--+--Grippidia
     `--+--Cymbospondylidae
        `--+--Mixosauria
           `--+--Besanosauridae
              `--+--Shastasauria
                 |  |-
-Shastasaurus
                 |  `-
-Shonisaurus
                 `--+-
-Californosauridae
                    `--+-
-Parvipelvia
                       `-
-Thunnosauria
```

McGowan & Motani, 2003 - based on taxonomy in table of contents (here refernce is made to supra-generic taxa, but otherwise the arrangement is the same)

The cladogram on the left is from Sander et al 2011 and reproduced under the Creative Commons Attribution License of the original paper. It represents the strict consensus (and hence most reliable but lowest resolution) of 72 most parsimonious trees. The three species of *Shastasaurus* are shown in bold. Note the paraphyletic nature of the Shastasauria. Interestingly, *Californosaurus* is here placed as more basal rather than crownward. The enigmatic Hupehsuchia



here appear as stem ichthyopterygia. MAK111123

Regardless of which hypothesis is preferred, the shastasaurs, like their predecessors the Cymbospondyls attained very large size. In the case of the Shonisaurs they became much larger, and in advanced forms less sea-serpent like and more stocky and deep bodied then is the case with *Cymbospondylus*. Here we see an example of convergent or parallel evolution with the toothed whales of the Cenozoic oceans; although in the rapid evolutionary tendency to huge size there is a similarity with the baleen whales, which likewise grew from medium-sized to enormous creatures in the space of some five or ten-odd million years (Miocene-Pliocene). Reaching lengths of 10 to 23 meters, and with bodies that were quite deep and sturdy, the shonisaurs were not only the largest ichthyosaurs, but also among the largest of the marine animals of the Mesozoic. These giant ichthyosaurs, which were far larger than any of the contemporary Triassic land-living archosauromorphs and early dinosaurs, would have lived a lifestyle much like that of the present day toothed whales, feeding primarily on cephalopods. They were probably slow swimmers, rowing themselves slowly along with their long paddle-like limbs. MAK100925

Descriptions

Merriamosauria:

Phylogentic definition: last common ancestor of *Shastasaurus pacificus* and *Ichthyosaurus* and all of its descendants (Motani 1999b), amended by Maisch & Matzke 2000 to last common ancestor of *Besanosaurus leptorhynchus* and *Ichthyosaurus communis* and all of its descendants.

Phylogeny: Ichthyosauria :: *Mixosaurus* + *: Shastasauria + Euichthyosauria.

Range: Middle Triassic to Late Cretaceous. Mostly Late Triassic and Jurassic forms.

Characters: tooth implantation aulacodont except in *Shonisaurus* (Shastasauria), which has unique implantation like *Cymbospondylus* [M97]; tooth roots not expanded [M97]. ATW020516

Links: Eyes. ATW020516.

References: Motani (1997) [M97].

Shastasauria: (= Shastasauridae) *Besanosaurus*, *Himalayasaurus*, *Metashastasaurus*, *Shastasaurus*, *Shonisaurus*.

Range: Early? Triassic to Late Triassic of Japan, China and North America

Phylogeny: *either* Merriamosauria: Euichthyosauria + * **:** Besanosaurus + (*Shastasaurus* + *Shonisaurus*) (monophyletic clade, according to Motani 1999b and Nicholls & Manabe, 2001)
or Merriamosauria **:** Besanosaurus + (*Shastasaurus* + (*Californosauridae* + *Shonisaurus* + (*Callawayia* + Parvipelvia))) (paraphyletic grade, according to Maisch & Matzke 2000)

Characters: medium to quite large in size; teeth isodont [S97]; implantation probably aulacodont in some species [Mo97]; **$** parapophysis diminishes and disappears along cervical series [S97]; **$** diapophysis elongates along cervical series [S97]; in *Shonisaurus*, diapophysis may split briefly into two dorsal & ventral, separate articulations over dorsal series [C80], [S97]; diapophysis separates from neural arch midway through dorsal series & moves down centra, becoming rounded instead of elongate [S97] (see also image at *Californosaurus*); no dorsal fin or semilunate caudal "fin"; less than 4 complete digits on fins [S97] [M97]; humerus very robust & usually as wide as long [M99]; humerus anterior flange reduced, thickened, and may be emarginated in the middle [M99]; humerus anterior flange tilted slightly dorsally [M99]; reduction of posterior humeral shaft proximally and distally [M99]; humerus with articular facet for radius enlarged, twice as wide as ulnar facet [M99]; deltopectoral ridge may run anterodistally or distally from deltopectoral crest, or posterodistally (plesiomorphic state) [M99]; humerus posterodistal tuberosity pronounced [M99]; humeral head may be directed proximodorsally (not proximally) &, if so, scapula glenoid facet tilted ventrally [M99]; movement still basically anguilliform.

Comments: An the basis of cladistic analysis, Motani 1999b shows the traditional family Shastasauridae are shown to be polyphyletic and paraphyletic, with *Cymbospondylus* representing a very primitive form (sister group to Mixosaurs and more derived ichthyosaurs) , while *Californosaurus* and *Toretocnemus* are not shastasaurs but euichthyosaurs. Maisch & Matzke 2000's cladistic analysis on the rejects the Shastasauria and considers *Toretocnemus* more basal than *Cymbospondylus*. Sander et al 2011's analysis makes the Shastasauria a paraphyletic grade. MAK100925

Links: Eyes; New Shastasaurid from Canada; Besanosaurus (Italian); modello del besanosauro; Paleontology and Geology Glossary: Be; EXN Science Wire: Daily news from the world of science; SVPCA 2000 -Abstracts L-M; NRC Research Press: Canadian Journal of Earth Sciences; Darren Naish. A new species of shastasaurus ...; Welcome to Prehistorics Illustrated; Dinosaurier-Interesse - Saurier- Ordnung der Ichthyosauria (German); DinoData Marine Reptiles Ichtyo; ON THE EVOLUTION AND HOMOLOGIES OF ICHTHYOPTERYGIAN FOREFINS; TERRITÓRIO DOS DINOSSAUROS (Portuguese: extensive discussion of *Shonisaurus*); Re- NEW RHYNCHOSAUR & TEMNOSPONDYLS (summarizes some new phylogenies); Scopriamo insieme.

References: Camp (1980) [C80], McGowan (1997) [M97]; Motani (1997) [Mo97]; Motani (1999) [M99]; Sander (1997) [S97]. ATW031003

Besanosaurus: *Besanosaurus leptorhynchus* Dal Sasso & Pinna 1996

Range: Middle Triassic of Europe

Phylogeny: *either* Shastasauria **:** (*Shastasaurus* + *Shonisaurus*) + *: . (Motani 1999b and Nicholls & Manabe, 2001)
or Merriamosauria **:** (*Shastasaurus* +

Fossil of *Besanosaurus leptorhynchus*, photo by Ghedoghedo, Wikipedia

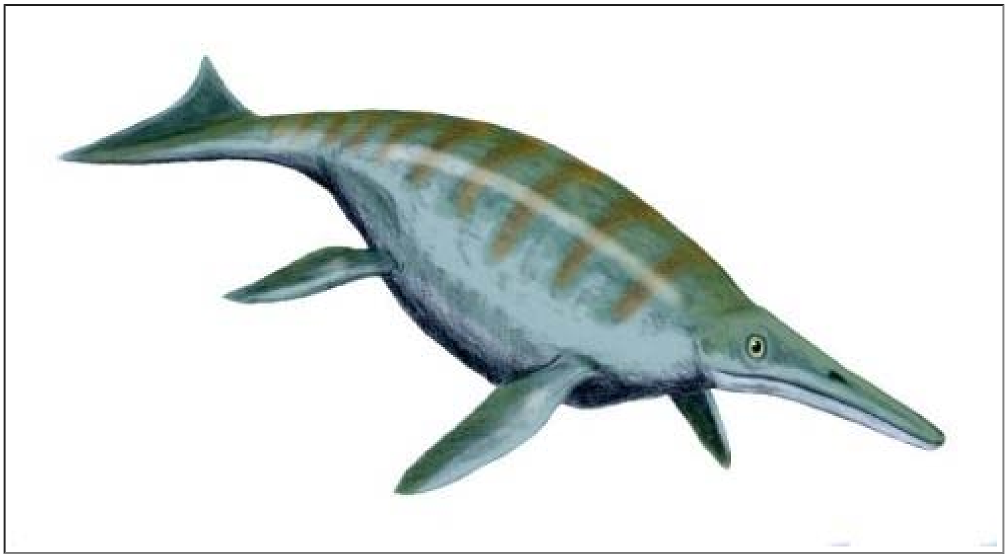
(*Californosauridae* + *Shonisaurus* + (*Callawayia* + Parvipelvia))) + * (Maisch & Matzke 2000)

Characters: teeth very small, isodontous (all of the same size and shape), snout very gracile and slender.

