Lepidosauromorpha: Overview

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--o Lepidosauria
         |--SPHENODONTIA
         `--SQUAMATA
```

Contents

The Kuehneosaur *Icarosaurus siefkeri*, an early specialised gliding lizard-like form from the Late Triassic of New Jersey. These animals were convergent with, but unrelated to, the Weigeltisaurids of the late Permian.
Digital artwork by Nobu Tamura, Wikipedia

Introduction

Along with the Archosauromorpha, the Lepidosauromorpha are one of the two main groups of Diapsid reptiles that emerged from younginiform-like ancestors some time during the middle or late Permian. All of these animals started out as small and lizard like, but the Archosauromorphs quickly developed large size and specialised forms, to dominate the Mesozoic world, wheras the Lepidosauromorphs retained their original lizard-like appearance and structure.

Although the archosaurian affinities of dinosaurs, crocodiles, pterosaurs and birds are clear, and likewise the lepidosaurian affinities of lizards, snakes, and the tuatara and its relatives, the problem is in deciding where the other various specialised forms that emerged during the Triassic period go on the reptilian evolutionary tree. Are Ichthyosaurs, Plesiosaurs, Thalattosaurs, Hupesuchians, Drepanosaurs, Choristoderans, and the Chelonia (turtles and tortoises; which are among the most ancient and specialised of all extant amniotes) closer to the lepidosauromorph or the archosauromorph stem, or did they branch off at an earlier time? The controversies are far from being solved.

For now, rather than force an answer, which will no doubt be refuted with future discoveries, I have decided to limit this unit to those animals whose Lepidosauromorph affinities are obvious, whilst relocating the other groups to separate units. MAK100929

Unit Back | Unit Home | Page Top | Page Next

last revised MAK100929

Lepidosauromorpha

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--o Lepidosauria
         |--SPHENODONTIA
         `--SQUAMATA
```

Contents

Taxa on This Page

1. Lepidosauromorpha

Lepidosauromorpha and Lepidosauriformes

The Lepidosauromorphs are one of the two major groups or clades of diapsids that evolved from earlier Permo-Carbiniferous ancestors, the other being the Archosauromorphs. The distinction between these two groups was confirmed by cladistic analysis (Benton, 1985; Gauthier et al 1988). These authors also included a number of basal taxa such as the younginiforms, *Palaeagama*, *Paliguana*, and *Saurosternon*, as well as the more derived forms: kuehneosaurs, rhynchocephalia and squamates (lizards and snakes). All of these taxa share a unique combination of synapomorphies, such as in the morphology of the forelimbs and girdles. But later studies showed that the position of some of the early forms was not so clear cut after all, and finally the younginiforms were banished from the Lepidosauromorphs altogether (Laurin 1991). Following soon after was the controversial thesis by Rieppel and deBraga (Rieppel 1994, Rieppel & deBraga 1996, deBraga & Rieppel 1997) that turtles (Chelonians, Testudines) are closely related to sauropterygians (plesiosaurs and their relatives), and that both groups are lepidosauromorphs (For an overview of all these developments, see Michel Laurin and Jacques A. Gauthier, Diapsid Phylogeny - Tree of Life page, although this essay, written in 2000, does not cover more recent papers). This was a revolutionary development, as up until then chelonians had almost always been included in the Anapsida on the basis of the lack of fenestration (openings) in the bones of the side of the skull). If Rieppel was right, then fenestrae can no longer be used as a reliable indicator of reptilian relationship. Thus Lepidosauromorpha become an important group that include not only lizards and snakes and their relatives (Lepidosauriformes), but turtles and tortoises, and plesiosaurs and pliosaurs (Sauropterygia). Unfortunately chelonian origins is a very controversal subject, and molecular phylogeny shows unanimously that - contrary to almost all morphological evidence, chelonians are actually archosaurs (well, archosauromorphs), that is, they are more closely related to birds and cerocodiles than to lizards and snakes. Which means that either they did not evolve from early sauropterygians after all, or, another heretical hypothesis, sauropterygians are also archosauromorphs. Again, this is contrary to conventional morphology, although some evidence does seem to be appearing. Some cladograms for example suggest that ichthyosaurs are the sister-group of sauropterygians, and that this clade is part of Archosauromorpha (Merck 1997), or that Ichthyosaurs are more basal Archosauromorphs relative to the Sauropterygia and Chelonia (who in turn are more basal relative to the Archosauria) (Borsuk-Bialynicka & Evans 2009 p.230). Which nicely ties in molecular with cladistic phylogeny. However, it goes totally against all morphological evidence, according to which Sauropterygians appear as Lepidosauromorphs (Lee, 2001) or as stem diapsids (Hill, 2005).

If Sauropterygians turn out not to be the sister group of lepidosaurs, then the lepidosauromorpha becomes synonym of the Lepidosauriformes, or vice-versa, and this clade is limited to groups of lizard like forms, very much overshadowed by its glamorous and diverse archosauromorph sibling. Although it should not be forgotten that the squamates are one of the real success stories of vertebrate evolution, thanks to their unique skull and jaw mobility. This reaches its highest development in the Snakes, who in this way are able to swallow prey much larger than themselves.

Mention should also be made of the rather surprising findings of Hill, 2005 who, using a very large taxonomic and character sample to test the phylogenetic position of turtles among amniotes, arrived at the findings that not only were Testudines and Lepidosaurs sister clades, but Turtles + Lepidosaurs are in turn the sister clade to Crown group Archosaurs (Dinosaurs + Crurotarsi). The whole thing is like this: Reptiliomorpha (Mesosauridae (Synapsida (Parareptilia (Captorhinidae (*Paleothyris* (Araeoscelida (*Claudiosaurus* (Younginiformes (Basal Archosauromorpha (Kuehneosauridae (Sauropterygia (Archosauria (Lepidosauria + Chelonia)))))))))))) , While with the starting clades this arrangement is in accordance with the consensus of with the general phylogeny of amniotes, the collapsing of Archosauromorpha and Lepidosauromorpha (represented by Kuehneosauridae) into a single stem, with Lepidosaurs way up in the crown goes against the entire Diapsid phylogenetic consensus. As with the contradiction between morphological and molecular data, here the computer intense cladograms contradict the obvious morphological approach (there is a similar contrast between early (Eugene Gaffney) and more recent (Joyce, Anquetin, Sterli, etc) turtle cladograms).

For now, I have retained the current consensus phylogeny, with the Archosauromorpha and Lepidosauromorpha as the two primary lines emerging from an unspecialised neodiapsid/younginiform stem, the Sauropterygians and Lepidosauriformes as sister taxa, and turtles as highly specialised Anapsids. Here following useful tabulation, the first four from Diapsid Characters and Anatomy (University of Bristol) and the last ones from Archosauromorpha (John Meck, study notes), can be used to distinguish the archosauromorpha from the Lepidosauromorpha / Lepidosauriformes / Lepidosauria:

Lepidosauromorpha	Archosauromorpha
• Sprawling posture/mediolateral excursion (primitive characteristic, shared with basal tetrapods), mediolateral means a more sinuous motion • Emphasis on lateral undulation of vertebral column (as above) • Large sternum for rib and muscle attachments • Wrist and hand unmodified (similar to primitive diapsids)	• Limbs are brought more directly under the body (allowing more erect and efficient posture and movement) • Lateral flexure of vertebral column eliminated (less serpentine movement). • Small sternum. • Carpus (wrist) and manus (hand) are more derived reflecting more upright stance
 *Planocephalosaurus*, a lepidosaur	 *Prolacerta*, an archosauromorph
• cervical (neck) vertebrae unmodified (similar to primitive diapsids)	• Overlapping cervical ribs (stiffening of neck) • Relatively long cervical vertebrae. (this and above mean a long relatively stiff neck)

MAK100929 revised MAK101030

Descriptions

Lepidosauromorpha: definition: lizards > buzzards

Range: from the Late Permian.

Phylogeny: Sauria: Archosauromorpha + * **:** Sauropterygia + Lepidosauriformes. (Rieppel (1989))

Characters: postfrontal borders upper fenestra [R89]; supratemporal absent; quadrate wide in posterior view, forming conch; quadrate bowed in lateral view; quadrate foramen absent; retroarticular process large; teeth absent on lateral pterygoid flanges; parasphenoid teeth absent; intercentra absent from trunk vertebrae; accessory vertebral articulations [R89]; dorsal ribs *holocephalous* [R89]; no bipedal specializations; rigid pectoral girdle; large sternum; overlapping scales.

Links: Lepidosauromorpha -- (lizards > birds); Reptilian Systematics; S. Karger AG, Basel - Brain, Behavior and Evolution Abstract 198, Vol. 50, No. 4, 1997; Reptilia.html; Lepidosauromorpha -- The Dinosauricon; PhyloCode Article 13; Diapsida.htm; serp_origem.pdf (Portuguese, English); Acrocoracoids & reptile phylogeny; Lepidosauromorpha (ToL: still nothing here); Untitled (Spanish: short, but useful discussion of anatomical changes in locomotion).

References: Rieppel (1989) [R89]. ATW0070113.

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

revised ATW080328, checked ATW030715, last revised MAK101012

Lepidosauromorpha: Lepidosauriformes

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--+--Marmoretta
         `--+--Sophineta
            `--o Lepidosauria
               |--SPHENODONTIA
               `--SQUAMATA
```

Contents

Taxa on This Page

1. Kuehneosauridae X
2. Lepidosauriformes

Cladistics, Frankensteins, and the Phylogenetic Position of *Paliguana*

Some years ago, *Paliguana*held a position of some prominence at this point in these phylogenetic proceedings. Simultaneously with the posting of this essay, the Paliguanidae disappeared from the site, just as they disappeared from the South African Karoo in the Early Triassic, 240 million years ago. Fortunately, this second mass extinction is somewhat less enigmaticand may only be temporary. However, it is an appropriate occasion to say a few words about the use and misuse of stem taxa.

Paliguana is known only from a partial skull described by Broome in 1903. It was immediately recognized as very lizard-like, as was (Huxley's?) *Paleagama* (or *Palæagama*), which is also known from a single, fairly complete, but badly preserved, specimen. Somewhat later, *Saurosternon*, a headless body with similar characteristics, was also recovered from similar exposures. Clearly, these were all basal diapsids -- too primitive to be lizards, but fairly close morphologically to that line and to each other. The temptation to put the ambiguous body of *Paleagama* together with the isolated skull of *Paliguana* proved too much, and so the Paliguanidae were born, the gaps being filled in with material from *Saurosternon*. In truth, they are a good match and, as Carroll (1988a) has pointed out, there is nothing which prevents them from belonging to the same, or closely related, genera.

However, the advent of computer cladistics had curious effects on the Paliguanidae. The first significant cladistic analysis of the basal diapsids was performed by Gauthier *et al*. (1988) and published back-to-back with Carroll's (1988a) defense of the Paliguanidae. The Gauthier group simultaneously conceived the taxon **Lepidosauriformes**. Their cladogram looked like this:

```
Lepidosauromorpha
|--Younginiformes
|--Paleagama
`--Lepidosauriformes
   |--Saurosternon
   |--Paliguana
   `--+--Kuehneosauridae
      `--Lepidosauria
         |--Squamata
         `--Rhynchocephalia
            |--Gephyrosaurus
            `--Sphenodontidae
```

Some of their analysis was attacked by Carroll (1988a) and others -- not without reason, as we shall see. After several years of good-natured academic banter, Clark & Hernandez (1994) published a description of an interesting new amphisbaenid-like creature, *Tamaulipasaurus*. In the process of discussing the phylogenetic relationships of this interesting new find, the authors off-handedly did a remarkable job of synthesizing the criticisms of the original cladistic study. Further, they did not stop at carping, but eliminated the offending characters, added new species, rescored the errors, and reran the analysis with a slightly more sophisticated software package. In a noble attempt to avert battles over mere nomenclature, these authors used numbers, rather than names, for the nodes. Their result, somewhat abbreviated, looks like this:

```
Node 1 (~Lepidosauromorpha)
|--Acerosodontosaurus
|--Paleagama
`--Node 2
   |--Node 12
   |  |--Tangasauridae
   |  `--Youngina
  `--Node 3 (~Lepipidosauriformes)
      |--Saurosternon
    `--Node 4
         |--Paliguana
      `--Node 5
            |--Kuehneosauridae
        `--Node 6
               |--Tamaulipasaurus
          `--Node 7 (~Lepidosauria)
                  |--Squamata
            `--Node 8
                     |--Gephyrosaurus
              `--Node 10
                        `--Sphenodontids
```

So far, so good. However, the devil is in the details. On careful inspection, it turns out that the synapomorphies of Node 4 are *entirely* composed of post-cranial characters. There is absolutely no anatomical support whatsoever for placing *Paliguana*, an isolated skull, at Node 4. Node 3 makes good sense. It consists most significantly of characters relating to the quadrate which, in turn, govern the ability of the jaw to exert pressure when closed. This is a very significant evolutionary development which is discussed at length by Carroll (1988) and in the main entry under Lepidosauriformes. However, Node 2 has just 1 synapomorphy: the medial centrale is significantly larger than the the lateral centrale -- a character of the "hand" which seems very easily influenced by local environmental conditions. *Paleagama* could not be scored on this character, nor could it be scored on any of the node 3 synapomorphies. Thus, there is also no support for placing *Paleagama* where it is, either. In short, just as Carroll (1988a) argued, there is no basis for separating *Paliguana*, *Saurosternon*, and perhaps even *Paleagama*. Combined, they give an interesting and useful description of a grade or hypothetical ancestral proto-lepidosaur, which one might call "Paliguanidae" so long as the monophyly of the group were taken with a grain of salt.

So why have the Paliguanidae been banished from the Notes? For several reasons. First, while there is no basis for separating these taxa, there is also no basis for uniting them in a phylogenetic context. More importantly, there is no reason to treat them as distinct phylogenetic entities at all, together or separately. As Feduccia (1999) has pointed out, there is not a great deal of utility in giving every scrap of lithified bone a Latin binomial. Unless there is enough information to place the fossil in a reasonably secure phylogenetic context, it makes no sense for phylogenetic taxonomy to recognize the fossil taxonomically. This simply leads to absurd results -- such as placing an isolated head in a category described only by post-cranial characters -- and cluttering cladograms with meaningless branches.

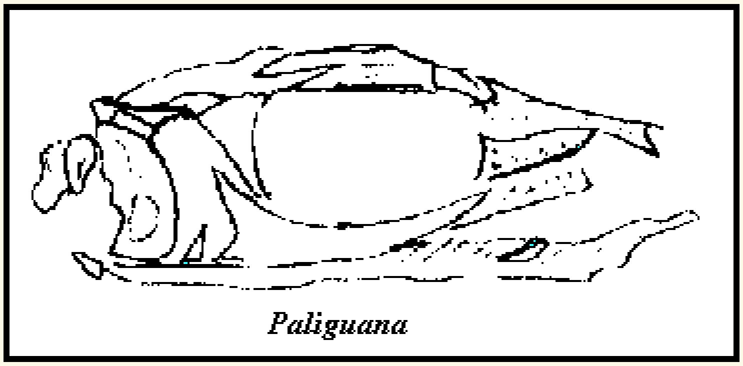
This is not to say that the paliguanids should be sold as paperweights. They are basal lepidosauriforms, or in that general neighborhood. They already have a taxonomic name: "Lepidosauriformes *incertae sedis*." If we are willing, as good cladists, to give up the idea of looking to nodes for an actual ancestor, then there is no reason not to refer a specimen to a node or stem group. The practice of refusing to do so reflects (a) a reaction to the Linnaean taxonomy's insistence on ancestry and (b) the sound logical principle that we can never be certain that a specimen is actually the last common ancestor of any two other specimens. However, a node is not only the LCA, but all of its descendants. All we know about the LCA are its synapomorphies. If a specimen has these characteristics, and has no characters which would render it unique, it should be referred to the node, *and to no other included taxon*, pending a more subtle analysis or additional material.

The same analysis applies to stem groups, such as Lepidosauromorpha = all Sauria closer to lizards than to birds, and Lepidosauriformes = all Lepidosauromorphs closer to lizards than to plesioraurs. *Paliguana* and *Saurosternon* are clearly that. But, as we have seen, they are no more than that. Thus, they are appropriately referred to the stem group, *incertae sedis* if one must; but, perhaps better, simply Lepidosauriformes. This is not an argument against rigor. *Paleagama* apparently lacks the synapomorphies for nodes 1, 2 or 3. At best, it is a diapsid.

In the last analysis Gauthier *et al*. (1988) and Carroll (1988a) are both correct. The exclusion of Paleagama has little impact on Carroll's (1988 & 1988a) hypothetical proto-Lepidosaur, and this construct forms a useful and appropriate model. However, there is no "Paliguanidae." The head and body *can* be analyzed together -- as a description of the basal Lepidosauriform morphotype.

Descriptions

Lepidosauriformes: *Paliguana*, *Saurosternon*. Lizards > plesiosaurs.



Range: from the Late Permian?

Phylogeny: Lepidosauromorpha: Sauropterygia + *. Kuehneosauridae + (*Marmoretta* + (*Sophineta* + Lepidosauria)).

Characters: **$** quadrate wide and bowed in lateral view; **$** retroarticular process large. Stem species intermediate between basic diapsid form and lepidosaurs: lower temporal bar absent; frontal-parietal suture apparently fairly loose on skull roof; quadrate articulation with pterygoid flexible or absent; dorsal end of quadrate enlarged to articulate with squamosal (*streptostyly*); no fenestration of scapulocoracoid or pelvis; vertebral centra amphicoelous; space for jaw musculature limited, but some kinesis acheived and development of space for pterygoideus allows force to be exerted by jaws when mouth is closed.

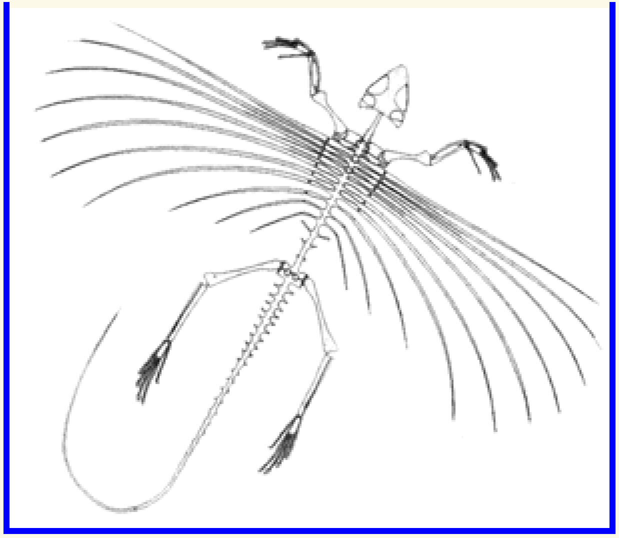
References: Carroll (1988a); Clark & Hernandez (1994); Gauthier *et al.* (1988).

Image: sketch after Carroll (1988). For purposes of the essay, note that this is *all* of *Paliguana*. ATW000301.

Kuehneosauridae: *Kuehneosaurus, Icarosaurus*.

Range: Late Triassic of North America & Europe

Phylogeny: Lepidosauriformes: (*Marmoretta* + (*Sophineta* + Lepidosauria) + *.



Characters: Unclear whether this is the sister of Lepidosauria or Sphenodontidae. Possibly a garbage taxon of basal Lepidosauria with some but not all lizard synapomorphies. Carroll includes Paliguanidae in this group.

Image: *Icarosaurus* from La scoperta dell'*Icarosaurus*.

Links: reptiles; Nathis Fauna Reptilelen Slangen en hagedissen (Dutch); Kuehneosaurus; Paleontology and Geology Glossary: K; Dinosaurios: Kuehneosaurus; A NEW TRIASSIC GLIDING REPTILE FROM THE DANVILLE BASIN; Chapter 14 The Evolution of Flight; La scoperta dell'Icarosaurus (Italian); Era Mesozoica Triassico - I Paracadutisti (Italian). ATW000226.

Page Back | Unit Home | Page Top | Page Next

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

contact us

checked ATW031006, last revised MAK100929

Lepidosauromorpha: Lepidosauria

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--+--Marmoretta
         |--Megachirella
         `--+--Sophineta
            `--o Lepidosauria
               |--SPHENODONTIA
               `--SQUAMATA
```