Comments: An unusually slim-snouted but large form, growing to 5 to 6 meters in length. Probably an eel-like swimmer. X-rays revealed the presence of embryos, indicating that these animals gave birth to live young. A smaller animal, *Mikadocephalus*, named in 1997 for a skull from Monte San Giorgio, may be related. Specimens attributed to the latter have also been reported from Spitsbergen (ref Darren Naish blog and Paleontology Newsletter no. 60 pp.81-2). Motani 1999b and Nicholls & Manabe, 2001 include *Besanosaurus* as a basal member of a monophyletic Shastasauria, whereas Maisch & Matzke 2000 consider Shastasauria a paraphyletic grade of intermediate ichthyosaurs

Links: Wikipedia

References: Maisch & Matzke 2000 p.68. MAK100923



Shonisaurus popularis from the Carnian of West Laurasia (but as an open ocean species probably of global distribution), illustration by Nobu Tamura (Wikipedia). Length of original animal 15 meters.

Shonisaurus *S. popularis* Camp

Range: Carnian, known from the Luning Formation (Upper Carnian), of Nevada

Phylogeny: *either* Shastasauria **:** Besanosaurus + (*Shastasaurus* + * **:** *Shonisaurus popularis* + *Shonisaurus sikanniensis*) (Motani 1999b and Nicholls & Manabe, 2001)
or Merriamosauria **:** Besanosaurus + (*Shastasaurus* + (*Californosauridae* + (*Callawayia* + Parvipelvia) + * **:***Shonisaurus popularis* + *Shonisaurus sikanniensis*)) (Maisch & Matzke 2000)
or Merriamosauria **:** (Parvipelvia + *Shastasaurus*) + * (Sander et al 2011)

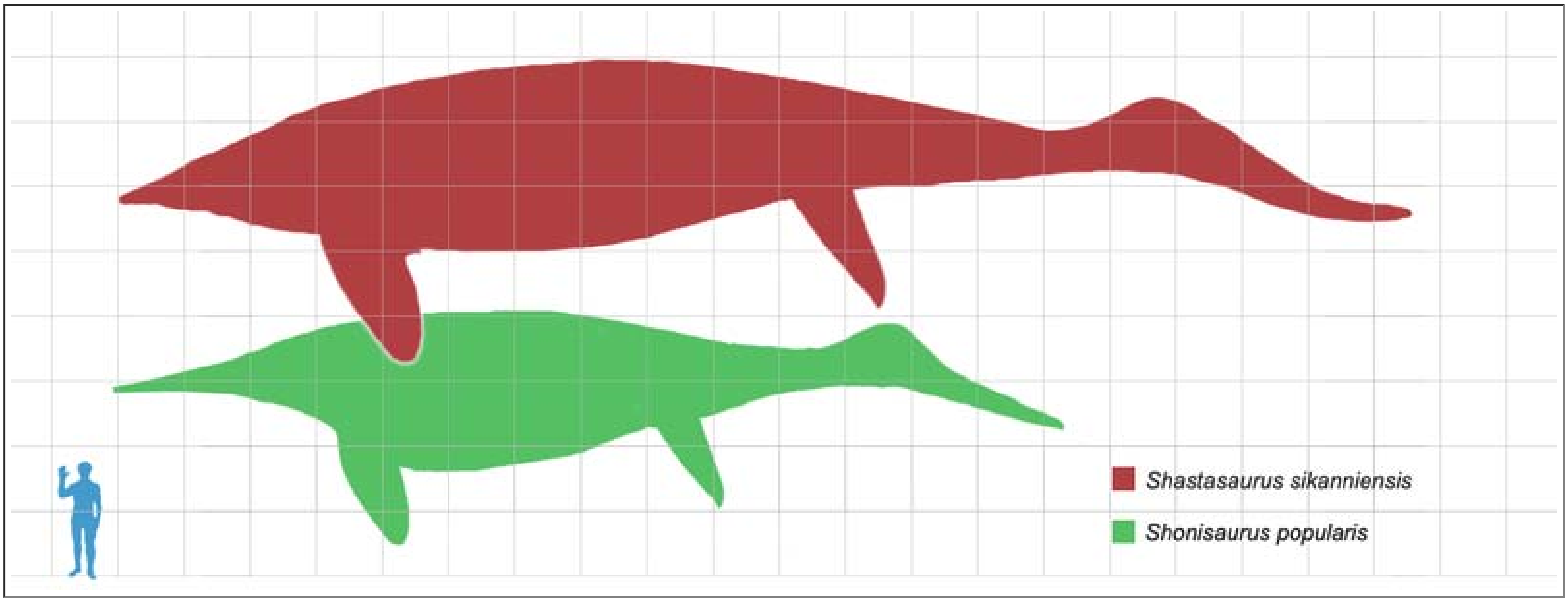
Characters: Very large ichthyosaur, over 12 m, very long but robust snout, coronoid very large, fore- and hindfins essentially tridactyl. scapula rather long and slender with reduced anterior and posterior extensions, thoracal and caudal vertebral centra very high, thoracals more than three times as high as long.

Note: Study of *Shastasaurus sikanniensis*, along with re-examination of *S. popularis*, suggests that *Shonisaurus* was not as deep-bodied as previously reconstructed (Nicholls & Makoto 2004), an attempt at a more accurate recomnstruction here

Comments: Camp divided this genus into three species found at different stratigraphic levels, but later workers have synonymised these. It is not impossible even so that these could represent a single chronospecies which increased in size with time. In 1984, this species was adopted as the State Fossil of Nevada.

Links: Shonisaurus popularis - Oceans of Kansas; THE ICHTHYOSAUR Nevada's State Fossil.; Shonisaurus - Lost Creatures Project (with pencil drawing with better proportions then the usual over deep-bodied reconstructions), Wikipedia

References: Camp 1980, Maisch & Matzke 2000 p.69. MAK100923, 111123



A comparison of the body sizes between giant Shastasaurs and an adult male human. *Shonisaurus popularis* is shown in green, and *Shastasaurus sikanniensis* in red. Grid segment = 1m. Diagram by Matt Martyniuk & Dmitry Bogdanov, Wikipedia.

Shastasaurus *S. pacificus, S. liangae, S. sikanniensis*

Range: Carnian - Norian

Phylogeny: *either* Shastasauria **:** Besanosaurus + (*Shonisaurus* + *) (Motani 1999b, Nicholls & Manabe, 2001)
or Merriamosauria **:** Besanosaurus + ((*Californosauridae* + *Shonisaurus* + (*Callawayia* + Parvipelvia)) + *) (Maisch & Matzke 2000)
or Merriamosauria **:** *Shonisaurus* + (Parvipelvia + * **:** *S. sikkanniensis* + (*S. liangae* + *S. pacificus*)) (Sander et al 2011)

Comments: Wikipedia: *Shastasaurus*' skull bore an unusually short, toothless snout compared to the long, toothed, dolphin-like snouts of most ichthyosaurs. It is likely that this strange snout indicates that Shastasaurus was a suction feeder, feeding primarily on soft-bodied cephalopods which lacked shells. In S. liangae, the only species with several well preserved skulls, the skull measures only 8.3% of the total body length (9.3% in a juvenile specimen). Unlike the related *Shonisaurus*, even juvenile *Shastasaurus* completely lacked teeth. The snout was highly compressed via a unique arrangement of skull bones. Unlike almost all other reptiles, the nasal bone, which usually forms the mid part of the skull, extended to the very tip of the snout, and all bones of the snout tapered to abrupt points.[3]

References: Sander et al 2011. MAK111123

Shastasaurus pacificus Merriam, 1895

Shastasaurus pacificus © University of California Museum of Paleontology - more photos

Synonyms: *Shastasaurus alexandrae* Merriam, 1902; *Shastasaurus osmonti* Merriam, 1902

Phylogeny: *Shastasaurus* **:** *S. sikkanniensis* + (*S. liangae* + *)

Characters: Centra (see photo right) very short , humerus, radius, and ulna (arm bones) shortened

Comments: Until recently, the genus *Shastasaurus* and the family Shastasauridae have been hard to define due to the fragmentary nature of the type specimens. *Shastasaurus pacificus* Merriam, 1895 (type species) and *Shastasaurus alexandrae* Merriam, 1902 (both from the Carnian, Hosselkus Limestone Formation, Shasta County, California, although *S. alexandrae* is now considered a synonym of *S. pacificus*) are included in this genus, but *Shastasaurus neoscapularis Shastasaurus neoscapularis* from the slightly later Pardonet Formation of British Columbia is a much more advanced form, similar to *Shonisaurus* on the one hand, and more advanced Ichthyosaurs on the other, and is relocated to a separate genus (*Callawayia* = *Metashastasaurus*). Like most shastasaurs, these were large ichthyosaurs, the various species increasing in size from early to later, ranging from about 3 to 10 meters in length (von Zittel & Eastman, 1932 p.280). The average size of *S. pacificus* was about 3 1/2 to 4 1/2 meters in length, about the size of a large dolphin. Both fore and hind fins were long and narrow, perhaps with only three digits each (longipinnate) (Hilton, 2003 p.88)

References: von Zittel & Eastman, 1932, Maisch & Matzke 2000 pp.67-8. Hilton, 2003, MAK100925, 111123

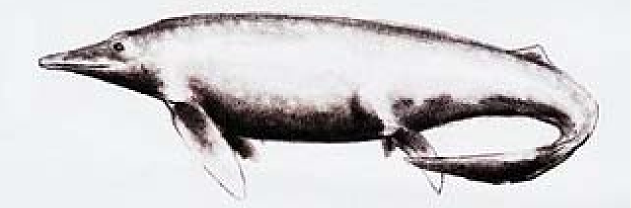
Shastasaurus liangae (Yin et al., 2000)

Synonyms: *Guanlingsaurus liangae* Yin et al., 2000

Phylogeny: *Shastasaurus* **:** *S. sikkanniensis* + (*S. pacificus* + *)

Comments: Wikipedia: *Shastasaurus liangae* was the first species to definitively show the unusual short-snouted, toothless nature of *Shastasaurus*. It is known from several good specimens, and was originally placed in the separate genus Guanlingsaurus. The largest specimen (YIGMR SPCV03109) measures 8.3 metres (27 ft) long. A juvenile specimen (YIGMR SPCV03108) has also been found, measuring 3.74 metres in length. (Sander et al 2011)

Shastasaurus sikanniensis



Synonyms: *Shonisaurus sikkanniensis* Nicholls & Manabe, 2004

Range: Norian (known from the Pardonet Formation (Norian) of British Columbia,)

Phylogeny: *Shastasaurus* **:** (*S. pacificus* + *S. liangae*) + *

Characters: Differs from *Shonisaurus* in having a fan-shaped scapula, and relatively longer vertebral centra.

Comments: The type specimen is considerably larger than *Shonisaurus popularis*, with an estimated length of 21 m. Teeth are known only in a few, small individuals, implying that they were present only in juveniles, and that adults were edentulous (toothless). This raises the question of what such big animals ate. It is likely that, as with most ichthyosaurs, these animals fed on belemnites (Mesozoic squid-like cephalopods), procuring larger volumes of food through suction feeding. "The large ceratobranchials of Shonisaurus imply powerfully developed gular muscles that control the tongue and floor of the mouth. This may have facilitated expansion of the gular region, creating a drop in intraorbital pressure, and allowing prey to be sucked in. A recent analogy would be the beaked whales (Family Ziphidae), which feed on squid, and are for the most part, edentulous. Beaked whales have throat grooves allowing for expansion of the gular region. Like Shonisaurus, they have large hyoid bones, larger than those in non-suction feeding dolphins." (Nicholls & Makoto 2004)

Update: Wikipedia: *S. sikkanniensis* was originally described in 2004 as a large species of *Shonisaurus*. However, this classification was not based on any phylogenetic analysis, and the authors also noted similarities with Shastasaurus. The first study testing its relationships, in 2011, supported the hypothesis that it was indeed more closely related to Shastasaurus than to Shonisaurus, and it was reclassified as *Shastasaurus sikkanniensis*. (Sander et al 2011)

References: Nicholls & Makoto 2004, Sander et al 2011 MAK100923, 111123

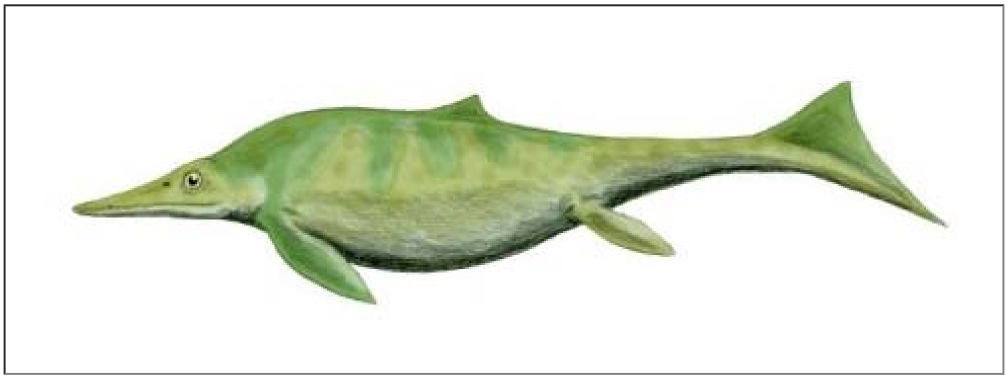
Euichthyosauria Motani 1999b

Range: Late Triassic to middle Cretaceous

Phylogeny: Merriamosauria: Shastasauria + *: *Californosaurus* + Parvipelvia. (Motani 1999b)

Comments: An the basis of cladistic analysis, Motani 1999b distinguishes the new taxon Euichthyosauria from the Shastasauria . The traditional Shastasauridae are shown to be polyphyletic, with *Cymbospondylus* representing a very primitive form (sister group to Mixosaurs and more derived ichthyosaurs) , while *Californosaurus* and *Toretocnemus* are not shastasaurs but euichthyosaurs. Maisch & Matzke 2000's cladistic analysis arrives at different results: *Mixosaurus* and *Toretocnemus* are more primitive than *Cymbospondylus*, and the disting\inction between Shastasauria and Euichthyosauria is rejected. MAK100925

Links: Phylogeny of the Ichthyopterygia. ATW020517.