Contents

Taxa on This Page

1. Lepidosauria
2. *Marmoretta* X
3. *Megachirella* X
4. *Sophineta* X

The Lepidosaurs

Although often overshadowed by their more charismatic big brothers, the archosaurs, the lepidosaurs are very much a success story in minature. An important element among micro- and meso-vertebrate faunas in the late Triassic and early Jurassic, when most lepidosaurs were rhynchocephalians, they underwent an extraordinary evolutionary radiation during the middle to late Jurassic with the appearance of the squamates. Today, lizard and snakes number over seven thousand species, second only to birds (Aves) as the most species-rich tetrapod group.

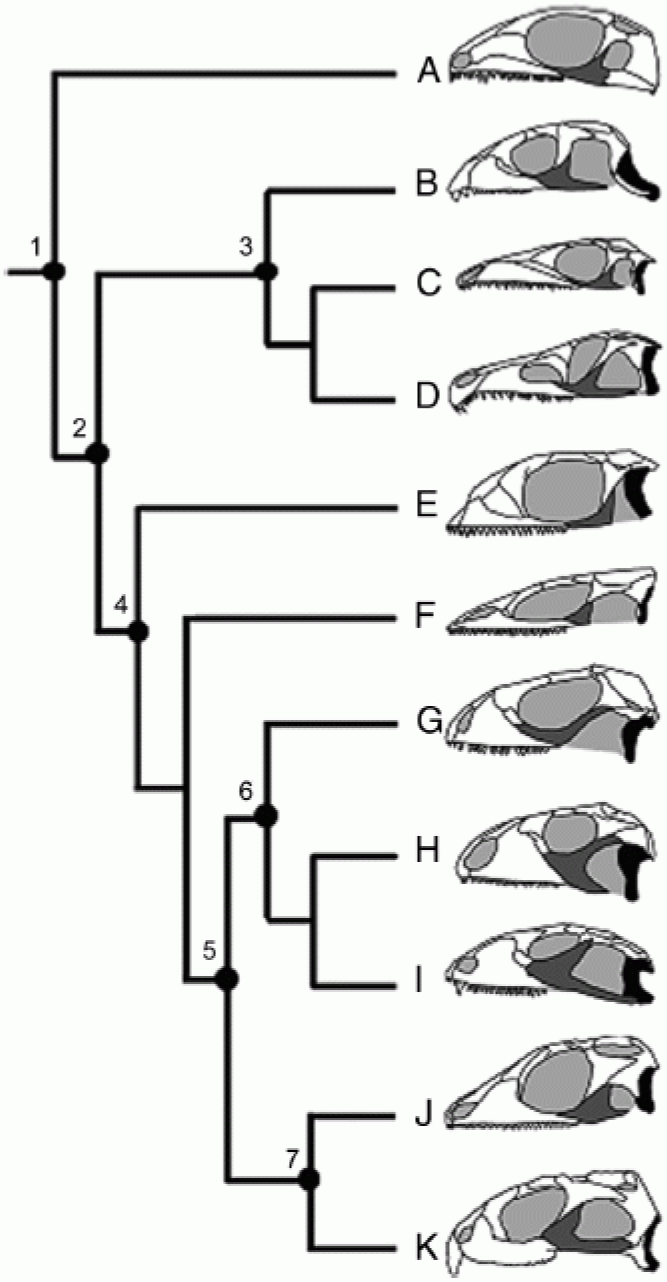
The Lepidosaurs emerged from an assortment of very lizard-like (in general appearance) lepidosauromorph/lepidosauriform taxa that flourished during the late Permian and early Triassic. During the early Triassic, these various basal forms gave rise to both the specialised gliding forms called kuehneosaurs, sauropterygians (probably), and the true Lepidosauria. All these reptiles doubt6less radiated into the ecological niches left by the end Permian extinction, which so devastated the mammal-like reptiles that until then had dominated terrestrial ecologies. This central group was mostly very small in size, focussing on small lizard niches that the archosauromorphs had not filled. Aong the stem of the main lepidosaur lineage (Crown Group Lepidosauria, to use cladistic terminology) were relict "living fossils" such as *Marmoretta* survived alongside lepidosaurs proper well into the Jurassic (Evans & Borsuk-Bialynicka 2009 p.198).

The higher Lepidosaurs divided into two subgroups, the Sphenodontia (Sphenodon and its relatives) and the Squamata (lizards and snakes). The Sphenodontia, also called Rhynchocephalia abd Sphenodontida, were very common and successful from the late Triassic to the late Jurassic, but diminished progressively through the Cretaceous and Tertiary. The squamates in contrast, which are rare or unknown prior to the middle Jurassic, went from strength to strength as the Cretaceous and Cenozoic progressed. One is reminded of the pterosaurs being supplanted by the birds in the Cretaceous. The difference between the two groups, and perhaps the reason for the success of the lizard and snake line, can be explained in terms of their differences in cranial morphology, and especially the evolution of streptostyly (anteroposterior (forward and back movement of the quadrate bone) and skull and jaw mobility (cranial kinesis) in general.

Streptostyly is achieved in lepidosaurs through partial or complete loss of the strong lower temporal bar. This has occurred a number of times among different lines of diapsids, as has the development of a complete lower temporal bar. Biomechanical analysis shows that streptostyly reduces certain stresses acting on the skull (the quadratomandibular joint force) during biting, but at the cost of limiting maximum bite force and decreasing skull robusticity. Thus a mobile quadrate has the advantage of reducing the possibility of fracture, but an akinetic skull allows for a more powerful bite. The development of a lower temporal bar would provide additional support for an immobile quadrate which could become highly stressed during forceful biting. (Moazen et al 2009)

The following diagram shows some a range of variations and modifications of the lower temporal bar among diapsids and especially lepidosauriformes

A simplified phylogeny of diapsid reptiles showing variation in the development of the lower temporal bar. Black indicates quadrate; dark gray, jugal. (A) the basal diapsid *Petrolacosaurus*; (B) the early rhynchosaur *Mesosuchus*; (C) the archosauromorph *Prolacerta*; (D) the archosauriform *Proterosuchus*; (E) the lepidosauriform *Kuehneosaurus* ; (F) the stem lepidosaur *Marmoretta*; (G) the extant squamate *Iguana*, representing a more or less unspecialised type; (H) the large herbivorous Cretaceous scincomorph *Polyglyphanodon*, (I) the related late Cretaceous lizard *Tianyusaurus*, unique among squamates in having a rhynchocephalian-like akinetic quadrate; (J) the basal rhynchocephalian *Gephyrosaurus*; and (K) the advanced extant rhynchocephalian *Sphenodon*. Nodes: 1, Diapsida, primitively lower temporal bar, fixed quadrate, robust epipterygoid; 2, Sauria, no lower temporal bar, fixed quadrate and epipterygoid; 3, Archosauromorpha, no lower temporal bar in basal taxa, but developed in Rhynchosaurs and Archosaurs; 4, Lepidosauriformes and 5, Lepidosauria, no lower temporal bar in basal taxa quadrate, epipterygoid sutured to pterygoid, large squamosal; 6, Squamata, quadrate/pterygoid overlap reduced, ligamentous, squamosal reduced, epipterygoid with synovial pterygoid joint, development of lower temporal bar in *Tianyusaurus* only; and 7, Rhynchocephalia, no lower temporal bar in basal taxa, developed in some descendants, quadrate, pterygoid, and epipterygoid firmly sutured. Text (slightly modified) and diagram from Moazen et al 2009 p.8274



Rather than being Mesozoic relics or "living fossils" with the extant Tuatara representing a type unchanged since the late Triassic, the Sphenodontia constitute a diverse evolutionary lineage that included baqutic, herbivorous, and other forms (Benton, 1986). The two lepidosaur groups therefore each persued very different adaptive stratigies, one developing a strong, immobile, skull for powerful biting, the other a reduced and highly mobile skull. Sphenodontians developed a complete lower temporal bar perhaps several times, whereas ancestral squamates lacked a lower temporal bar and then underwent a reduction of other elements as well, and a reduction of the connections between them. In advanced Sphenodontia such as *Sphenodon* the quadrate, pterygoid, and epipterygoid extensively overlap and are firmly sutured together. In an advanced squamate such as *Varanus*, the contacts are substantially reduced, allowing greater mobility (Moazen et al 2009 p.8273), such as being able to move the upper jaw relative to the braincase. This ability is especially developed in snakes, and allows them to open their mouths extremely wide to swallow large prey.

Descriptions

Megachirella: *Megachirella wachtleri* Renesto & Posenato 2003

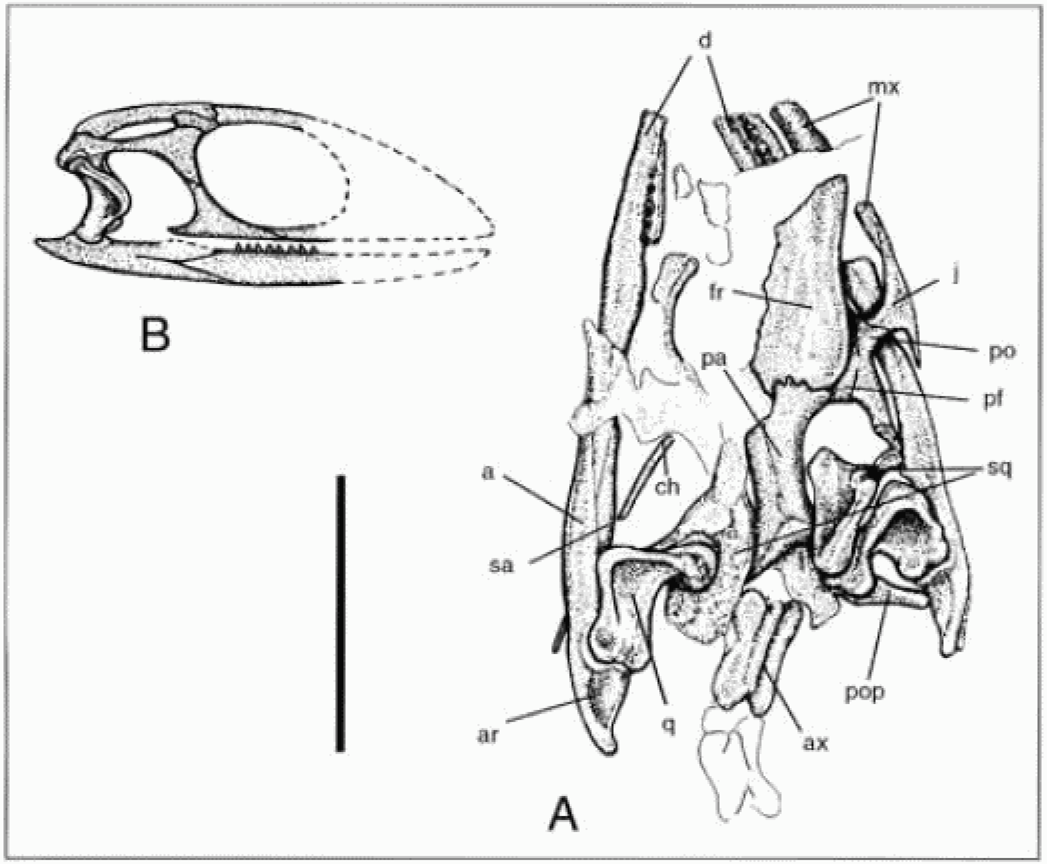
Range: middle Triassic (Anisian) of Northern Italy

Phylogeny: Lepidosauriformes: Lepidosauria + *.

Comments: A stem Lepidosauriform, similar to *Marmoretta*. The species name honours Michael Wachtler, who discovered the specimen.

Links: - Megachirella detailed page and life illustration by Prof. Silvio Claudio Renesto. MAK101003

Reference: Renesto & Posenato 2003



Megachirella wachtleri gen. et sp. n.; KUH 1501 holotype. A) drawing of the preserved portions of the skull; scale bar equals 1 cm. B) tentative reconstruction of the preserved portion of the skull in lateral (left) view. Abbreviations are: a) angular; ar) articular; ch) ceratohyal; d) dentary; f) frontal; j) jugal; mx) maxilla; pa) parietal; pf) postfrontal; po) postorbital; pop) process of the opisthotic; pra) prearticular; q) quadrate; sq) squamosal.

Megachirella wachtleri, Anisian of Northern Italy. Diagram from Renesto & Posenato 2003 p.468

***Marmoretta*:**

Range: middle Jurassic (Bathonian) of England, related species at Guimarota, Portugal (Late Jurassic: Kimmeridgian) (Evans & Milner 1994)

Phylogeny: Lepidosauriformes: (*Sophineta* + Lepidosauria) + *.

Comments: Relict Jurassic genus, shares primitive features in common with kuehneosaurs. Possibly aquatic.

Reference: Evans, 1991

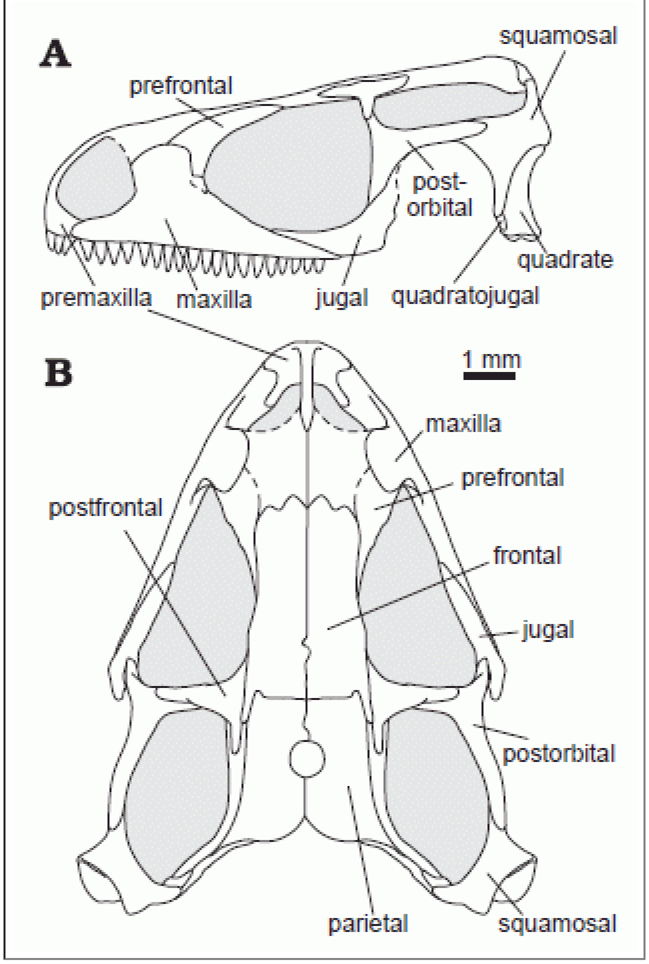
Sophineta: *Sophineta cracoviensis* Evans & Borsuk-Bialynicka 2009

Range: Early Triassic (earliest Late Olenekian) of Poland

Phylogeny: Lepidosauriformes: *Marmoretta* + (Lepidosauria + *).

Characters: small (skull ~ 1cm, body with-out tail ~3 cm), relatively short preorbital region, tall facial process of the maxilla, reduced lacrimal, and pleurodonty, all derived features that resemble early crown-group lepidosaurs rather then stem-taxa.

Comments: sister taxon of Lepidosauria, shares features in common with the basal rynchocephalian *Gephyrosaurus* (Evans & Borsuk-Bialynicka 2009)



Sophineta cracoviensis, Olenekian of Poland. Skull reconstruction in lateral (A) and dorsal (B) views. Diagram from Evans & Borsuk-Bialynicka 2009 p.182

Lepidosauria:

Range: from the Late Triassic

Phylogeny: Lepidosauriformes **:** Kuehneosauridae + (*Marmoretta* + (*Sophineta* + * **:** Rhynchocephalia + Squamata).