Californosaurus perrini, an ichthyosaur from the Late Triassic of, naturally, California. Illustration by Nobu Tamura (Wikipedia). .

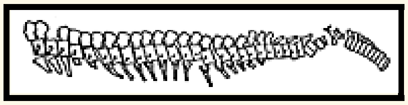
Californosaurus *C. perrini*

Synonyms: *Delphinosaurus*, *Perrinosaurus*, *Toretocnemus*?

Range: Late Triassic of North America

Phylogeny: *either* Euichthyosauria: Parvipelvia + *. (Motani 1999b)
or Merriamosauria **:** Besanosaurus + (*Shastasaurus* + (*Shonisaurus* + (*Callawayia* + Parvipelvia) + *)) (Maisch & Matzke 2000)

Characters: ~3 m; somewhat elongated; 45-50 dorsal vertebrae, centra long, rib articulations as in shastasaurs [S97] (see also image); tail sharply down-turned, with possible semilunate caudal fin; phalanges circular & widely spaced, giving large, rounded flipper [C80].



Comments: The most basal of the **euichthyosaurs** is ***Californosaurus*** Kuhn, 1934. (Synonym: *Delphinosaurus*; *Toretocnemus* has been restored as a distinct genus). *Californosaurus* is known from the Lower Hosselkus Limestone of California. Although it is a Triassic species, it has the "fishy" appearance and medium size (3 m) of many Jurassic forms. *Californosaurus* is distinguished by a smaller number of pre-sacral vertebrae (45 or 50) than is usual in ichthyosaurs, but each vertebra is somewhat elongate Camp (1980: 195), so it still has the normal body length. The tail (*right*) is sharply bent downwards, giving the animal a shark-like caudal (tail) fin; a characteristic of later ichthyosaurs. The phalanges (finger and toe bones) are quite circular and widely spaced, giving a more rounded flipper. The skull is not known.

Links: Paleontology and Geology Glossary: C; The Journal of Vertebrate Paleontology.

References: Camp (1980) [C80]; Sander (1997) [S97]. ATW020517.

Callawayia / Metashastasaurus:

Synonym: *Shastasaurus neoscapularis*

Range: Late Triassic (early Norian), Pardonet Formation of British Columbia

Phylogeny: Euichthyosauria **:::** Parvipelvia + *. (Considered the sister taxon to *Shonisaurus* by Nicholls & Manabe 2001 who place it in a monphyletic Shastasauria)

Characters: length ~ 2 meters; post-cranially, resembles the shastasaurids, e.g. latipinnate (humerus short, forefin tridactyl), but differs from *Shastasaurus* in having a radically different scapula, like that of typical Jurassic taxa like *Ichthyosaurus* and *Stenopterygius*, and the shape of the scapula and fibula. The skull, with its large orbit, narrow postorbital region, small maxilla, and a parietal ridge and postparietal shelf is unlike *Shastasaurus* but similar to that of more advanced ichthyosaurs (McGowan, 1994; Nicholls & Manabe, 2001)

Comments: Previously named *Shastasaurus neoscapularis* but differs significantly from the type species, *Shastasaurus pacificus*, e.g. in morphology of the frontals, and therefore needs to be allocated a new genus. Named *Metashastasaurus* by Nicholls & Manabe 2001. Unfortunately, the same specioes was simultaneously being redescribed by Maisch & Matzke 2000 who allocated it to their new genus *Callawayia*. This occurred while Nicholls & Manabe, 2001 was in press, and was unknown to the latter authors. *Metashastasaurus* thus becomes a junior synonym of *Callawayia*. Nicholls and Manabe note (in an addendum) that Maisch knew that their work was in progress and thus the publication of the name *Callawayia* represents a breach of the ICZN Code of Ethics . (Darren Naish - Dinosaur Mailing List). The result (as well as disagreement over phylogeny constituting the so-called "ichthyosaur wars". I'm not sure of the current status of the name *Metashastasaurus*, although it has been used in preference to *Callawayia* in at least one paper - see Shang & Li 2009 MAK100925

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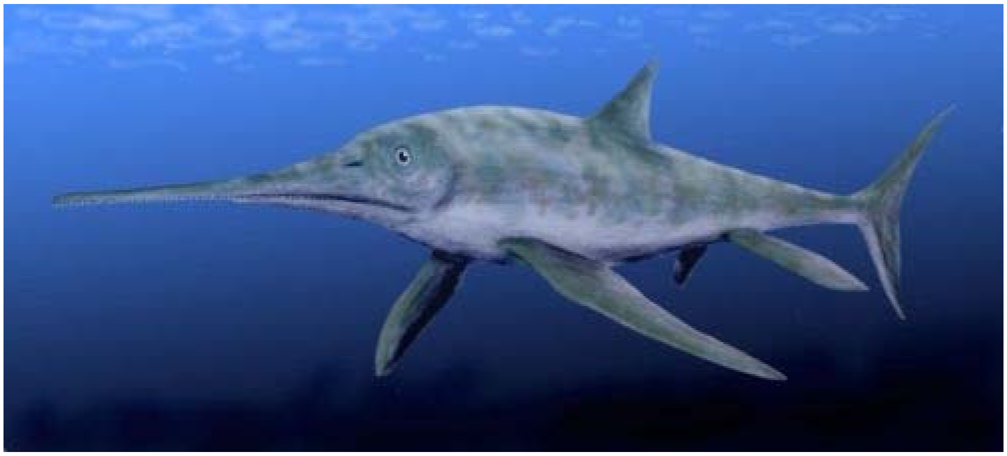
Ichthyosauria: Temnodontosaurs and Eurhinosaurs

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                  `--o Parvipelvia
   |                     |--Temnodontosaurus
   |                     |--Eurhinosauria
   |                     `--+--Thunnosauria
   |                        `--Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Taxa on this Page

1. Eurhinosauria X
2. Parvipelvia X
3. *Temnodontosaurus* X

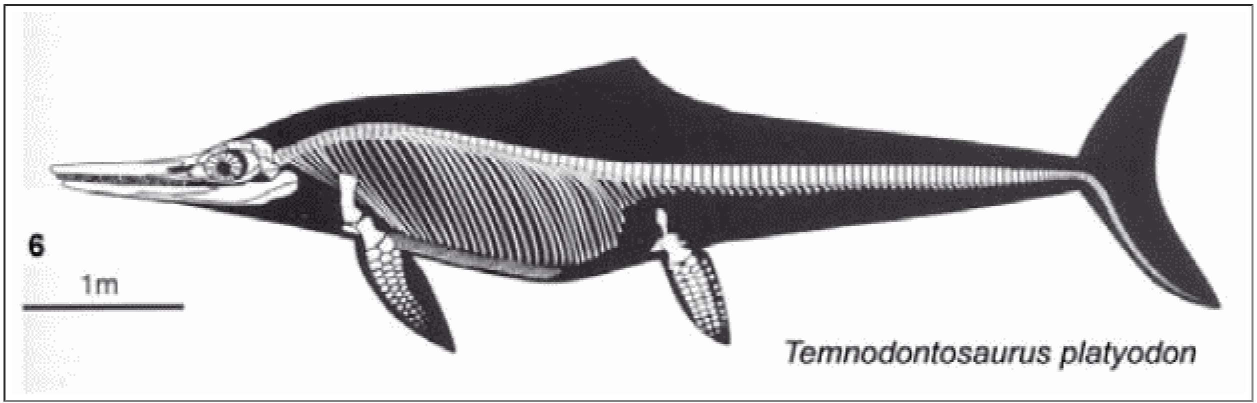


Eurhinosaurus longirostris, an Ichthyosaur from the Early Jurassic of Germany. Illustration by Nobu Tamura, Wikipedia

By the Jurassic, at level of the **Parvipelvia**, many ichthyosaurs had developed very large eyes. *Temnodontosaurus*, one of the most basal Jurassic forms, had some of the largest eyes (26 cm diameter), although this was at least partially a function of its very large size (9 m). From this we may speculate that the one of the distinguishing features of the Jurassic ichthyosaurs was an ability to move off the continental shelves into deep water. Stomach contents of the same species confirm this suspicion. Although *Temnodontosaurus* had a reasonably varied diet, its menu seems to have been particularly strong in squid which are often found at considerable depth. ATW020517.

Another Early Jurassic group, the **Eurhinosauria** is harder to make sense of. These ichthyosaurs evolved an upper jaw which was substantially longer than the lower jaw. The overall appearance was thus of a swordfish. The eurhinosaurs appear to have been designed for a very fast, pursuit mode of prey capture.

Descriptions



Temnodontosaurus platyodon, Early Jurassic (Sinemurian) of England. Length 5 to 9 metres. While highly streamlined relative to earlier forms, this less specialised Parvipelvian had not yet attained the more completely fish-like form of the higher specialised Thunnosaurs such as *Ichthyosaurus* and *Ophthalmosaurus*. The fins (paddles) are of the elongate, "longipinnate" type. From McGowan and Motani, 2003

Parvipelvia: *Hudsonelpidia, Suevoleviathan*

Phylogentic definition: last common ancestor of *Hudsonelpidia*, *Macgowania*, *Ichthyosaurus* and all of its descendants.

Range: Late Triassic to mid-Cretaceous

Phylogeny: Euichthyosauria: *Californosaurus* + *: *Temnodontosaurus* + Eurhinosauria + Thunnosauria.

Characters: Jurassic ichthyosaurs and transitional forms with mosaic of Jurassic characters (large orbit, notched phalanges on digit I, short postorbital skull, etc). ATW020517.

Temnodontosaurus: (= *Leptopterygius*) *T. platyodon, T. eurycephalus*.

Range: Late Triassic to Early Jurassic of Europe. [C97a]

Phylogeny: Parvipelvia: Eurhinosauria + Thunnosauria + *.

Characters: to 9 m; largest eye ever measured; long, narrow jaw; numerous large teeth set in a dental groove [M97]; fusiform body, triangular dorsal fin; fish-like caudal fin long, rather long, narrow paddles of approximately equal length; stomach contents indicate unspecialized diet, heavy in squid; viviparous.

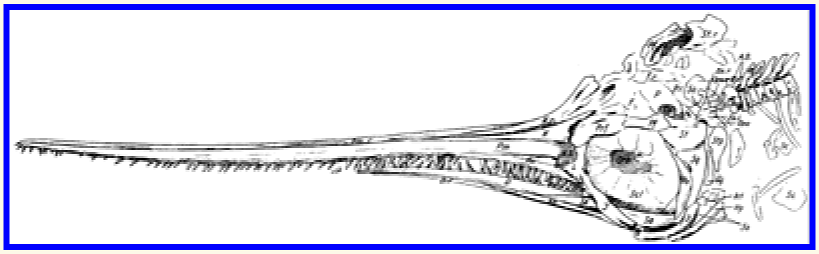
Image: (*right*) from the Max Salas Gallery at Prehistorics Illustrated

Mounted fossil of *Temnodontosaurus trigonodon*, Staatliches Museum für Naturkunde Stuttgart.
Photo by Ghedoghedo, Wikipedia

Links: Preparing Mary the ichthyosaur at Charmouth Fossils; Paleontology and Geology Glossary: Te; Dinosaurs: Model & Collectible Pricelist (see image at right); marinhos.htm (Spanish); BBC News | SCI/TECH | Monster eyes from the deep; temnodon; Diets; Eyes; An overview of the Jurassic Cliffs in Dorset; ??? (Japanese); Untitled Document (*T. risor* is a juvenile of *T. platyodon*); ??????(????) (Japanese).

References: Callaway (1997a) [C97a], McGowan (1991) [M91]; McGowan (1997) [M97]. ATW030104.

Eurhinosauria: *Eurhinosaurus*, *Excalibosaurus*, *Leptonectes*.



Range: Early Jurassic

Phylogeny: Parvipelvia: *Temnodontosaurus* + Thunnosauria + *.

Characters: 2-7 m; maxilla elongate and substantially longer than lower jaw; maxilla with teeth along entire length, but directed laterally (as in pristids?)

Comments: A group of large ichthyosaurs which show a tendency towards a swordfish-like elongation of the upper jaw. Eurhinosauria Motani 1999b is rejected by Maisch & Matzke 2000 in favour of Leptonectidae

Links: Eurhinosaurus; eurhino (German); Charitable Trust Artifacts; Excalibosaurus; ¿¡¿ì¸®³ë»ç¿ì·ç½º (Korean); English.

References: McGowan (1995) [M95]. ATW020517.

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Ichthyosauria: Thunnosauria

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                 `--+--Parvipelvia
   |                    |--Eurhinosauria
   |                    `--o Thunnosauria
   |                       |--Stenopterygius
   |                       `--+--Ichthyosaurus
   |                          `-
-Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Overview
Ancestral Ichthyosaurs
Mixosaurs and Cymbospondyls
Shastasaurs and basal Euichthyosaurs
Temnodontosaurs and Eurhinosaurs
Thunnosaurs
Ophthalmosaurs
Dendrogram
References

Taxa on this Page

1. *Ichthyosaurus* X
2. *Stenopterygius* X
3. Thunnosauria X

Descriptions

Thunnosauria: *Chacaicosaurus*

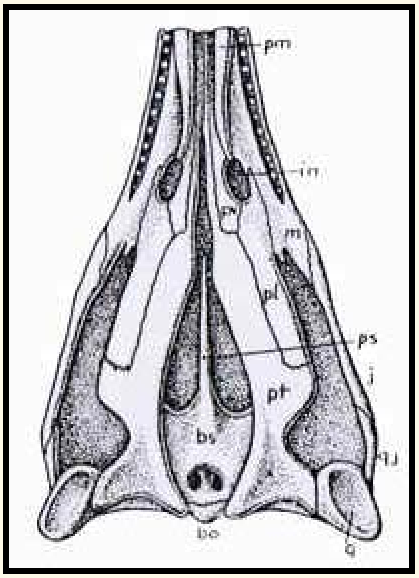
Range: Late Triassic, but mostly Early Jurassic to middle Cretaceous

Phylogeny: Parvipelvia: *Temnodontosaurus* + Eurhinosauria + *: *Stenopterygius* + (*Ichthyosaurus* + Ophthalmosauria).

Characters: diapophyses & parapophyses round [S97]; diapophysis on anterior spine attaches to neural arch & moves down centrum to fuse with parapophysis in sacral vertebrae [S97]; parapophysis also moves ventrally, but not as much; caudal vertebrae with 1 articular facet [S97]; pubis & ischium rod-like [M97].

References: McGowan (1997) [M97]; Sander (1997) [S97].

Note: It will be disappointing if this turns out not to be a clade, since it is so aptly named. These are, indeed, the tuna-lizards. ATW020517.



Stenopterygius: *S. quadriscissus* Quenstedt

Range: Early Jurassic to Middle Jurassic of Europe & South America.