Characters: Determinate growth with epiphyses on terminal ends of long bones; post-parietal and tabular absent; fused astragalus and calcaneum; kidney sexual segment; thin stapes. Thyroid fenestration. Significance: hearing (lost in sphenodontids, strong foot action & ability to jump?

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

Lepidosauromorpha: Dendrogram

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--o Lepidosauria
         |--SPHENODONTIA
         `--SQUAMATA
```

Contents

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Paliguana
      |--Kuehneosauridae
      `--+--Marmoretta
         |--Megachirella
         `--+--Sophineta
            `--o Lepidosauria
               |--SPHENODONTIA
               `--SQUAMATA
```

Page Back | Unit Home | Page Top | Page Next

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

contact us

last revised MAK100929

Lepidosauromorpha: References

Abbreviated Dendrogram

```
o DIAPSIDA
|--ARCHOSAUROMORPHA
`--o LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   `--o Lepidosauriformes
      |--Kuehneosauridae
      `--o Lepidosauria
         |--SPHENODONTIA
         `--SQUAMATA
```

Contents

Benton M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97-164.
Lepidosauromorpha and Lepidosauriformes

Benton M. J. 1986, The demise of a living fossil. *Nature* 323, 762. pdf
The Lepidosaurs

Borsuk-Bialynicka, M, & Evans, S.E. (2009). A long-necked archosauromorph from the Early Triassic of Poland. *Paleontologica Polonica* 65: 203�234. pdf
Lepidosauromorpha and Lepidosauriformes

deBraga, M & O Rieppel (1997) *Reptile phylogeny and the interrelationships of turtles*, **Zool. J. Linnean Soc.** 120: 281-354.
Lepidosauromorpha and Lepidosauriformes

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp.
Lepidosauriformes

Carroll, RL (1988a), *Late Paleozoic and early Mesozoic lepidosauromorphs and their relation to lizard ancestry*, in R Estes & G Pregill (eds.), **Phylogenetic Relationships of the Lizard Families**, Stanford Univ. Press, pp. 99-118.
Lepidosauriformes

Clark, JM & RR Hernandez (1994), *A new burrowing diapsid from the Jurassic La Boca formation of Tamaulipas, Mexico*, **J. Vert. Paleontol.**, 14: 180-195.
Lepidosauriformes.

Evans, S.E. 1991. A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological Journal of the Linnean Society* **103**, 391�412.
Marmoretta.

Evans, S.E. and Borsuk-Bia�ynicka, M. 2009. A small lepidosauromorph reptile from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 179�202.pdf
The Lepidosaurs, *Sophineta*

Evans, S. E., and A. R. Milner. 1994. Middle Jurassic microvertebrate assemblages from the British Isles; pp. 303�321 *in* N. C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, Cambridge
Marmoretta.

Gauthier J., R. Estes, & K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. In: R. Estes and G. Pregill (ed.) *Phylogenetic relationships of the lizard families*: 15-98. Stanford: Stanford University Press. pdf
Lepidosauromorpha and Lepidosauriformes, Lepidosauriformes

Hill, Robert V.. 2005. Integration of Morphological Data Sets for Phylogenetic Analysis of Amniota: The Importance of Integumentary Characters and Increased Taxonomic Sampling. *Systematic Biology* 54(4):530-547. pdf.
Lepidosauromorpha and Lepidosauriformes

Laurin M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. Zoological Journal of the Linnean Society 101: 59-95.
Lepidosauromorpha and Lepidosauriformes

Lee, M. S. Y. 2001. Molecules, morphology, and the monophyly of diapsid reptiles. Contrib. Zool. 70: 121�138.
Lepidosauromorpha and Lepidosauriformes

A phylogenetic analysis of the euryapsid reptiles. Journal of Vertebrate Paleontology 17: 65A.
Lepidosauromorpha and Lepidosauriformes

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ (2009) Biomechanical assessment of evolutionary changes in the lepidosaurian skull. *PNAS* 106: 8273�8277. pdf
The Lepidosaurs

Renesto S. and Posenato, R. (2003) A new lepidosauromorph reptile from the Middle Triassic of the Dolomites. *Rivista Italiana di Paleontologia e Stratigrafia* 109 (463-474). pdf *Megachirella*

Rieppel, O. 1994 Osteology of Simosaurus gaillardoti and the relationships of stem-group sauropterygia. *Fieldiana Geology* 1462: 1-85.
Lepidosauromorpha and Lepidosauriformes

Rieppel O. & M. deBraga. 1996. Turtles as diapsid reptiles. **Nature** 384: 453-455.
Lepidosauromorpha and Lepidosauriformes

Page Back | Unit Home | Page Top | Page Next

Last revised MAK101002

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

contact us

Page by MAK111113

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

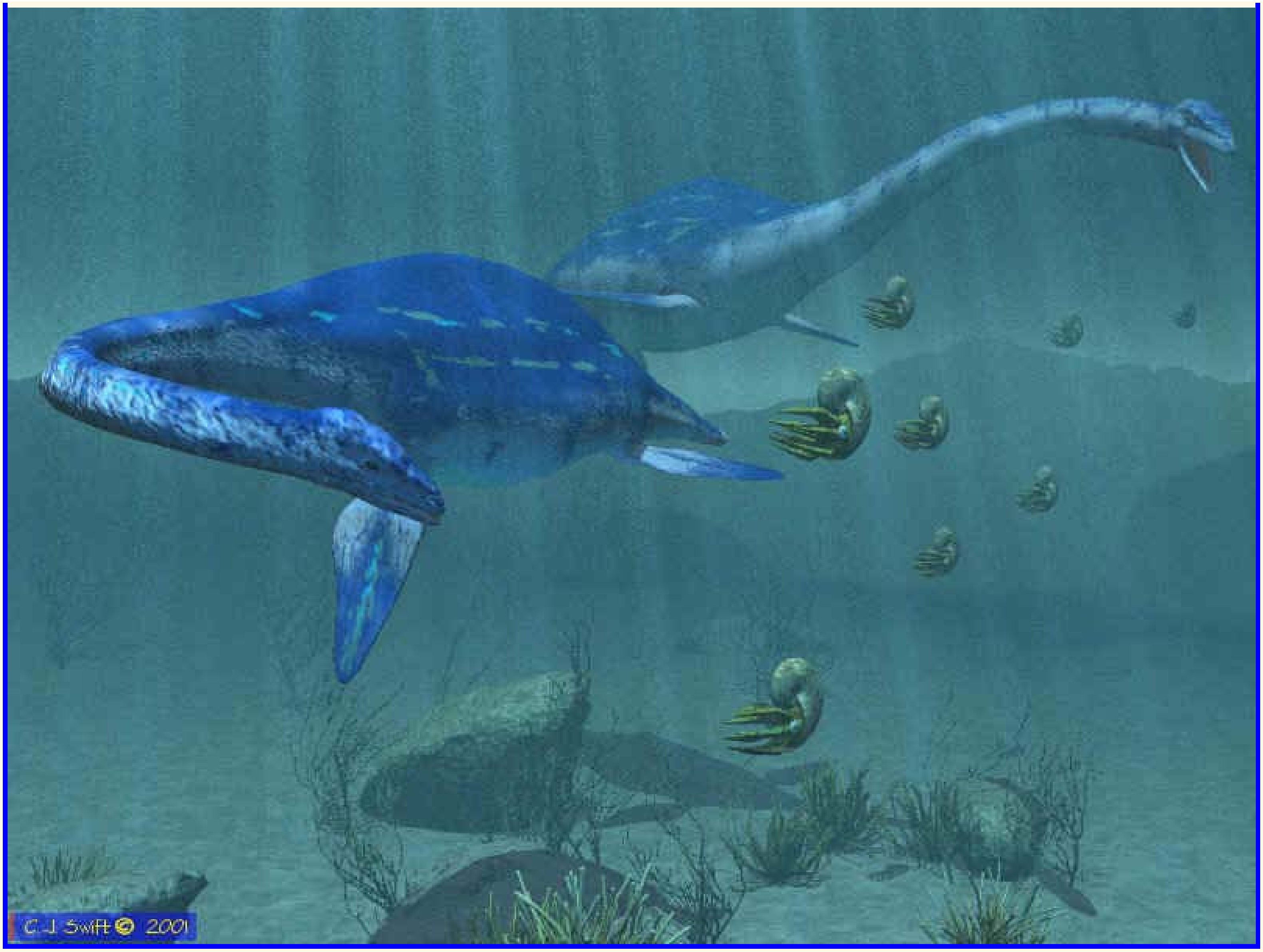
Sauropterygia: Overview

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|Lepidosauromorpha
|--SAUROPTERYGIA
|  |--Placodontia
|  |==Pachypleurosauridae
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Introduction



Two muraenosaurs: "Somewhere Under Tethys" © Colin Swift, based on a mesh from Gruppo Iride. Reproduced by permission.

Page Back | Unit Home | Page Top | Page Next

checked ATW050512

Sauropterygia

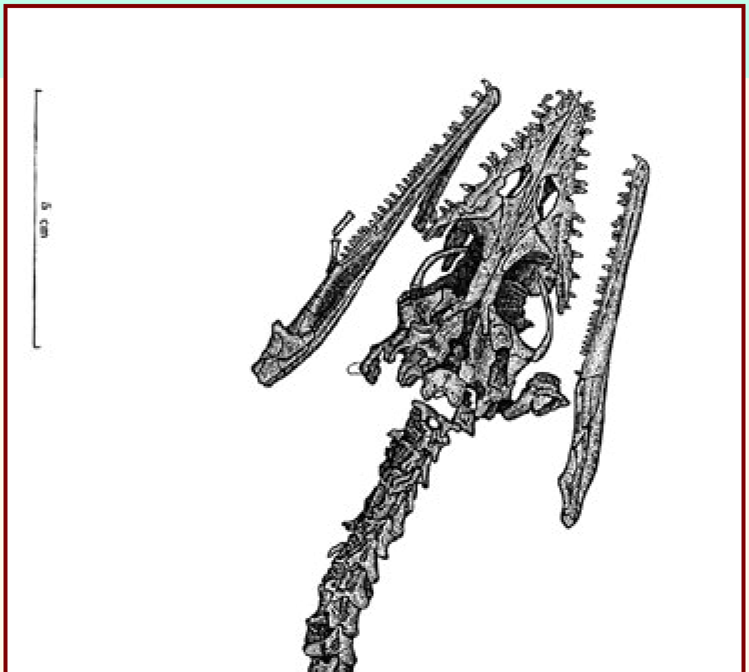
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--Sauropterygia
|  |--Placodontia
|  `--Nothosauria
|     |--Wumengosaurus
|     |==Pachypleurosauridae
|     `--+--Nothosauridae
|        `--Plesiosauria
|           |--Pliosauroidea
|           `--Plesiosauroidea
|              |--Elasmosauridae
|              `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

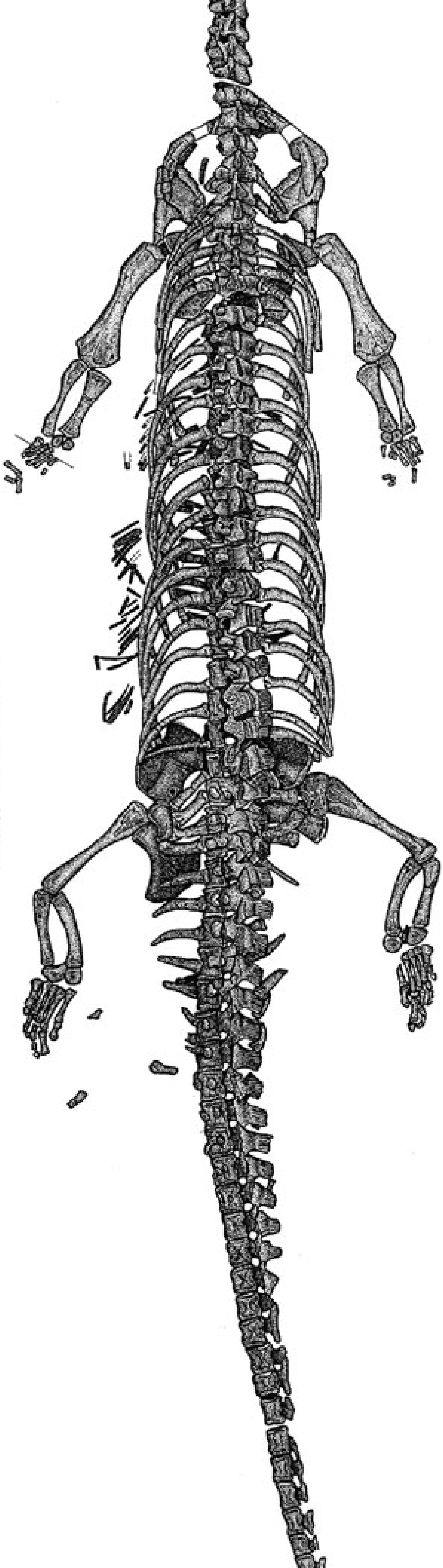
Taxa on This Page

1. Nothosauria X
2. Sauropterygia X
3. *Wumengosaurus* X



Sauropterygia

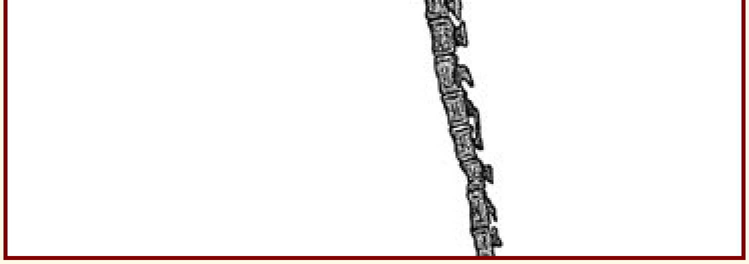
The **Sauropterygia** or "lizard flippers" are an important group which includes a wide range of aquatic lizard-like, crocodile-like, long-necked "Loch Ness monster"-like, and large-headed killer whale-like aquatic reptiles. Among the great prehistoric success stories, they first appeared at (or just before) the very start of the Mesozoic and flourished right until the end of the era. Yet as with the Ichthyosauria, they are so specialized their ancestry and evolutionary relationships are still somewhat obscure (see comments on Sauropterygian origins.



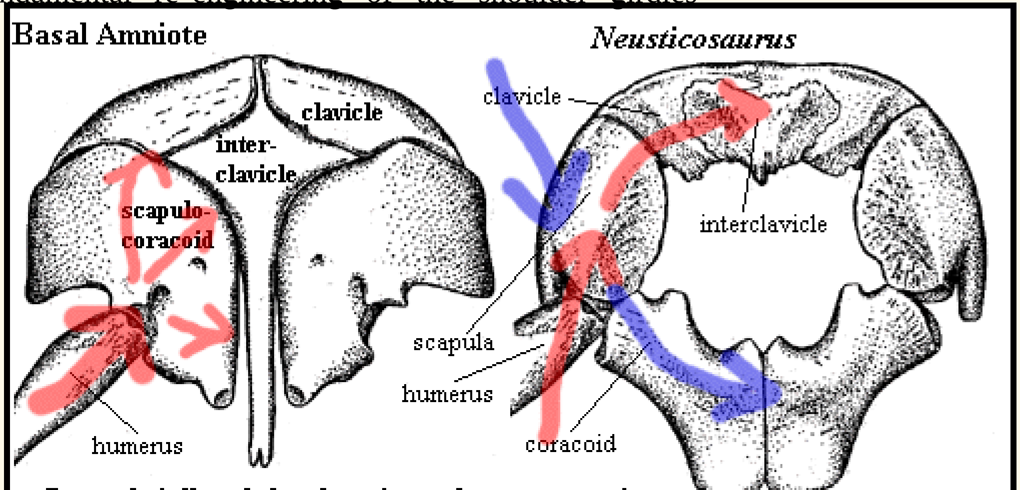
Earlier forms (pachypleurosaurs) were mostly small amphibious lizard-like animals with slender, elongated limbs and small heads, that lived in estuarine and near-shore environments. They quickly increased to several meters in size and ventured further out to sea, although still retaining amphibious traits and sinuous lizard-like form (nothosaurs). By the Middle Triassic there were a number of divergent lineages. In addition to the line leading to the successful Jurassic plesiosaurs, there were several divergent branches of early sauropterygians, including pachypleurosaurs, several lines of nothosaurs, and the transitional pistosaurs. These early divergent branches show successive stages in adaptation to oceanic life.

The Carnian extinction took out most of these early Sauropterygia, but the one surviving group, the plesiosaurs, underwent a tremendous evolutionary radiation around the very end of the Triassic period and the very start of the Jurassic, diverging rapidly into variously lineages in a typical example of a macroevolutionary adaptive radiation. It is not yet clear whether this event coincided with and was caused by the full development of the plesiosaur locomotor plan, or whether it was simply opportunistic factors, such as the mass extinction of potential competitors in the Rhaetian turnover, that allowed the plesiosaurs to exploit the potential of a previously evolved locomotor plan (see below). In any case by the early Jurassic there were a diverse range of long- medium- and short-necked forms, some with small heads others with large. These were all open ocean types, completely adapted for marine life, and usually 3 metres or more in length. The two principal morphs were the plesiosaurs (long necked "Loch Ness monster" types) and pliosaurs (reptilian killer whales). However, the evolutionary relationships of the Plesiosauria are complex, and it appears that long-necked and short-necked types occurred in a number of lineages.

The Sauropterygia are united by unique derived features features of the skull and shoulder girdle. As Carroll & Gaskill (1985) note, the fundamental relations of the shoulder girdle elements are altered in the Sauropterygia. The figure illustrates the differences in shoulder structure between a basal amniote (adapted from Carroll, 1988) and the basal sauropterygian, *Neusticosaurus* (adapted from Carroll & Gaskill 1985). In the terrestrial amniote, force is directed by the humerus against the plate-like scapulocoracoid, which dissipates the force over a wide area and is, in turn, supported by extensive contact with the dermal bones



of the clavicle and interclavicle. In the sauropterygian shoulder, a direct, medially directed force would probably cause the shoulder girdle to collapse. However, the anterior and posterior strains caused by paddling and steering simply bind the girdle more strongly together by forcing the interclavicles and coracoids against their opposite numbers. The fundamental re-engineering of the shoulder girdles suggests that the strains involved were considerable, *i.e.*, that the sauropterygians were fast, agile swimmers.



Pectoral girdles of a basal amniote and a sauropterygian (Neusticosaurus) in ventral view

A remarkably similar arrangement was evolved in the pelvic girdle of derived sauropterygians, *e.g.* plesiosaurs, and both girdles were connected by a net of gastralia (stomach ribs) probably reinforced by stout ligaments. This arrangement and the problems of plesiosaur locomotion, will be covered on a subsequent page. MAK991206, ATW061220.

Descriptions

Sauropterygia: definition variable in the literature. Used here as placodonts + plesiosaurs.

Range: Early Triassic to Late Cretaceous.

Phylogeny: Lepidosauromorpha: Lepidosauriformes + * **:** Placodontia + Nothosauria.

Characters: Postorbital skull elongated; upper fenestra enlarged; "euryapsid" (lower temporal arch lost) [CG85]; quadrate rigid (primitive) [CG85]; elongate neck (>7 cervicals); limbs relatively large [CG85]; curved humerus; radius equal length to ulna. ATW061216.

Comments: The Sauropterygian can be divided into six main types. The *Pachypleurosauridae* represent an ancestral lineage or series of lineages, all are morphologically quite similar, small lizard-like near shore forms, they include both slow and fast growing types. The *Placodontia* are highly specialised armoured turtle like forms with variable diet (molluscivore, seaweed, filter feeding, etc). The *Nothosauridae* are larger forms otherwise resembling the pachypleurosaurs. The *Pistosauridae* are intermediate between pachypleurposaurs and nothosaurs on the one hand, and crown group sauropterufgia (Plesiosauria) on the other. The *Pliosauroidea* started out as small to medium sized long-necked and small headed types, but later became medium to very large short-necked and large headed forms. These were the superpreditors of the middle Jurassic through to mid Cretaceous, immortalised in the popular geek consciousness as the mythical 25 meter *Liopleurodon* of *Walking With Dinosaurs* fame (in fact 8 to 12 meters was more realistc, still a very respectable size for an apex predator). Finally the *Plesiosauroidea* are your standard "loch ness monster" or "antediluvian sea monster", with a small head on a long sinuous neck, and a broad turtle like body. Some advanced forms however became secondarily pliosaur-like. MAK111125

Sauropterygian origins: At one time included with the Ichthyosuria, polyphyletic Protorosauria (*Protorosaurus* + Araeoscelida), and a seperate Placodontia in the Subclass Euryapsida (Colbert, 1969); the Placodonts were then given their own subclass Kuhn 1969. Later Carroll 1981 derived the pachypleurosaurs, and hence the Sauropterygia as a whole, from the late Permian diapsid *Claudiosaurus*. *Claudiosaurus* itself he placed in the Lepidosauromorpha. Other workers however considered *Claudiosaurus* a more primitive form, predating the Archosaur-Lepidosaur divide (e.g. Benton 1985, see Diapsid phylogeny) , and this is the current consensus position which we have followed here. Rieppel on cladistic grounds returned to Sauropterygia to the Lepidosauromorpha (minus *Claudiosaurus*), and made them the sister group of the Placodontia, thus revising in part the Euryapsida; alternatively the Placodontia are included in the Sauropterygia, but distinct from pachypleurosaurs + (nothosaurs + (plesiosaurs))). More recently John Merck returned the Ichthyosaurs to the Euryapsida as (Thalattosauria + Euryapsida (Ichthyopterygia + Sauropterygia), but moved them from basal lepidosauromorpha to basal archosauromorphs (ref: DML posting (Tom Holtz). This gives three possible, and perhaps equally plausible, hypotheses for sauropterygian origins: as stem neodiapsids derived from *Claudiosaurus* or a similar form, as stem lepidosauromorphs, or as stem archosauromorphs. MAK111102

Links: Sauropterygia -- The Dinosauricon; Sauropterygia; Turtle Origins; Literature - Sauropterygia; muschelkalk lipperland (German: never saw this site before. Very nice.); ???????? (Japanese); Untitled Document; Literature - Sauropterygia; Sauropterygia after Rieppel, 1997, 1998ab and Rieppel & Hagdorn, 1997; Fossil Room; some additions to Re: MOSASAURS AND PLIOSAURS; MOSASAURS AND PLIOSAURS; muschelkalk lipperland (German).

References: Carroll & Gaskill (1985) [CG85]. ATW061216.

Changing classifications of the Sauropterygia		
Colbert, 1969:	Carroll 1988:	Benton 2005:
Subclass Euryapsida Order Protorosauria Order Ichthyosauria Order **Sauropterygia** Suborder Nothosauria Suborder Plesiosauria Superfamily Pistosauroidea Superfamily Pliosauroidea Superfamily Plesiosauroidea Order Placodontia Subclass Diapsida	Subclass Diapsida Order Placodontia (*incertae sedis*) Infraclass Lepidosauromorpha Superorder Lepidosauria Superorder **Sauropterygia** nbsp; Family Claudiosauridae (*incertae sedis*) Order Nothosauria Order Plesiosauria Superfamily Pliosauroidea Superfamily Plesiosauroidea Infraclass Archosauromorpha	Subclass Diapsida Order Araeoscelidia Infraclass Ichthyosauria *sedis mutabilis* Infraclass Lepidosauromorpha Superorder Lepidosauria Superorder **Sauropterygia** Order Placodontia Order Nothosauroidea Suborder Pachypleurosauria Suborder Nothosauria Order Plesiosauria Suborder Pliosauroidea Suborder Plesiosauroidea Infraclass Archosauromorpha

The above represent Linnaean/Evolutionary rank-based classifications, which allow ancestral taxa, and should not be confused with Cladistic clade-based phylogenies which do not. Both methodologies are equally valid and complementary; it is not the case that one "disproves" the other. MAK111103

Nothosauria: plesiosaurs > placodonts. This was traditionally the name for a paraphyletic group including pachypleurosaurs and nothosaurs. Since a lot of good work was done on the plesiomorphic state of the group, we insert it here as a stem group supporting Sauropterygia. Most references prior to about 1990 use "nothosaurs" to refer to this group, rather than to Nothosauridae.

Range: Early Triassic to End Cretaceous

Phylogeny: Sauropterygia : Placodontia + * : Pachypleurosauridae + Eusauropterygia. ATW061220

Characters: "euryapsid" (lower temporal arch lost)

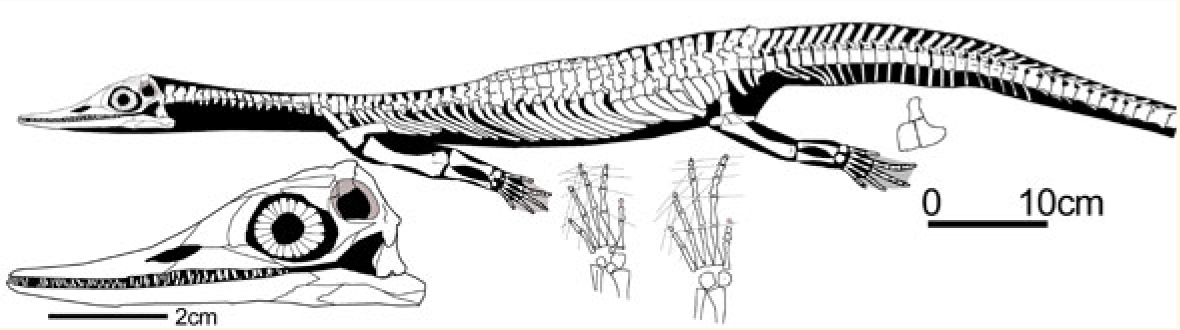
[CG85]; quadrate rigid (primitive) [CG85]; quadrate embayed [R89]; pterygoids usually meet ventrally covering braincase, occluding interpterygoid vacuities [CG85]; pterygoid with parasagittal ridges medial to LTF (possibly pterygoideus muscle) [CG85]; tooth implantation typically thecodont [R89]; increase in neck length by increasing number of vertebrae (but number in trunk is primitively almost constant) [CG85]; scapula and coracoid separately ossified [CG85]; cleithrum & sternum absent [CG85]; clavicles & interclavicle form solid bar anteriorly & ventrally [CG85]; large opening between medial surfaces of scapulae & coracoids [CG85]; ventral margin of scapula broadly underlying posterior clavicle (opposite of usual tetrapod arrangement) [CG85]; interclavicle small & ventral to clavicles [CG85] **[1]**; coracoid posterior to surface of glenoid [CG85]; humerus remains relatively straight [R89]. ATW061220

Comment: the phylogenetic position of the placodonts is unclear, due to their highly specialised nature and lack of obvious characteristics that can be compared with run of the mill sauropterygia. It is quite likely that they diverged later from pachypleurosaurs, in which case Nothosauria characteristics given here are simply plesiomorphic sauropterygian traits which are lost by ancestral placodonts. Assuming this is so (and there don't presently seem to be any peer review papers pushing thsi line, so it's just the present author on his soap box) Nothosauria would become a junior synonym for Sauropterygia. If Pachypleurosauria turn out to be paraphyletic as well, that would mean that Sauropterygia = Nothosauria = Pachypleurosauridae. See also comments on *Wumengosaurus*, below. MAK111125

Notes: [1] See images at Sauropterygia and *Nesticosaurus*.

References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]. ATW061220.

Wumengosaurus: *W. delicatomandibularis* Jiang et al 2008



Range: middle Anisian (Middle Triassic) of Panxian, Guizhou Province, southwestern China.

Phylogeny: Sauropterygia (= paraphyletic Pachypleurosauridae?) **:** Pachypleurosauridae + Placodontia + Nothosauridae + Pistosauroidea + *.

Characters: From the abstract of Jiang et al 2008: "unique specialization of the jaws that form an elongate pointed rostrum furnished with numerous small, monocuspid and vertically oriented teeth with a basally expanded crown and pointed tip, which is quite unlike any other sauropterygian known. Other diagnostic characters include: frontals paired; parietal unpaired; pineal foramen located centrally in broad parietal skull table; two carpal ossification; ilium with distinct preacetabular process at the base of the dorsally extending iliac blade; pubis plate-like and of rounded contours; two tarsal ossifications. The curved and distally expanded humerus, the reversed topological relationship of the clavicle and scapula, and the presence of three sacral ribs indicate sauropterygian affinities of the new taxon, whereas the 'butterfly-shaped' or 'cruciform' facet for the neural arch on the dorsal centrum surface indicate its eosauropterygian status."

Comments: The five known specimens show morphological variation, like that of *Keichousaurus*, *Neusticosaurus*, and *Serpianosaurus*. Originally considered by Jiang et al (2008) pachypleurosaurid with an unusually elongated rostrum, hence the species name. Wu et al. (2011) restudied this species is restudied on the basis of three new specimens. They revised Jiang et al (2008)'s analysis, rejected the idea of a monophyletic

Pachypleurosauria, and questioned *Wumengosaurus* placement in the Pachypleurosauria. They suggest instead that *Wumengosaurus* might represent the basal-most member of a monophyletic clade that includes the Nothosauroidea and those taxa assigned to the paraphyletic Pachypleurosauria. David Peters tested *Wumengosaurus* against *Stereosternum*, *Hupehsuchus*, and *Utatsusaurus* and argued that they form a single clade with Wumengosaurus more derived than Stereosternum but more basal than Hupehsaurus, Utatsusaurus, and the Ichthyopterygia. The present author however feels that, whilst the taxa Peters lists are similar in appearance, this can be better explained in terms of convergence (*Wumengosaurus* being an ichthyosaur-mimicking sauropterygian rather than a proto-ichthyosaur. Similarily, if the basal placement of Placodonts and *Wumengosaurus* (rather like the original basal placement of Mesoauria in the Sauropsida prior to the Reptilia) is due to their specialised adaptations and loss of shared character traits (synapomorhies) rather than their never having those traits in the first place, the placodonts, *Wumengosaurus*, nothosaurs, and pistosaurs are all groups that evolved from an original pachypleurosaur ancestral assemblage (rather like the bubble-ancestor in romerograms), the details of which need to be still worked out. MAK111125

Graphic: skeletal reconstruction (right), David Peters, Reptile Evolution. Photo of fossil (left), MarineReptile.org (Triassic and Later Marine Vertebrate Symposium, Guanling, China)

Links: Wikipedia

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

revised ATW080328, checked ATW030715, revised MAK111125

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

Sauropterygia: Placodontia

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--+--Paraplacodus PLACODONTIA
|  |   `--+--Placodus
|  |       `--Cyamodontoidea
|  |           |--+--Cyamodus
|  |           |  `--Henodus
|  |           `--Placochelyidae
|  |               |--Placochelys
|  |               `--Psephoderma
|  `--Nothosauria
|     |--Wumengosaurus
|     |--Pachypleurosauridae
|     `--+--Nothosauridae
|        `--Plesiosauria
|           |--Pliosauroidea
|           `--Plesiosauroidea
|              |--Elasmosauridae
|              `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Taxa on This Page

1. Placodontia X
2. *Placodus* X
3. *Psephoderma* X
4. Cyamodontoidea X
5. *Cyamodus* X
6. *Henodus* X
7. Placochelyidae X
8. *Placochelys* X

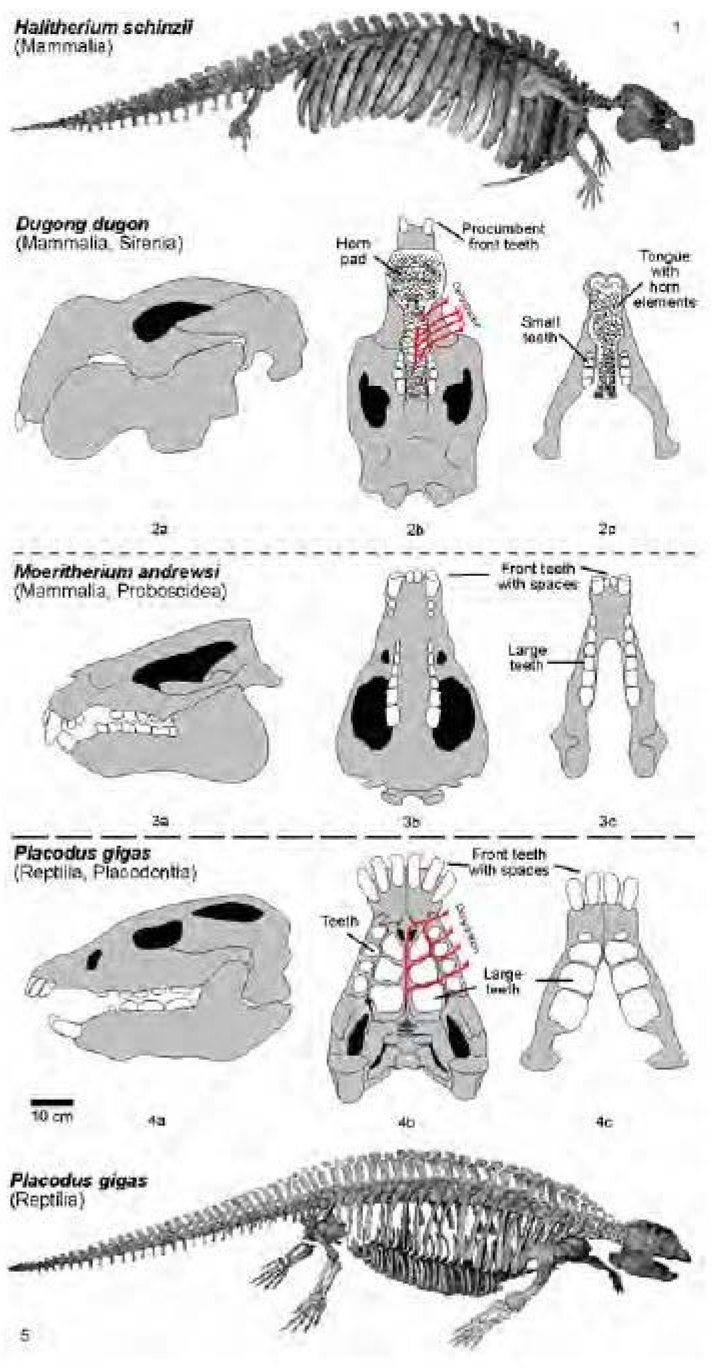
Evolutionary relationships

Like the thalattosaurs, hupehsuchians, hevetticosaurs, omphalosaurs, and ichthyosaurs, the placodonts are one of those specialsed groups of Triassic marine reptiles that are hard to place on the reptilian phylogenetic tree. Both a return to life in the sea, and specialised habit, conspire to create evolutionary forms very different from their ancestors. Who would have guessed for example that whales are descended from even-toped ungulates? For the most part, the consensus has been that they are diapsids, perhaps related to, but distinct from, the Sauropterygia, and being included with them, for example by Colbert and Romer, in the subclass Euryapsida. German Palaeontologist Oskar Kuhn in contrast gave them a subclass all of their own, considering they did not show clear relationships with any established reptile group (Kuhn 1969). In the last few decades however a number of systematists have firmly restablished the placodonts within the duiapsida, this time within the Sauropterygia, the only controversy being whether they are basal to (e.g. this cladogram) or more derived than (e.g. Storrs 1993 fig 3) the Pachypleurosaurs. In the view of one of the authors (MAK), the Pachypleurosauridae are a paraphyletic assemblafge (i.e. Pachypleurosauridae cladistically defined = Sauropterygia) so the question becomes irrelevant anyway.