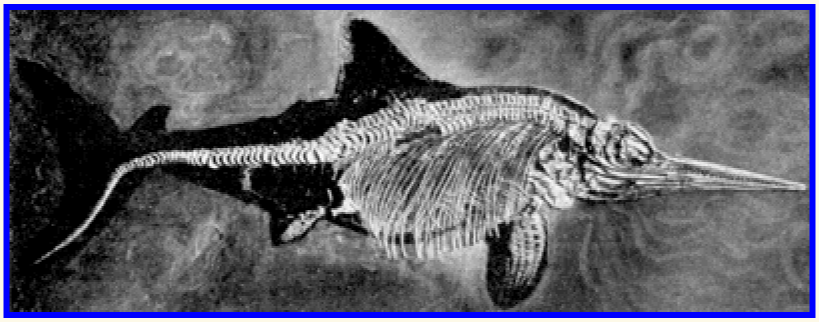
Phylogeny: Thunnosauria: (*Ichthyosaurus* + Ophthalmosauria) + *.

Characters: to 2-3 m; generally similar to *Ichthyosaurus*; small head; see image for unusual structure of skull; exceptionally large orbit compared to size of head; dramatic overbite; narrow paddles (hence the name).

Image: fossil replica image from **www.fossilien.de**. Larger image and various close-ups at this site.

Links: Prehistoric World Images - Stenopterygius - Jurassic reptile; Stenopterygius; Stenopterygius quadriscissus; Weight; Biology 356 (detail of forelimb); jurassic images (another strikingly beautiful image from Doug Henderson); Dinosaurios: Stenopterygius; Fossilienverkauf (remarkable selection of photos); Gallery of fossil amphibians, reptiles and birds; Bernstein, Fossilien, Ammoniten, Repliken und vieles mehr zum Kaufen; Neuigkeiten aus der Wissenschaft; Bilder aus der Fossilien-Sammlung von Armin Bauer; Ichthyosaur Stenopterygius quadriscissus (fossil image); Stenopterygius ステノプテリギウス (model); Dinowelt-Stenopterygius; Ichthyosaurier Stenopterygius quadriscissus Quenstedt - ... (fossil images); [스테노프테리기우스(Stenopterygius)] (Korean: several good images); Gallery of fossil amphibians, reptiles and birds (very nice, but tiny image); 標本解説 ステノプテリギュウス. ATW020517.

Ichthyosaurus:



Range: Late Triassic(!?) to Early Jurassic of Europe & North America. [C97a]

Phylogeny: Thunnosauria:: Ophthalmosauria + *.

Characters: ~2 m; jaws of equal length; maxilla relatively small [M97]; orbits enlarged [M97]; narrow posorbital region [M97]; pronounced dorsal fin; nares very close to orbits; polydactyly;

Links: Ichthyosaurus teunuirostris (Italian); The No. 973: Owen's Ichthyosaurus; The Field Museum of Natural History Ichthyosaurus; Marine Reptiles: Ichthyosaur: Ichthyosaurus; Ichthyosaure - Reptile marin de l'Ere Secondaire; Dinosaurios: Ichthyosaurus; Hawkins 1834 - Page 14 - The Ichthyosaurus Chiroligostinus (not certain this is *Ichthyosaurus* itself, but an incredible site all the same).

References: Callaway (1997a) [C97a]; McGowan (1991) [M91]; McGowan (1997) [M97]. ATW020517.

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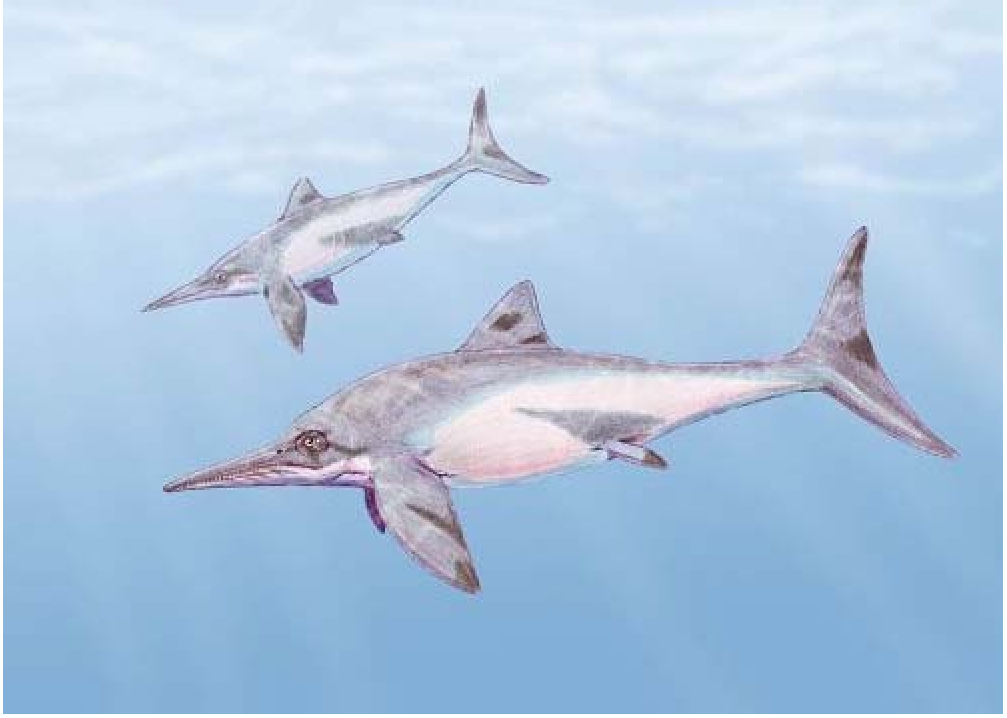
Ichthyosauria: Thunnosauria

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                 `--+--Parvipelvia
   |                    |--Eurhinosauria
   |                    `--o Thunnosauria
   |                       |--Stenopterygius
   |                       `--+--Ichthyosaurus
   |                          `--o
Ophthalmosauria
   |                             |-
-Brachypterygius
   |                             `--+-
-Ophthalmosaurus
   |                                `-
-Platypterygius
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

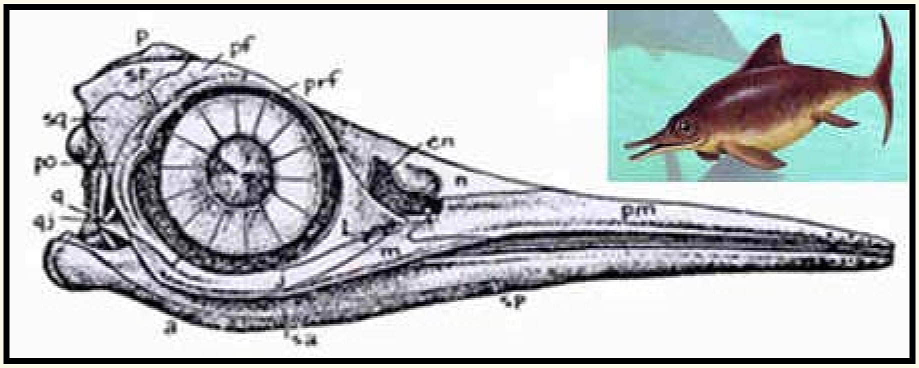
Taxa on this Page

1. *Brachypterygius* X
2. Ophthalmosauria X
3. *Ophthalmosaurus* X
4. *Platypterygius* X



Platypterygius kiprijanoffi (Early Cretaceous, Russia)
illustration by Dmitry Bogdanov (Wikipedia)

Descriptions



Ophthalmosauria: *Aegirosaurus*, *Brachypterygius*, *Caypullisaurus*, *Nannopterygius*, *Ophthalmosaurus*, *Otschevia*, *Paraophthalmosaurus*, *Platypterygius*, *Plutoniosaurus*, *Simbirskiasaurus*, *Undorosaurus* (= Ophthalmosauridae)

Range: Middle Jurassic to Late Jurassic

Phylogeny: Thunnosauria **:** *Ichthyosaurus* + * **:** Ophthalmosauria **:** *Brachypterygius* + (*Ophthalmosaurus* + *Platypterygius*).