Significantly, Placodonts were metabolically active, as they have the most advanced have the most advanced fibrolamellar bone tissue within the Sauropterygia (Klein 2010 p.23). This implies they may not have been as basal as they are portrayed in most sauropterygian phylogenetic hypotheses. Rather, as with the Mesosauria, which are placed by cladistic analysis at either the base of the Anapsida or the base of the Amniota, their highly specialsed nature and lack of easily recognisable shared characteristics means it is hard to know where they branched off. One possibility is that they are derived from fast-growing and hence physiologically more advanced, if otherwise morphologically primitive, pachypleurosaurs of the *Anarosaurus* type. MAK111103

Triassic sea cows

For as long as we've read about placodonts, one thing is always agreed upon. They used their large flat teeth to eat hard shelled food. For example, Wikipedia says: "Their diet consisted of marine bivalves, brachiopods, and other invertebrates. They were notable for their large, flat, often protruding teeth which they used to crush molluscs and brachiopods, which they hunted on the sea bed (another way in which they were similar to walruses). The palate teeth were adapted for this durophagous diet, being extremely thick and large enough to crush thick shell." It's probably not worth chasing up further refrences, though if you are curious a simple google search with the appropriate keywords should do the trick. This is not the case with all taxa - Darren Naish for example has written a fascinating post on Henodus the filter feeder. But Henodus was a late abbarent genus, remarkable for its toothlessness.



Convergent development in 1. *Halitherium* from the Oligocene of Europe, 2. the extant *Dugong*, 3. the Eocene *Moeritherium*, and 4-5. *Placodus* from the Middle Triassic of the central European Germanic Basin. (Both Placodus and Halitherium are about 2.5-3.0 meters in length). Diagram from Diedrich 2011, Copyright © 2011 SciRes.

Descriptions

Placodontia: (placodonts > plesiosaurs) *Paraplacodus*, *Placodus*, *Henodus*.

Range: Early to Late Triassic of Europe, North Africa & the Middle East.

Phylogeny: Either Sauropterygia **:** Nothosauria + * *or*, perhaps phylogenetricxally more accurately (if rather less cladistically rigorously)

Sauropterygia/paraphyletic pachypleurosauridae ::: * ; MAK111102

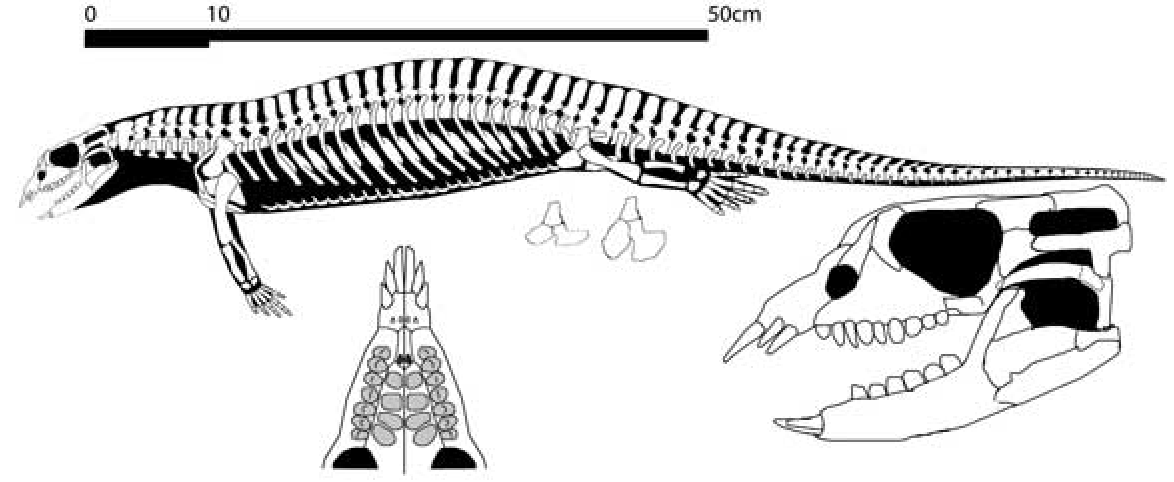
Skeleton of *Placodus gigas*, Staatliches Museum für Naturkunde, Stuttgart. Photo by Ghedoghedo. Wikipedia, GNU Free Documentation/Creative Commons Attribution.

Characters: Marine or amphibious, short (1-3m), very-wide walrus- or sea cow like bodies, relatively unspecialized for aquatic life. Massive consolidated skull; large flat teeth or plates; buck-toothed (procumbent) premaxillary teeth; neck short; pachyostosis; centra deeply amphiocoelous; long neural & transverse processes; ribs massive, giving body rather square outline; tail short; limbs and pectoral girdles poorly ossified; pelvis plate-like; dermal plate armor common, some with epidermal scutes; molluscivores.

Links: Placodonts by Darren Naish, Oceans of Kansas **Best on the Web**; Wikipedia; Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; Paleontology and Geology Glossary: Pl to Po (very basic coverage); Placodonts (very basic coverage). Checked MAK111102

Note: related to turtles, according to some. After studying pachypleurosaurs, we're a lot more sympathetic to this point of view. ATW061216, rev'd ATW080328.

Paraplacodus *P. broilli* Peyer 1931



Range: Middle Triassic of Continental Europe

Phylogeny: Basal Placodontia

Size: length 1.5 meters

Comments: Although a good ancestral type from which more advanced placondonts could be derived, this primitive placodont was already a highly specialised animal. MAK111102

Graphic: © David Peters Reptile Evolution, reproduced with permission.

Placodus Agassiz

Range: Middle Triassic of

Continental Europe

Phylogeny: Placodontia : Cyamodontoidea + *.

Characters: Skull not much longer than broad, superiorly arched, the snout somewhat produced. Premaxillae and symphysis of lower jaw with cylindro-conical incisors. On either side of the palate and on the dentary are three large rectangular pavement teeth ; maxillae with a single series of depressed, conical teeth. Detached teeth are abundant in the Muschelkalk of Southern Germany and France, rare in the Wellendolomite and Alpine Keuper - Zittel, 1902, *Text-book of Palaeontology*, vol.2 pp.187-8 (Public domain)

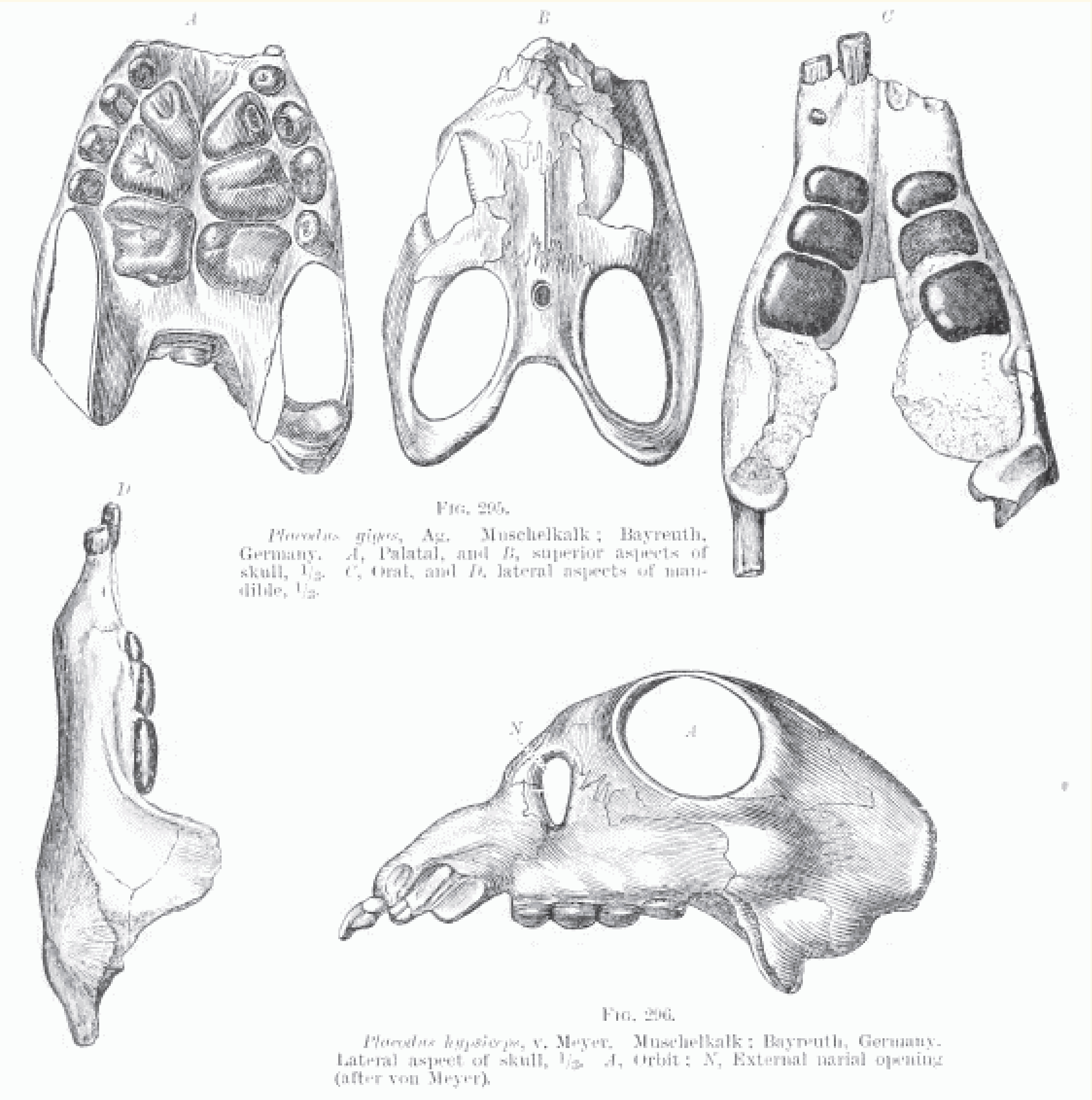


Fig. 295.

Placodus gigas, Ag. Muschelkalk ; Bayreuth, Germany. *A*, Palatal, and *B*, superior aspects of skull, 1/3. *C*, Oral, and *D*, lateral aspects of mandible, 1/3.

Fig. 296.

Placodus hypsiceps, v. Meyer. Muschelkalk : Bayreuth, Germany. Lateral aspect of skull, 1/3. *A*, Orbit ; *N*, External narial opening (after von Meyer).

Size: length to 2 metres

Comments: this is the classic placodont, a stocky body, long tail, short neck, short, heavy, dome-like skull, and distinctive large pavement like teeth. It is generally believed that the teeth were an adptation to a diet of shellfish, but Diedrich 2011 presents a strong case that they were actually an adaptation to eating seaweed. There is already the beginning of the armour that reaches such prominance in more advanced members of the group. Quoting Wikipedia: "The vertebral processes of Placodus dove-tailed into each other and were firmly connected, so that the trunk was rigid. The abdomen was covered with a special armor formed of the bent, right-angled abdominal ribs. Equipped with dense bones, heavy belly ribs, and a row of bony knobs above the backbone, Placodus was a heavily built and negatively buoyant creature that would have had no trouble staying on the seafloor to feed. This body armour would have offered protection from predators as well, but would have also hampered mobility on land, making Placodus slow and clumsy out of water." MAK111101

Image: Zittel, *Text-book of Palaeontology*

Cyamodontoidea

Range: Middle to Late Triassic of Europe

Phylogeny: Placodontia **:** *Placodus* + * **:** (*Cyamodus* + *Henodus*) + Placochelyidae

Comments: The higher placodonts, defined by more extensive armour and details of the skull. Reduced or absent premaxillary teeth and a turtle-like carapace composed of interlocking scutes -

References: Rieppel 2001; Naish, Placodonts

Cyamodus , v. Meyer. *C. rostratus*, Miinster sp

Range: Middle Triassic of Muschelkalk ; Bavaria.

Phylogeny: Cyamodontoidea **:** Placochelyidae + (*Henodus* + *).

Characters: Skull triangular, snout much compressed. Supratemporal vacuity elongated oval, nearly three times as large as the orbits, which are placed in anterior third of the skull. Anterior nares small, separate, nearly terminal. On either side of the palate are placed two or three rounded or elliptical-crushing teeth, the hindmost at least twice the size of the anterior. - Zittel, 1902, *Text-book of Palaeontology*, vol.2 p.188 (Public domain)

Henodus *H. chelyops*, Huene 1936

Range: Late Triassic of Gipskeuper (Early Carnian) of Tübingen, southern Germany.

Phylogeny: Cyamodontoidea **:** Placochelyidae + (*Cyamodus* + *.)

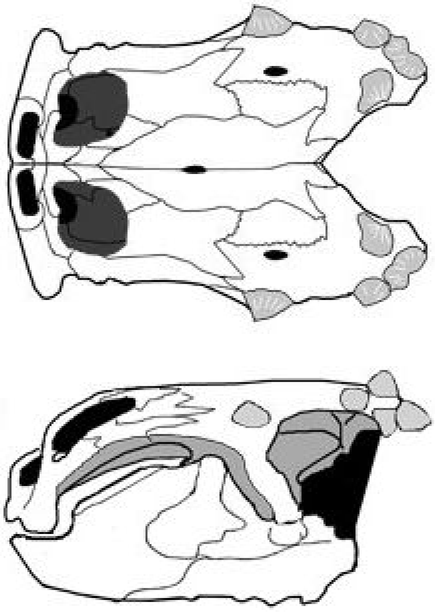
Characters: Skull broad and flat rostrum short; maxillary without tooth plates but with deep grooves (supporting baleens); palatine with single posterior tooth plate; upper temporal fenestra vestigial or absent (Rieppel 2001)

Size: overall length of about 1.2 meters

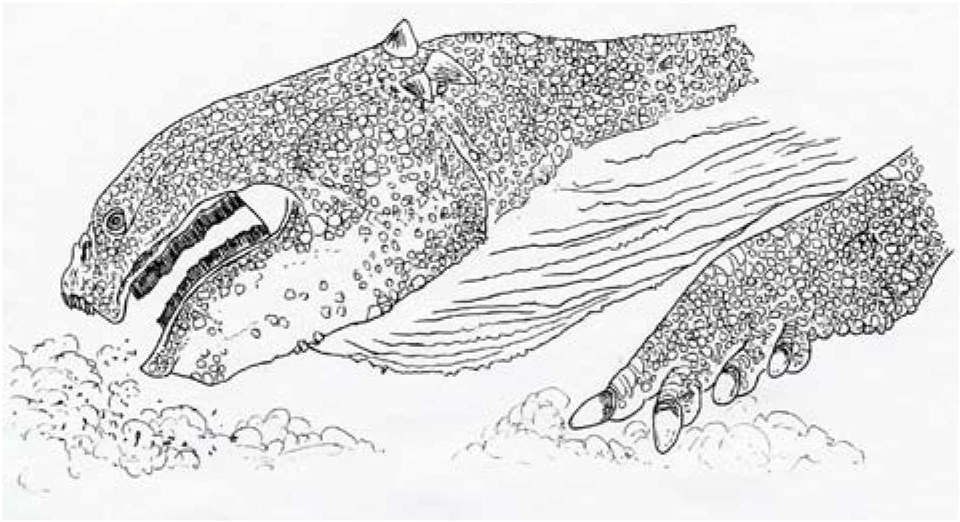
Comments: The only known non-marine placodont, it inhabited brackish or possibly freshwater lagoons, and may have fed on fishes and crustaceans as well as molluscs. As with the Ladinian *Placochelys*, it was a member of the Placodonta that had evolved to look like turtles, with a broad armoured carapace. The back and belly were covered with an armour of irregular, many-sided bony plates, the whole being completely covered with horn. The square toothless snout was equipped in life with a strong horny beak, another parallel with a modern turtle. Originally it was considered to be an advanced species, but recent research indicates that Henodus may actually represent a primitive form, and its late appearance in the fossil record explained by the fact that it was restricted to a peculiar environment that is not preserved in older rocks of the same region. [Rieppel and Zanon 1997).

Amazingly, this animal was actually a filter feeder, as Darren Naish explains. To quote:

> "the rediscovery in the 1990s of striations within the jaw grooves (originally reported in 1936) indicate that *Henodus* had baleen-like material fringing its jaws. Furthermore, long overlooked is that the premaxillae support a ventrally projecting flange with a sharp cutting edge. Even more surprising is that this cutting edge exhibits a row of toothlike denticles along its anterior surface. When considered together and compared with the feeding adaptations of turtles, these features suggest that *Henodus* was a filter feeder that employed depression of the heavy lower jaw and expansion of the throat to suck in food particles. It may have engulfed swimming invertebrates, filtered burrowing forms out from the substrate, or used the premaxillary flange and denticles to scrape algae off rocks or to cut off pieces of other kinds of aquatic vegetation. Clearly, reappraisal of this bizarre placodont has revealed hitherto unsuspected diversity in the ecology of Mesozoic marine reptiles."