Characters: extra *zeugopodial* element anterior to radius, with associated extra digit.

Comments: The only middle Jurassic through to Cretaceous ichthyosaurs. Cladistic analysis by Motani 2000 and Maisch & Matzke 2000 show the Ophthalmosaurs to be the most specialised and advanced ("derived" to use the technical cladistic term) of all the fish-like Ichthyosaurs. However Lawrence, 2008 used a species level analysis in which the Ophthalmosauria appear as a paraphyletic basal group between the basal Parvipelvian *Suevoleviathan* and a paraphyletic Eurhinosauria.

Ophthalmosaurus icenicus, from the Oxford Clay, in Peterborough, England. Photo by Captmondo (Wikipedia).

Links: Charmouth 180 million years BC and the Ichthysaur; Geology Field Trip Guide - Kimmeridge, Dorset - Kimmeridge Clay Fossils; Diving; Untitled Document (JVP abstract); Re- NEW RHYNCHOSAUR & TEMNOSPONDYLS (questioning monophyly). ATW030613.

Brachypterygius

Synonyms: *Grendelius* and *Otschevia*

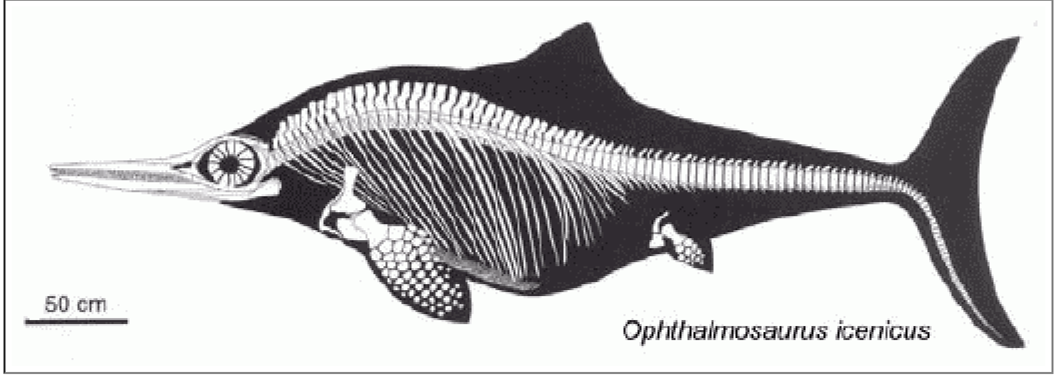
Range: Late Jurassic (Early Kimmeridgian to Late Tithonian), known from England and European Russia (central Laurasia).

Phylogeny: Ophthalmosauria **:** (*Ophthalmosaurus* + *Platypterygius*) + *

Characters: Large ichthyosaur, exceeding 5m in total length, skull with moderately large orbit, large, well developed dentition retained in adults , maxilla very long anterior to external naris (Maisch & Matzke 2000 p.79), very broad forepaddles, hence the name (latipinnate) (von Zittel & Eastman, 1932? p.281)

Comments: the most basal of the Ophthalmosaurs. (Motani 1999b). MAK100925

Ophthalmosaurus



Ophthalmosaurus icenicus, Middle Jurassic (Callovian), England and France, representing the Thunnosaur type. Length about 4 meters. In contrast to all other (less specialised) ichthyosaurs, the body is more rounded (the streamlined "tear-drop" shape), the dorsal fin high, and the fins (paddles) of the shorter and broader "latipinnate" type (convergent with *Mixosaurus*). From McGowan and Motani, 2003

Range: Middle to Late Jurassic, known from England, France, Russia, Wyoming, and Argentina

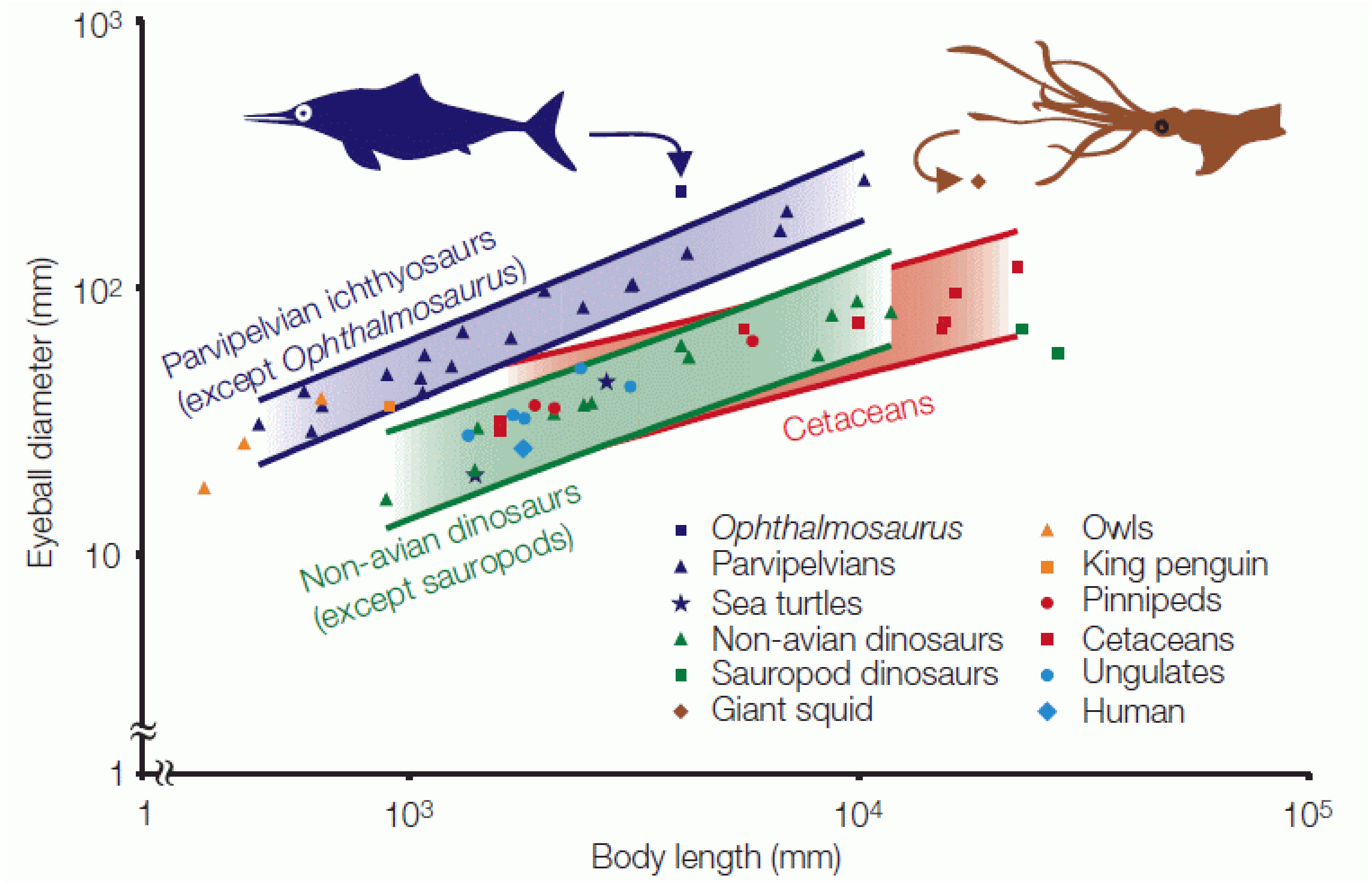
Phylogeny: Ophthalmosauria **:** *Brachypterygius* + (*Platypterygius* + *)

Characters: About 4 meters in length, skull with long snout and very large orbit, postorbital skull segment very short, dentition reduced in adults and only at the anterior tips of the jaws, humerus with three facets of subequal size (Maisch & Matzke 2000 p.78; Storrs et al 2000 p.199)

Comments: Had the largest eyes (more than 220 mm in diameter) for any ichthyosaur in prortion to its body length, may have dives to depths of 500 metres or more (Motani et al 1999). A great number of species, which differ only slightly in details. Clearly this was a very successful animal over an extended period of time. Very streamlined "teardrop" shape

Links: Ophthalmosaurus icenicus - Natural History Museum; BBC - Walking with Dinosaurs - Fact Files; Discovery of the ichthyosaur Ophthalmosaurus (Reptilia) in the Late Jurassic of the Boulonnais; Ophthalmosaurus sp.; Ophthalmosaurus (Portuguese); Dinosaurios: Ophthalmosaurus (Spanish); Wikipedia ATW030613, MAK100920

References: Maisch & Matzke 2000



Logarithmic plot of eyeball diameter against body length. Bands show 95% confidence ranges for the least-square regression lines for parvipelvian ichthyosaurs except *Ophthalmosaurus*, non-avian dinosaurs except sauropods, and cetaceans. Sauropod dinosaurs hade smaller than average eyes, *Ophthalmosaurus* larger than expected. The giant squid, Architeuthis, has the largest eyes for any extant organism (and as the diagram shows, about equal to the largest ichthyosaur eyes). Eyeball diameters for dinosaurs and ichthyosaurs are based on the external diameter of the sclerotic rings. From Motani et al 1999. For more information presented in a non-technical manner, see also Ryosuke Motani's page on Eyes of ichthyosaurs

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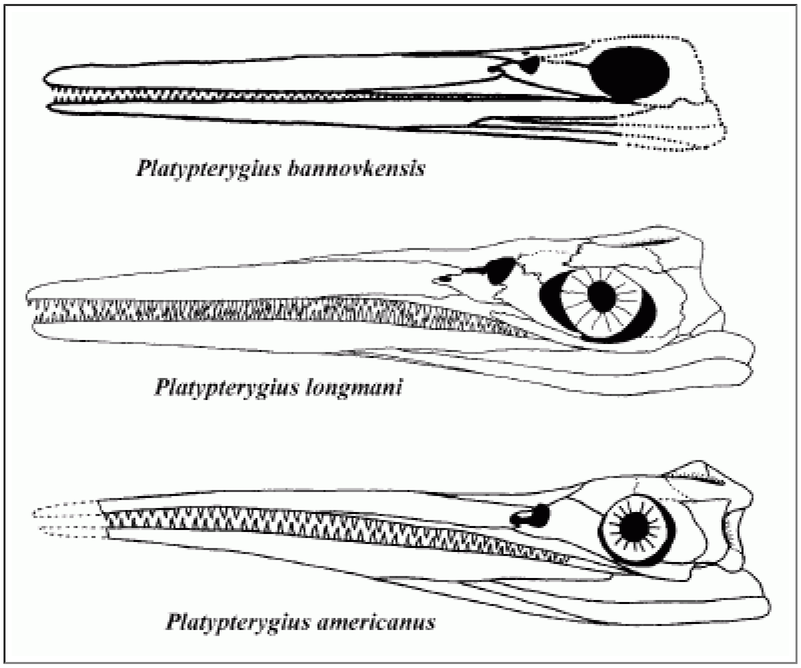
Platypterygius

Range: Cretaceous, cosmopolitan