The strange skull of *Henodus*. Note how far forward the eyes are. The spikes on the skull are reminiscent of ankylosaurs. Drawing copyright © David Peters, Reptile Evolution. See Darren Naish's Tetrapod Zoology page (right)for a close up photo and more detailed drawing



life restoration of *Henodus*, drawing copyright © Darren Naish, Tetrapod Zoology . At first it's hard to see the eyes, because we're used to them being positioned towards the back of the head. In Henodus they are over the front of the jaw, close to the nostrils

Links: Henodus, filter-feeding Triassic marine reptile; Wikipedia, Dinosaur fact net, Reptile evolution, About com (basic info), Checked MAK111102

References: *Dixon et al 1988*, Kuhn 1969, Naish 2000

,

Placochelyidae Romer, 1956

Range: Late Triassic of Europe

Phylogeny: Cyamodontoidea **:** (*Cyamodus* + *Henodus*) + * **:** *Placochelys* + *Psephoderma*

Comments: intrerpreted as reptilian rays, with flattened bodies and very long, slim tails (Mazin & Pinna 1993, ccited in Naish); narrow triangular skulls, pointed and toothless beaks, extensive, turtle-like carapaces; Naish, Placodonts

---

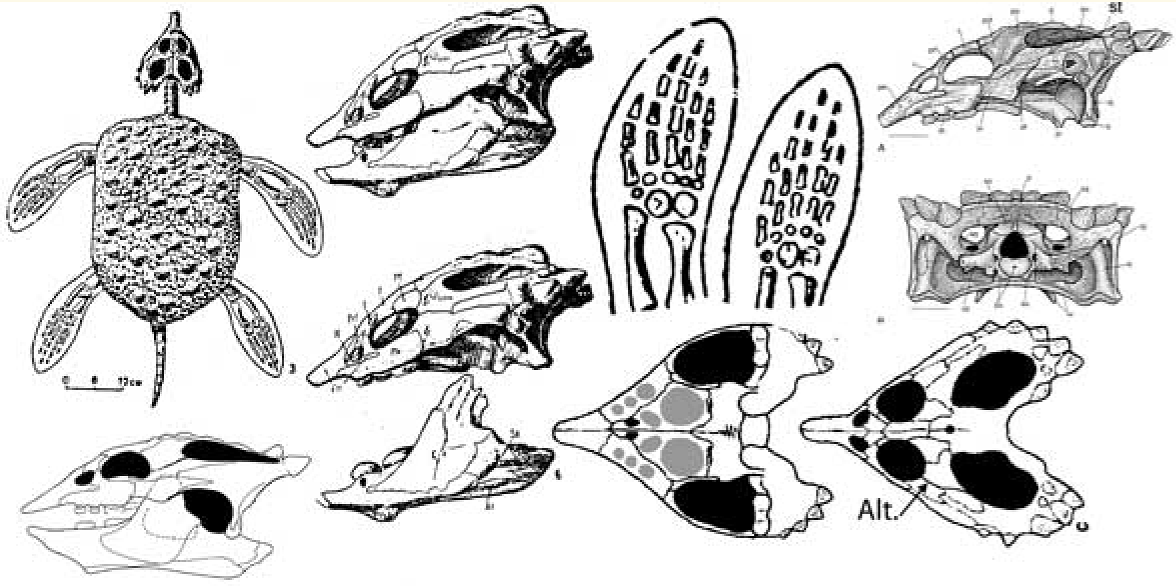
Placochelys *P. placodonta* Jaeckel 1902

Range: Late Triassic of Europe

Phylogeny: Cyamodontoidea **:** (*Cyamodus* + *Henodus*) + * **:** *Placochelys* + *Psephoderma*

Size: 90 cm

Characters: Shell highly



convergent with turtles. Three small, rounded teeth on each maxilla

Comments: intrerpreted as reptilian rays, with flattened bodies and very long, slim tails (Mazin & Pinna 1993, ccited in Naish); narrow triangular skulls, pointed and toothless beaks, extensive, turtle-like carapaces; Naish, Placodonts

Graphic: David Peters Reptile Evolution, adapted from Kuhn 1969.

Psephoderma

Range: Late Triassic (Latest Middle Norian (Calcari di Zorzino of Northern Italy) to Rhaetian) of Tethys Europe

Phylogeny: Cyamodontoidea : (*Cyamodus* + *Henodus*) + * : *Placochelys* + *Psephoderma*

Size: Norian specimens are at least 50% longer in linear dimensions than Rhaetic forms (the largest complete specimen is 180 cm long, but isolated teeth indicate it grew larger) so it is possible that these might be a different subspecies or even species.

Characters: two teeth on each maxilla, the posterior (rear) one larger

Comments: ray-analogue; the body is very broad and flattened. The discoidal carapace armour is in two parts, making the animal more mobile, there is a long thin tail, which does not seem to have been used in swimming. At least two species are known: the Tethyan *P. alpinum* and *P. anglicum* from the Rhaetian of England.

Graphic: photo by Ghedoghedo of *Psephoderma alpinum*, at the *Museo di Storia Naturale di Milano* Wikipedia, GNU Free Documentation/Creative Commons Attribution

Links: *Psephoderma* by Dr Silvio Renesto **Best on the Web**; Wikipedia; Psephoderma and nothosaurid by Kahless ; Paleo sculpture by Hirokazu Tokugawa; Paleobiology database, Prehistoric blog - Psephoderma (Polish) Checked MAK111102

Page Back | Unit Home | Page Top | Page Next

revised ATW080328, checked ATW030715; new page MAK111102

Palaeos
SAUROPTERYGIA
VERTEBRATES
PACHYPLEUROSAURIDAE

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

Sauropterygia: Pachypleurosauridae

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Pachypleurosauridae
|  |  |--Hanosaurus
|  |  `--+--+--Dactylosaurus
|  |     |  `--Anarosaurus
|  |     `--Serpianosaurus--Neusticosaurus
|  `--Eusauropterygia
|     |--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

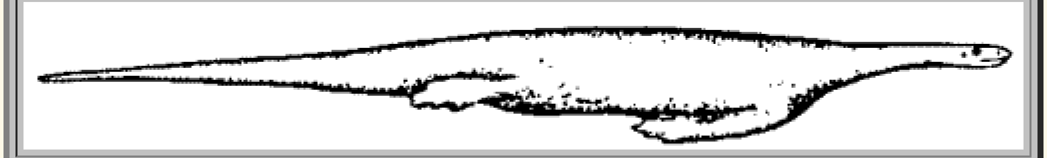
Contents

Taxa on This Page

1. *Hanosaurus* X
2. Pachypleurosauridae X

The Pachypleurosaurs

The pachypleurosaurs were small, lightly built lizard-like reptiles, generally less than a meter (the



***Neusticosaurus* edwardsii. Middle Triassic - Tethys Sea; length about 60 cm.**

smallest about 20 cm). They were clearly related to the nothosaurs, with which they were contemporary. For a long time the pachypleurosaurs were included among the nothosaurs, and originally even placed in the same family Nothosauridae. It is now coming to be realized that they represent a distinct group that was only related via a primitive sauropterygian common ancestor.

The neck is long but, unlike the Nothosauridae, the head is very small (like *Claudiosaurus*), so pachypleurosaurs probably fed on very small fish and Crustacea. Relatively small dorsal temporal openings in the skull also clearly distinguish the pachypleurosaurs from the nothosaur genera (and their close relatives) such as *Lariosaurus*, *Ceresiosaurus*, *Corosaurus*, *Paranothosaurus* and *Simosaurus*, in all of which the upper temporal openings are much larger than the orbits. The tail is deep and would have been used as a swimming organ. The legs were semi-flattened to serve as paddles, but the hips and shoulders were still powerful and functional enough to provide support on land. It is likely that these animals were able to crawl about on land like modern seals, dragging themselves by their strong forelimbs. As with the nothosaurids they were semi-aquatic forms, mostly lagoonal but also venturing out to sea, perhaps not unlike the modern marine iguana in that respect. Their small size meant however they probably did not venture out far, being primarily near-shore forms. MAK991211.

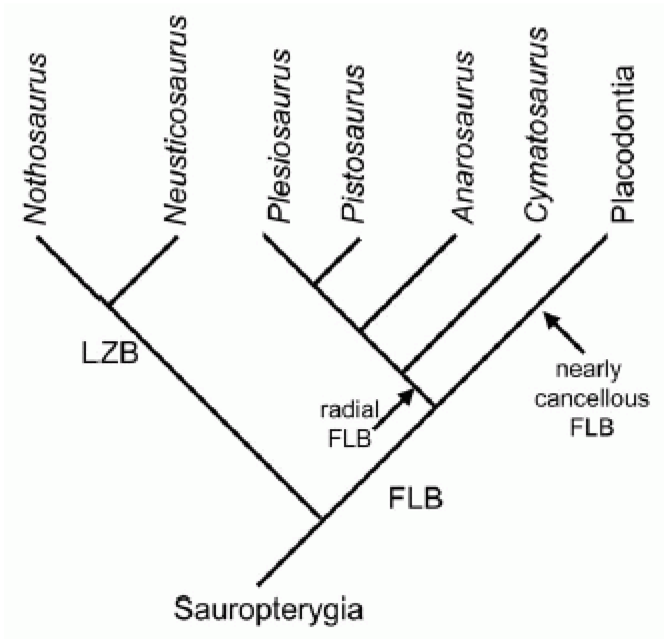
Clade or Grade?

Pachypleurosaurs are often portrayed as a monophyletic clade (Rieppel, 1989, Lui et al 2011) and sister group to the Eusauropterygia (Storrs 1993, Rieppel, 2000). The problem with this approach, as with Guathier's groundbreaking work on the theropod dinosaurs (Gauthier 1986), is that they don't take into account reversals (loss of shared character traits (synapomorhies)). convergences can also provide a misleading signal. Such cladograms produce *hypotheses* where there is an infinite regress of sister taxa and ghost lineages, in which no ancestor-descendent relationship can ever be recovered. Statistical parsimony analsyes give variying ersults, but often show these monophyletic ancestrors to in fact be a paraphyletic grouping of early ancestral types and persistantly primitive later types, as happened with the Ceratosauria; and with the pachypleurosauria where for example *Keichousaurus* is now understood as basal nothosaur Holmes et al 2008. Similarly, Wu et al. (2011) restudy, using new material, of the abarrent basal pachypleurosaur *Wumengosaurus* reject Jiang et al (2008) (who originally named the species) original assement of a monophyletic Pachypleurosauria, replacing it with a clade that includes the Nothosauroidea and those taxa assigned to the paraphyletic Pachypleurosauria.

The nothosaurs themselves still tend to be understood monophyletically, although they raise the same problem of ancestor-descendant relationship as they are intermediate in organisation between pachypleurosaurs and higher sauropterygia (pistosaurs and plesiosaurs). Here it is worth considering the possibility of a basal nothosaur like *Simosaurus* as ancestral to both specialised nothosaurs and plesiosaurs. Alternatively the pistosaurs and plesiosaurs may be derived from a primitive pachypleurosaur-like ancestor such as *Corosaurus*. MAK111125

Finally, long bone histological studies of Triassic sauropterygia reveal two quite different bone growth patterns, and imply a paraphyletic or even polyphyletic pachypleurosauria, quite distinct from the conventional gross-morphology based tree topologies (Klein 2010). Although one may question how much undistorted phylogenetic signal such studies provide, since various functional factors come into play as well (Cubo et al 2005), this is certainly one more factor to key into the overall picture.

Physiological diversity



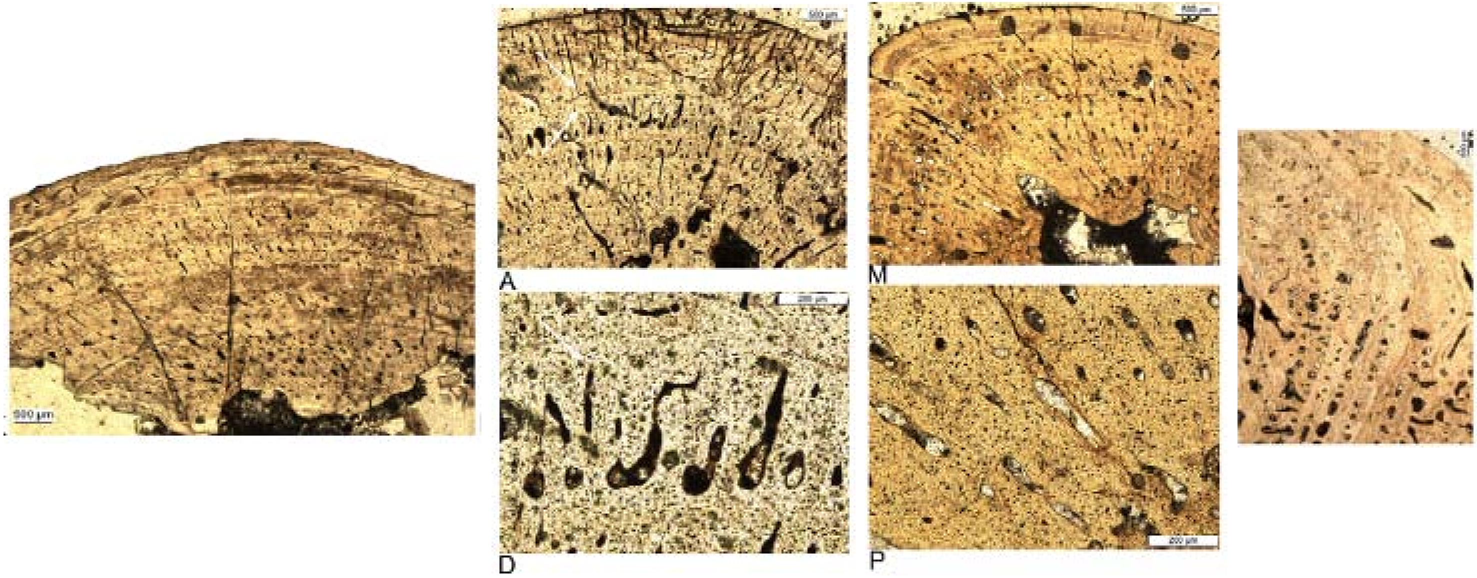
Phylogeny based on bone tissue types in Sauropterygia long bones, which differ markedly from standard tree topologies. Taking only bone histological data, pachypleurosaurs are polyphyletic because *Neusticosaurus* shows lamellar-zonal bone whereas *Anarosaurus heterodontus* has incipient fibrolamellar bone. *Cymatosaurus* already shows a radial vascular pattern and distinct layers of fibrolamellar bone within the parallel-fibered bone tissue. Placodonts have the most advanced bone tissue within Sauropterygia. LZB = Lamellar-zonal bone tissue type, FLB = Fibrolamellar bone tissue type. This hypothesis is not yet supported by a data matrix or phylogenetic analysis and thus remains provisional. Diagram and caption from Klein 2010, Creative Commons attribution license.

We think of the pachypleurosaurs as pretty uniform. All share a common long-necked and small headed but otherwise standard lizard-like form. The long neck itself may be a common aquatic adaptation, as it is also found in prolacertiformes and choristoderans. It seems however that these creatures were very metabolically diverse, as three distinct bone histologies are known (Klein 2010). This diversity dates back even to the early-middle Triassic (Anisian age) indicating a rapid evolutionary radiation. The two main types are:

The *lamellar-zonal bone (LZB) type*, the standard low metabolic reptilian type, which is the primtive or plesiomorphic condition for amniotes. It consists of lamellar bone with only low to moderate vascularization, and bone tissue is dominated by longitudinally arranged simple vascular canals (Klein 2010 p.3). Growth tends to be sporadic, indicating ectothermic metabolism. This bone type is associated with lepidosaurs, crocodiles, and turtles This is found in the *Serpianosaurus*-*Neusticosaurus* lineage (Hugi et al 2011). Surprisingly, nothosaurs (*Nothosaurus* (Klein 2010) and *Ceresiosaurus* (Hugi 2011) also shows this typical lamellar-zonal bone type, but not more advanced forms such as Pistosaurs. The implication may be that these two are related, and that nothosaurids evolved distinct from other higher sauropterygia ((Klein 2010).

The *fibrolamellar bone (FLB) type* in contrast involves a complex bone structure deposited very rapidly. It is highly vascularized (many blood vessels) and dominated by radial, laminar or irregularly arranged vascular canals. The FLB type is produced by fast growth rates. It always occurs in association high metabolic rates, and is typical of dinosaurs, extant birds, and large mammals. Growth is not only rapid but also constant, as evident in sauropods, large herbivorous mammals, and most birds. However, growth can also be cyclically interrupted, as in the case of many nonavian dinosaurs. (Klein 2010 p.3, see further references therein). Among sauropterygia, it is found in the pachypleurosaur *Anarosaurus* and in pistosaurs such as the basal *Cymatosaurus* and the more derived *Pistosaurus*, as well as in the crown group Plesiosauria (plesiosauroids and pliosauroids). What is extraordinary is that morphologically *Anarosaurus* is a very basal pachypleurosaur; we see here a disjunction between gross morphology and metabolism, which reminds us of the need for a total evidence approach.

The fibrolamellar pachypleurosaurs themselves are divided into two further groups, referred to in Klein 2010 as histotype A and histotype B. Both are dominated by a radial pattern of vascularization. However, vascular density is distinctly higher in histotype B. On average, vascular canals take up between 5% to 10% of histotype A bone tissue, but between 10% to nearly 20% in histotype B. Histotype B is associated with *Anarosaurus*, whereas, curiously, the somewhat less metabolically intense histotype A (although still superior to the nothosaur condition) is assocuiated with the ore advanced form, *Cymatosaurus*, although this association si tentative because *Cymatosaurus* is not known with certainty from postccranial material. In any case, this indictaes a whole range of different metabolic types evolving alongside each other. Finally, a sample of placodont bone vascular density is even higher than in histotype B, dominated by very large longitudinal canals, indicating an even higher level of metabolism. (Klein 2010)



Nothosaurus *Cymatosaurus* *Anarosaurus* Placodont

Histological details of sauropterygian long bones. Left, typical of *Nothosaurus* bone tissue and growth pattern, showing typically reptilian pattern of growth rungs and few haversian canals. Center, Typical histotype A bone tissue and growth pattern, attributed to *Cymatosaurus*, showing spaces for large blood vessels, hence rapid growth. Lower image is the same as the higher, but magnified. Right, Typical histotype B bone tissue and growth pattern (*Anarosaurus heterodontus*). Far right, cross section of cross section of placodont femur Photos from Klein 2010, Creative Commons attribution license.

If fibrolamellar bone was inherited by the Sauropterygia from a terrestrial ancestor, this could place their origin in the Archosauria, where fibrolamellar growth appears to be basic (Ricqles et al 2008 cited in Klein 2010) rather than the Lepidosauromorpha. Ironically, this would then enable Chelonii (turtles) to be both related to Sauropterygia (as proposed by Rieppel and others) *and* nested in the archosaurs (as molecular phylogeny seems to show). The problem is that this goes as much against all available morphology as crown archosaurian turtles do; if sauropterygians are archosauromorphs they much more likely branched off at a very basal level [1] On the other hand, the fact that *Neusticosaurus* and *Nothosaurus* show the more primitive, lamellar-zonal bone structure, supports the hypothesis of Lepidosauromorph origin (Lepidosauromorpha having retained the basal amniote lamellar-zonal condition) and implying that fibrolamellar bone developed multiple times within the Sauropterygia (Klein 2010 p.23).

It is however very unlikely that small lizard-like pachypleurosaurs were endotherms or in any way metaboloically similar to dinosaurs, birds, or mammals. There are limits to the reliability of such studies as metabolic indicators; Haversian or fibrolamellar bone is fairly common in young crocodilians and sometimes found in adults, it has also been found in turtles and tortoises, and temnospondyl amphibians, but is often absent in small birds, bats, shrews and rodents. (Enlow 1963, Reid 1984, Reid 1997 cited via Wikipedia, Ray et al 2009). In all other respects, pachypleurosaurs were classic reptiles with elongated bodies and broadly lizard-like appearance, lacking for example the long limbs and parasaggital (erect) gait of mammals and higher archosaurs (rauisuchia, dinosaurs, and birds). Endothermy would also have been a distinct disadvantage for a small aquatic animal due to loss of body heat. However, fibrolamellar bone does indicate rapid growth (Ray et al 2009). We can assume then that the sauropterygia adopted a number of distinct growth strategies. At one extreme there was the slow growing and classic reptilian regime of the neusticosaurs and nothosaurs; on the other the ultra-rapid growth of the anarosaurs and placodonts, which had an even higher metabolic growth rate when young than the pistosaurs and plesiosaurs. Once adult size was reached, anarosaurs and placodonts probably settled down to a typically reptilian liefstyle.

The question is, how much did these ontogenic, metabolic, and physiological processes factor in to phylogeny? On the basis of histological data alone, most current sauropterygian clades - Nothosauria, Pachypleurosauridae and Eusauropterygia - would be rejected, although the higher Pistosauroidea and the Plesiosauria are retained. *Neusticosaurus* is now related to *Nothosaurus*, whereas the basal pachypleurosaur *Anarosaurus* is relocated to the pistosaur clade, all of which gives a very different dendrogram topology. Further studies are required, ideally incorporating gross morphological, histological, and stratographic or stratocladistic methodologies, in order to arive at a better understanding of early sauropterygian phylogeny. MAK111101

Notes:

[1]John Merck favours thalattosaurs and Euryapsida (Ichthyopterygia + Sauropterygia) as the sister group to all other archosauromorphs (referenced in DML posting (Tom Holtz), see also Tom Holtz webpage) Cladograms given by Borsuk-Bialynicka & Evans, 2009 using using the data matrix of Müller 2004 also present thalattosaurs, ichthyosaurs and sauropterygia as basal archosauromorphs. Because of the uncertainty regarding the placement of these groups we have retained more traditional phylogenies, at least until further research confuiirms their archosauromorphian status

---

Descriptions

Pachypleurosauridae: Nopsca 1928. *Neusticosaurus* Seeley, 1882; *Anarosaurus* Dames, 1882; *Dactylosaurus* Bardet, 1992; *Hanosaurus* Lee, 1958; *Serpianosaurus* Rieppel 1989. *Pachypleurosaurus* and *Phrygosaurus* are considered *nomina dubia*, and have been sunk into *Neusticosaurus* and *Serepianosaurus*, respectively.

Range: Middle Triassic (possibly Early Triassic in China) (possibly to Late Triassic [CG85] [RK95] in Europe) of Central Europe & China. [R95].

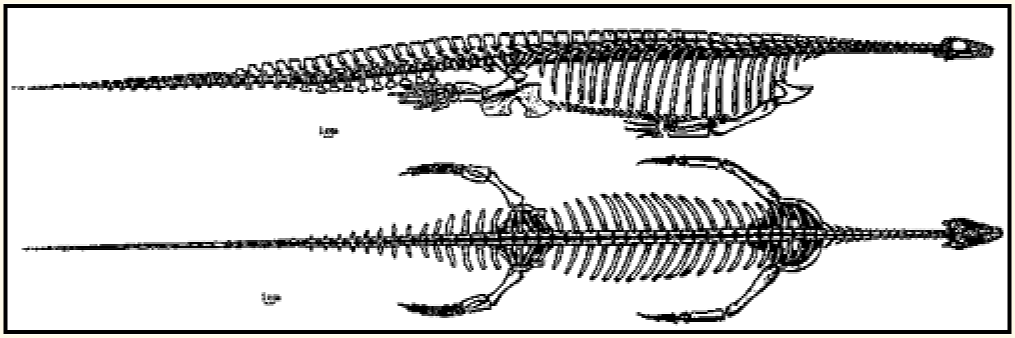
Phylogeny: Nothosauria **:** Eusauropterygia + * **:** *Hanosaurus* + ((*Dactylosaurus* + *Anarosaurus*) + (*Serpianosaurus* + *Neusticosaurus*)).

Characters: S-M size (<150 cm) [CG85]; similar to nothosaurs; skull unusually small [CG85]; skull not depressed as in Nothosauridae [R89]; prefrontal broad & domed [RK95]; frontals with concave lateral margin participating in orbit [RK95]; postorbital skull shorter than preorbital [R89] [RK95]; upper fenestra smaller than large orbit [CG85]; strong upper bar; no lower temporal bar [CG85]; UTF usually small [R89]; postorbital primitively enters margin of UTF [R89]; quadrate embayed (impedence-matching ear for airborne vibrations & thus amphibious?) (primitive) [R89] [RK95]; jaw joint not behind *occipital condyle* [R89] [RK95]; pterygoids expanded to completely cover braincase ventrally [CG85]; ectopterygoid absent [R89] [RK95] (*contra* [CG85]); jaws not elongated; jaw with retroarticular process bearing dorsal trough [RK95] **[3]**; anterior teeth nor strongly *procumbent* [RK95]; vertebrae *amphicoelous* throughout [R89]; long (18 cervicals) neck; dorsal vertebrae have low neural spines, thickened and dense (*pachyostosis* -- see Note); pachyostosis extends to ribs in more derived species; 3 sacral vertebrae; dorsoventral extension of vertebral spines near base of tail; girdles poorly ossified (thus obligate marine?); limbs not highly derived for aquatic life; sexual dimorphism in forelimb [ORS99]; interclavicle, posterior process rudimentary or absent [RK95]; radius slightly longer than ulna [RK95]; juveniles with entepicondylar foramen distal edge of ossified portion of humerus [R95]; iliac blade reduced to narrow dorsal process [RK95]; restricted to epicontinental & coastal areas. Appear to have originated in China and migrated to Europe via the northern border of Tethys Sea [RK95]. ATW070113.

Comments: Pachypleurosaurs are small (generally less than a meter), primitive, superficially lizard-like forms. Near-shore, coastal dwellers, they preferred equatorial regions and flourished briefly from the early Middle Triassic (Early Anisian) to the early Late Triassic (early Carnian). In size and appearance they were not very different to earlier Permo-Triassic diapsids like *Claudiosaurus*, from which they may have evolved (see note on conflicting sauropterygia hypotheses). Although specialised in a number of features, which has led to them being considered a monophyletic clade, they are the obvious ancestors for all other sauropterygians, and indeed, the only possible ancestral forms in the fossil record from which the other types could have evolved (through increase in size and loss of specialised features). Metabolically diverse, bone histology shows that they included both slow growing and fast growing lineages. MAK111125

Notes: [1] Pachyostosis, the thickening of bones, is common in recently aquatic tetrapods. Examples include mammalian Sirenia (e.g. manatees) and an unusual plesiosaur, *Pachycostasaurus*. deRicqlès (1989). *But see* Gaudant & Meunier (1996). This may have more to do with ballast for a benthic habit.

[2] The current belief is that the pachypleurosaur line forms part of the bridge between the Sauropterygian stem (*e.g.* placodonts) and the Eusauropterygia (*e.g.* plesiosaurs). The connection is an admittedly difficult one to make, but the fossil record gives few options. To make this phylogenetic region yet stranger, a prolonged stare at the pachypleurosaurs tends to bring turtles to mind -- yet another taxon of still-uncertain affinities. Look, for example, at the way the dorsal and caudal ribs seem to rise up above the level of the sacrum (the fused area of bone at the intersection of the pelvis and the spine) in some photographs of the nothosaur, *Keichousaurus*. Turtles are the only group of vertebrates with both sets of limb girdles inside the rib cage. Yet it would take little modification to give this unique character to a pachypleurosaur. The pachyostosis of the ribs, from which the group derived its name, is similar to the broad, heavy ribs of turtles. Although pachypleurosaurs themselves are unarmored, one group of placodonts has strikingly turtle-like armor. This relationship between sauropterygians and turtles was widely defended at the end of the last century. It seemed to fall apart, on details of skull anatomy among other things. However, the concept has recently been revived by Olivier Rieppel and others. The idea has also gained some support from DNA cladistics which tends to place the turtles up above the diapsid split, although their placement is sometimes (perhaps embarrassingly) closer to archosaurs than to lepidosaurs. However, given the total absence of (other?) living sauropterygians, a little uncertainty is only to be expected.



[3] The "trough" may be the same as what Sander (1989) identifies as a pit to receive the posterior process of the quadrate in *Neusticosaurus*. See Some Jaw Notes.

References: Carroll & Gaskill (1985) [CG85]; O'Keefe *et al*. (1999) [ORS99]; Rieppel (1989) [R89]; Rieppel (1995) [R95]; Rieppel & Hagdorn (1997); Rieppel & Kebang (1995) [RK95]. ATW070113.

Further note A monophyletic Pachypleurosauridae is supported by Rieppel 1989 Storrs 1993, Rieppel 1998 and Jiang et al 2008 but rejected by Holmes et al 2008 and Wu et al. 2011. Perhaps a distinction could be made between what seem to be a paraphyletic assemblage or evolutionary grade of basal forms and specialised monophyletic lineages of more typical pachypleurosaurs MAK111125

Hanosaurus: *H. hupehensis* Young 1972

Range: Middle Triassic (Anisian) Jialingjiang Formation of Nanzhang, Hubei province, China

Phylogeny: Pachypleurosauridae **:** ((*Dactylosaurus* + *Anarosaurus*) + (*Serpianosaurus* + *Neusticosaurus*)) + *.

Characters: elongate skull with long posterior orbits, no lower temporal opening, elongate supratemporal opening (Lucas, 2001,p p.115-6)

Comments: known from an incomplete skull and some postcrania, and originally interpreted as a thalattosaur, cladistic analysis by Reippel 1998 shows this species to be a basal pachypleurosaur close to *Keichousaurus*, and supports a sister group relationship between thalattosaurs and sauropterygia. This was further supported by Li et al 2011 who also make the Saurosphargidae the sister group of the Thalattosauriformes. However Holmes et al 2008's analysis presents *Keichousaurus* as a very primitive (basal in cladistic speak) nothosaur, and hence the the pachypleurosaurs as paraphyletic. It may still be that *Keichousaurus* and *Hanosaurus* are closely related, with one evolving to the nothosaurian condition, another to the pachypleurosaur state, although such ancestor-descendent interpretations fall outside cladistic methodology, which is based on phylogenetic hypotheses limited solely to sister group relationships MAK111125

Page Back | Unit Home | Page Top | Page Next

checked ATW090306, revised MAK111125

Sauropterygia: Pachypleurosauridae: *Dactylosaurus* & *Anarosaurus*

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Wumengosaurus
|  |--Pachypleurosauridae
|  |  |--Hanosaurus
|  |  `--+--+--Dactylosaurus
|  |     |  `--Anarosaurus
|  |     `--Serpianosaurus--Neusticosaurus
|  `--Eusauropterygia
|     |--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Taxa on This Page

1. *Anarosaurus* X
2. *Dactylosaurus* X

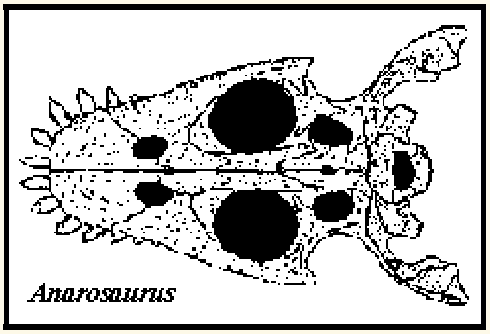
The Cast System

Pachypleurosaurs did not fare well in World War II. A number of important museum collections in Europe were destroyed during this war, including holotypes in the collections of, for example, the Zoologisches

Museum für Hamburg (now the Zoologisches Staatsinstitut und Zoologisches Museum), the Bristol City Museum, the Museo Civico di Storia Naturale di Milano, and Hiroshima University. In fact, from a historical perspective, the single most frequently-mentioned cause of destruction for vertebrate holotypes is bombing. And, of all wars fought in the last 200 years, World War II was the most destructive to fossils by a very large margin, due to the extensive, relatively unselective, bombing of metropolitan centers. *See*, for example, Benton *et al*. (2000) (holototype of *Thecodontosaurus antiquus*), Smith *et al*. (2001) (Stromer collection of Bahariya vertebrates), Leonard *et al*. (2005) (holotype of *Lithornis*), Dubrovo & Sanders (2000) (undescribed *Patriocetus sp*.), Grande & Bemis (1998) (holotype and only specimen of *Amiopsis*); Bennett (1996) (one of two specimens of "*Gnathosaurus*"), Damiani (2001) (only specimen of *Cyclotosaurus ebrachiensis*).

Dactylosaurus and *Anarosaurus* were the earliest European pachypleurosaurs. They are known only from very rare material excavated in Poland **[1]** and Germany. At the beginning of the war, the holotype of *Anarosaurus* was deposited in Göttingen, while two referred specimens were kept in Dresden and Jena, respectively. *All three* were destroyed. Thus, we have only casts made in the 1920s and 1930s. *Dactylosaurus* apparently differed from *Anarosaurus* in having much greater resistance to Allied bombing. No *Dactylosaurus* material was lost in the war. However, both known specimens of *Dactylosaurus* were natural molds to begin with.

Thus, both genera are now represented only by impressions. We are fortunate that pachypleurosaurs seem have had pleasant dispositions and thus left good impressions; and that their custodians had been disposed to impress a number of casts which were impressed upon various institutions for disposition in relatively bomb-proof structures, so that they may still be impressed for dispositive confirmation of the original published impressions, if one is so disposed .... But enough of that. The point, if any, of that extended linguistic exercise is that casts, like English words (and pachypleurosaurs for that matter), tend to diversify, accumulating small variations which may confuse interpretation.



Anarosaurus pumilio was initially distinguished from other pachypleurosaurs based on some oddly *spatulate* anterior teeth and a suite of metric characters. However, Rieppel & Kebang [RK95] found that the various casts had warped a bit over the years, making the metric characters unverifiable. Worse, they were unable to verify the shape of the teeth. One cast showed some indications of this feature, but it also showed other variations from the type. They therefore referred it to a new species, *A. heterodontus*. This creates some difficulty, in that the new species is mainly distinguished by having a characteristic supposedly apomorphic for the old.

Dactylosaurus was initially believed to have two species: *D. gracilis* and *D. schroederi*, each represented by a single specimen. Rieppel & Kebang conclude that these are juvenile and adult of the same species, *gracilis*. That's well enough, but the holotype of the genus becomes the *juvenile*. This is seriously awkward, since the juvenile differs in material respects from the adult form. We are forced to admit that, as a consequence, we ultimately gave up on *Dactylosaurus*. ATW070125

---

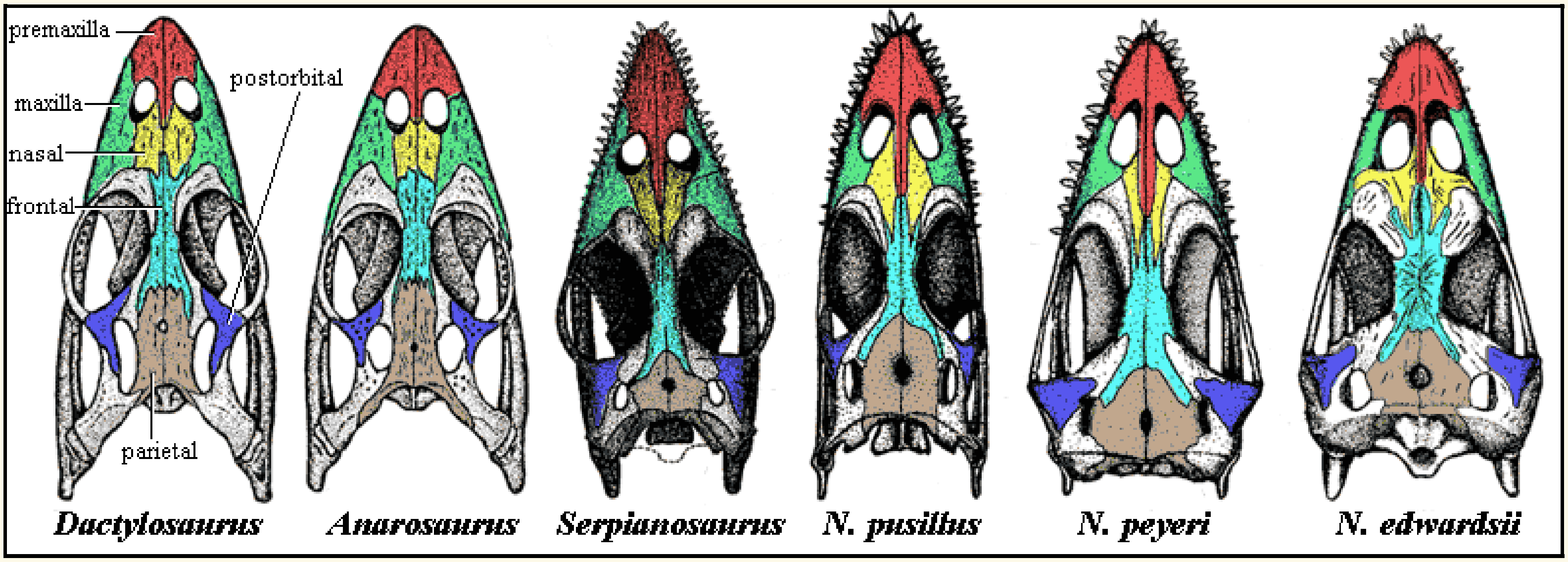
[1] *Dactylosaurus* is from Upper Silesia -- part of Germany at the time it was discovered, but now Polish territory. The historical information related to both genera is taken from Rieppel & Kebang [RK95]

The European Pachypleurosaurs

In spite of our own failings, the best efforts of the RAF, the limited stratigraphic range of the fossils, and many other difficulties, the European pachypleurosaurs still make a really interesting little group of closely-related species. It is one of the few such systems for which one can expect meaningful answers to questions about evolutionary trends. To our knowledge, no one has turned over this particular rock to see what might lie under it. We lack the qualifications to do the job, but we couldn't resist the temptation to take a peek at a few of the sights.