Phylogeny: Ophthalmosauria : *Brachypterygius* + (*Ophthalmosaurus* + *)

Characters: average size 5 meters long, but larger species upto 9 meters, skull over 1 meter long in adults, long and slender snout, small orbit, teeth massive with square roots. first three cervical vertebrae fused, tail fin relatively low, the body is generally long, longer flippers than other members of the group

Comments: The most derived of the Ophthalmosaurs, and the only currently recognized genus of Cretaceous ichthyosaurs. The best-known species are *Platypterygius longmani* from the Aptian of Queensland and *Platypterygius americanus* from the Early Cretaceous of Wyoming. The type-species, *P. platydactylus* was originally known from a fairly complete skeleton but this was destroyed in World



Skull reconstructions of three species of *Platypterygius* (not to scale). From top to bottom, *P. bannovkensis*, *P. longmani*, and *P. americanus*. Drawings from Maisch & Matzke 2000 p.119.

War II. Arkhangelsky 1998 has divided the genus into four subgenera, *Pervushovisaurus*, *Tenuirostria*, *Platypterygius* and *Longirostria*, but Maisch & Matzke 2000 reject this approach. Fossilized stomach contents of *P*. *longmani* show the diet included fish, cephalopods, and immature turtles. (Kear et al 2003)

Links: *Platypterygius*, Melbourne Museum: *Platypterygius*, Platypterygius (Russian, useful page with googl;e translation); Wikipedia, Platypterygius americanus (flickr pghoto - Royal Tyrrell Museum), Ichthyosaurs (includes Opalised fossils)

References: Maisch & Matzke 2000 p.82; Storrs et al 2000 pp.200-1

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Ichthyosauria: Dendrogram

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |     `--o Ichthyopterygia = ICHTHYOSAURIA
   |        |--Utatsusaurus
   |        `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                 `--+--Parvipelvia
   |                    |--Eurhinosauria
   |                    `--+--Thunnosauria
   |                       `--Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Contents

```
o DIAPSIDA
|==Younginiformes �X
`--+--o Ichthyopterygia X
   |  |--Utatsusaurus �X
   |  `--+--Grippidia �X
   |     `--Ichthyosauria X
   |        |--Cymbospondylus �X
   |        `--+--Mixosaurus �X
   |           `-- Merriamosauria X
   |              |--Besanosaurus �X    (paraphyletic Shastasauria)
   |              `--+--Shonisaurus �X
   |                 |--o Shastasaurus �X
   |                 |  |--S. sikkanniensis �X
   |                 |  `--+--S. liangae �X
   |                 |     `--S. pacificus �X
   |                 `--o Euichthyosauria X
   |                    |--Californosaurus �X
   |                    `--+--Callawayia/Metashastasaurus
   |                       `--o Parvipelvia X
   |                          |--Temnodontosaurus �X
   |                          |--Eurhinosauria �X
   |                          `--o Thunnosauria X
   |                             |--Stenopterygius �X
   |                             `--+--Ichthyosaurus �X
   |                                `--o Ophthalmosauria �X
   |                                   |--Brachypterygius
   |                                   `--+--Ophthalmosaurus
   |                                      `--Platypterygius
   |
   |?--Omphalosauria
   |?--Hupehsuchia
   `--o Sauria MH
      |
      |--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

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Ichthyosauria: References

Abbreviated Dendrogram

```
DIAPSIDA
|==Younginiformes
`-+--+?--Thalattosauria
   |   `--o Ichthyopterygia / ICHTHYOSAURIA
   |       |--Utatsusaurus
   |       `--+--Ichthyosauria
   |           `--+--Merriamosauria
   |              `--+--Euichthyosauria
   |                 `--+--Parvipelvia
   |                    |--Eurhinosauria
   |                    `--+--Thunnosauria
   |                       `--Ophthalmosauria
   `--+--LEPIDOSAUROMORPHA
      `--ARCHOSAUROMORPHA
```

Contents

Ichthyosaurs

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