The European pachypleurosaurs are *Dactylosaurus, Anarosaurus, Serpianosaurus*, and three species of *Neusticosaurus*: *N. pusillus, N. peyeri, and N. edwardsii*. They have little or no stratigraphic overlap and occur in the order listed. Rieppel & Kebang (1995); Sander (1989). So we're looking at a rather clean replacement series, with no reason to suspect extensive bushiness to the local phylogenetic tree. Undoubtedly, some bushiness existed. Mutations being random, divergence in all directions is to be expected. The wonder is that, over the roughly 10 million years during which pachypleurosaurs are found in Europe, many of the variations seem to be headed in a fairly uniform direction. That is, we seem to be looking at bona fide long-term trends based on natural selection.

We're not going to try and guess what factors were applying selective pressures. The point is that the critters don't seem to have specialized to subdivide their ecological niche. Rather they kept moving along a trajectory. It isn't easy to say what that trajectory accomplishes in a functional sense. Let's look at a few examples from the skull.



In general, the skull becomes more triangular. The posterior extension of the jaw becomes consistently shorter, and the jaw articulation is actually anterior to the occipital condyle in *N. edwardsii*. The entire postorbital region of the skull takes on an increasingly blocky or inflated appearance, with a corresponding increase in the relative size of the squamosal. The orbit generally becomes larger, and the jugal bar longer and less curved.

The posterior process of the premaxilla becomes longer and cuts more and more deeply between the nasals. *Dactylosaurus* has a small posterior process which separates the anterior ends of the nasals and extends no further than the posterior rim of the nares. *Anarosaurus* may even lack a posterior process, contrary to the trend. However, the four species of the *Serpianosaurus-Neusticosaurus* group show progressive elongation of the process so that, in N. edwardsii, the premaxilla reaches the frontals and may entirely eliminate the midline contact of the two nasals. In *Serpianosaurus*, *N. pusillus* and *N. peyeri*, the suture between the nasals is superficially covered by the premaxilla, but the nasals continue to meet.

At the same time, the maxilla retreats from the midline. In *Dactylosaurus*, the maxillae broadly extend up the side of the snout, reaching well above the mid-point of the orbit and ending in a wide suture with the nasals. This broad ascending extension gradually becomes reduced to a narrow ascending process, losing a little altitude with respect to the orbit. In *N. edwardsii*, the ascending process is lost completely. Oddly, throughout the trajectory, the maxilla maintains control of the posterior margin of the naris.

The center of mass of the frontals and parietals consistently moves back on the skull, although the anterior margin of the frontals continues to send increasingly elaborate processes both anteriorly and posteriorly. Some of this posterior movement is at the expense of the parietal, which becomes more block-like. In fact, the parietals are wider than long in

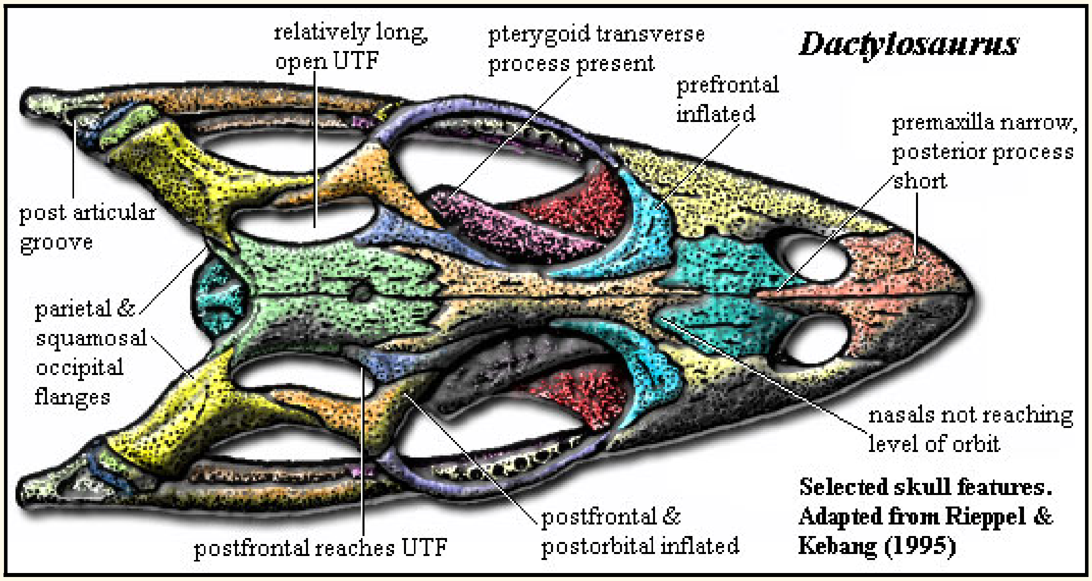
N. edwardsii. In the process, the upper temporal fenestra tends to become smaller and (except in *N. peyeri*) rounder. The posterior process of the postorbital consequently evolves from a long lower border for the UTF into a sharp intrusion into the body of the squamosal.

A few functional features seem clear enough. The entire system of sutures on the skull table is becoming more complex, more tightly knit and -- probably -- less flexible. The jaw muscles must have shifted considerably in the process, possibly trading efficiency and gape for speed.

Given these general trends, and the remarkably linear course of evolution in the European pachypleurosaurs, we might hazard a guess as to what was going on. At least one possibility is that pachypleurosaurs were specialist hunters trapped in a classic predator-prey arms race. Whatever habits *Neusticosaurus* may have had, the early pachpleurosaurs were almost certainly restricted to shallow waters. Other things being equal, prey animals in shallow waters will have less room to escape. When conditions are optimal -- analogous to, say, senior year in high school -- selection favors those with big mouths, rapid growth, and superior dating skills. However, specialist feeders are subject to drastic population bottlenecks when, for whatever reason, prey is absent. Then -- as in the junior year of college -- selection favors individuals who can move quickly, cover more territory, and aren't too picky. In a restricted basin like the Central European *Muschelkalk*, a coastwise range increase isn't possible. The only way to increase range is to dive deeper and, if possible, stay down longer. Thus, the most severe evolutionary pressures, over the long run, will be for diving efficiencies: stiffer neck and body, a more hydrodynamic skull, and a stronger, more pressure-resistant skull.

Maybe. It's only a scenario. ATW070127.

Descriptions



Selected skull features. Adapted from Rieppel & Kebang (1995)

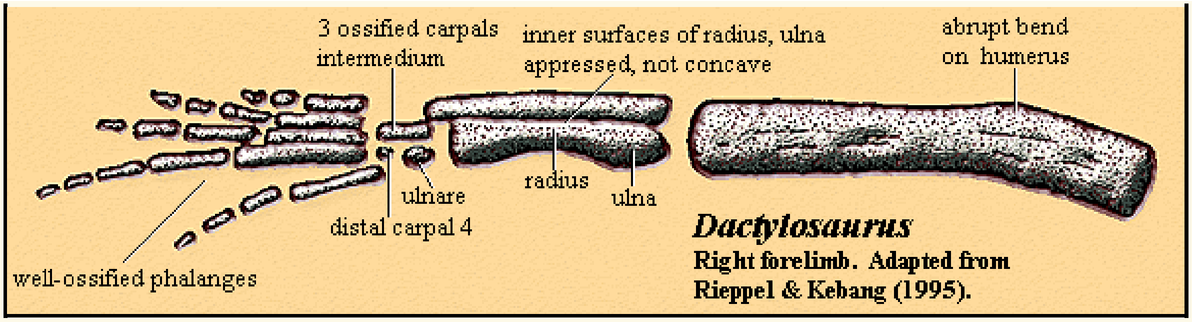
Dactylosaurus: Gürich 1884. *D. gracilis* Gürich 1884. *D. schroederi* Nopcsa 1928 is a junior synonym of *D. gracilis* [RK95].

Range: Middle Triassic (Anisian?) of Europe

Phylogeny: Pachypleurosauridae :::: *Anarosaurus* + *.

Characters: nasals meet & suture broadly [RK95]; process of frontal separates nasals and prefrontal **[1]** [RK95]; *UTF* large, *reniform* [RK95]; postfrontal & postorbital enter margin of UTF [R89] [RK95]; 17 cervical vertebrae [RK95]; cervical ribs with anterior process [RK95]; dorsal centra slightly inflated [RK95]; prezygapophyses appear as deep groove in lateral view, accommodating postzygapophyses of preceding vertebra so that articulation lies in transverse plane, restricting lateral bending [R89]; dorsal ribs without pachyostosis [RK95]; pectoral girdle standard pachypleurosaur plan (see *Neusticosaurus*) [RK95]; coracoid proximal expansion weak [RK95]; *deltopectoral crest* not differentiated [RK95]; *entepicondyle* not identifiable [RK95]; ulna and radius relatively gracile [CG85]; three ossified carpals [RK95]; intermedium long and rectangular [RK95]; manual phalanges 2-3-3-4-3, with unguals on at least 1&2 [RK95] .

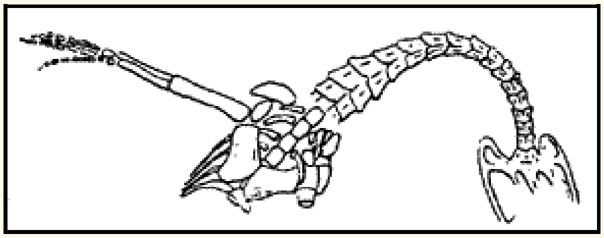
D. gracilis Gurich 1884 is known from only the anterior end of the skeleton (below), but the forelimb, especially



Dactylosaurus

Right forelimb. Adapted from Rieppel & Kebang (1995).

the ulna and radius, are much slimmer than those of *Neusticosaurus*. *D. gracilis* is the smallest known pachypleurosaur, it reached an adult degree of ossification (adult hardening of the bones) at a much smaller size than other forms. However, Rieppel & Kebang [RK95] believe the holotype is a juvenile.



Links: Plesiosaur Directory - Classification - Dactylosaurus; The systematic status of Hanosaurus hupehensis (phylogeny); Fossil Room (same); Species:Dactylosaurus gracilis.

Notes: [1] This is unclear. One side of Rieppel & Kebang's [RK95] reconstruction shows this feature, but the other side does not (see figure above). The specimen drawing of the cast on which the description was based shows no sign of a frontal-maxilla contact on either side.

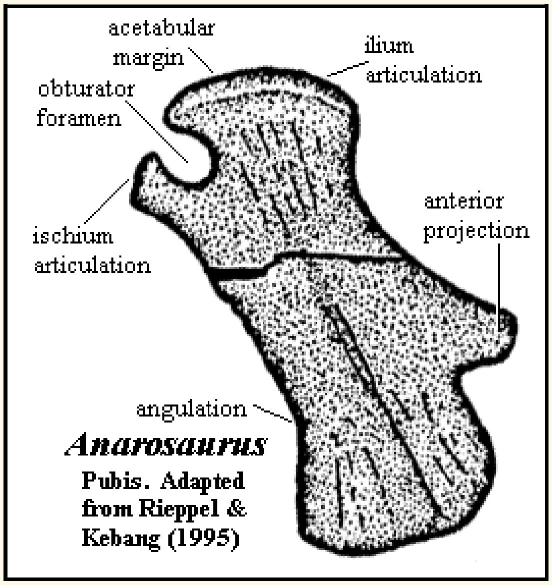
References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]; Rieppel & Kebang (1995) [RK95]. MAK991210, ATW070113.

Anarosaurus**:** Dames, 1890. *A. pumilio* Dames 1890; *A. heterodontus* Rieppel & Kebang 1995; *A. multidentatus* Huene, 1958, has been referred to *Cymatosaurus* (Nothosauridae).

Range: Middle Triassic of Europe (Lower Muschelkalk -- Anisian epoch).

Phylogeny: Pachypleurosauridae **::::***Dactylosaurus* + *.

Characters: quite small; premaxilla broad, forming anterior half of naris [RK95]; premaxilla with slender posterior process not extending beyond posterior margin of naris [RK95]; prefrontal well-separated from postfrontal [RK95]; frontals partially fused, long & slender [RK95]; parietal foramen small [RK95]; parietal forms *UTF* medial margin [RK95]; parietal with tapering processes extending onto occiput [RK95]; UTF larger than in *Serpianosaurus* or *Neusticosaurus* [R89] [RK95]; postfrontal participates broadly in UTF [RK95]; postorbital ventral process with facet receiving jugal [RK95]; postorbital reaches & broadly participates in upper temporal fenestra [CG85] [R89] [RK95]; supraoccipital large, with low crest along midline [RK95]; pterygoid lateral edge with distinct ventral ridge along anteromedial & medial margins of *subtemporal fossa* [RK95]; *retroarticular process* with trough on dorsal surface [RK95] **[2]**; some anterior teeth with crown having *spatulate* expansion [RK95] **[1]**; anterior teeth elongate [R89]; 45 presacral vertebrae [RK95]; 19-20 cervical centra with ventral surface bearing paired longitudinal keels [RK95]; cervical vertebrae with *pachyostosed* neural arches bearing low spines [RK95]; cervical ribs distinct with anterior processes close to articular head [RK95]; large number (25-26) dorsal vertebrae [RK95]; dorsal centra slightly constricted [RK95]; ribs without pachyostosis [R89] [RK95]; gastralia with 5 elements [R89] [RK95]; 2 gastralia per vertebra [RK95]; 3 sacrals with slight proximal expansion [RK95]; humerus slightly curved, with concave medial margin, well-developed deltopectoral crest & broadly expanded distal region [RK95] humerus ectepicondylar groove present [RK95]; *entepicondylar foramen* well set off from distal end [RK95]; ischium with narrow acetabular region, strongly convex anterior & posterior margins, & widely expanded ventral portion with convex ventral margin [RK95]; *obturator foramen* open [RK95]; pubis with distinct anteriorly-directed process **[3]** [RK95]; femur ~30% longer than humerus (proportionately much larger than in other pachypleurosaurs) [CG85] [RK95]. ATW070113



Anarosaurus

Pubis. Adapted from Rieppel & Kebang (1995)

Comment: strangely for such a primitive form, *Anarosaurus* possessed fibrolamellar bone like that of pistosaurs and plesiosaurs, implying rapid growth and perhaps greater physiological and (at least when young) metabolic development. This is unlike the lamellar-zonal bone type of the stratigraphically later and morphologically more derived (advanced) Neusticosaurus which one would expect to be more advanced in this respect. It is also different to that of *Nothosaurus* (Klein 2010) and *Ceresiosaurus* (Hugi 2011). It may or may not indicate a phylogenetic relationship with primitive pistosaurs such as *Cymatosaurus*. MAK111103

Links: classification; Untitled Document; Species:Anarosaurus pumilio; Triassic- Netherlands;

Notes: [1] the holotype was lost or destroyed during World War II. Rieppel & Kebang [RK95] worked from deteriorating casts made 70 years earlier by Nopsca. Sensibly, they assumed that the older observations were correct, although they could not completely confirm this point with the existing material. Our illustration is probably from Zeitl, who had studied the original material.

[2] This might be the same as the facet for the posterior process of the quadrate as described for *Neusticosaurus*. See **Jaw Notes**.

[3] The same structure is found in younger specimens of *Serpianosaurus* [R89].

References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]; Rieppel & Kebang (1995) [RK95]. MAK991210, ATW070113.

Page Back | Unit Home | Page Top | Page Next

checked ATW050109

Sauropterygia: Pachypleurosauridae: *Serpianosaurus*

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Wumengosaurus
|  |--Pachypleurosauridae
|  |  |--Hanosaurus
|  |  `--+--+--Dactylosaurus
|  |     |  `--Anarosaurus
|  |     `--+--Serpianosaurus
|  |        `--Neusticosaurus
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

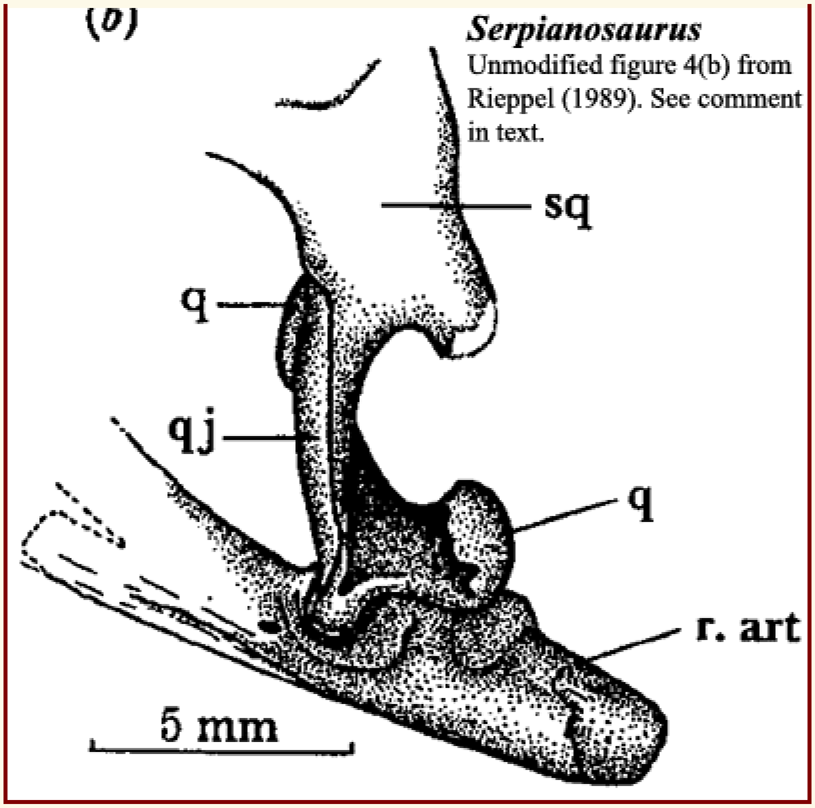
Contents

Taxa on This Page

1. *Serpianosaurus* X

Descriptions

Some Jaw Notes



Serpianosaurus
Unmodified figure 4(b) from Rieppel (1989). See comment in text.

Superficial Problems: There seems to be a little confusion about the structures near the jaw articulation in the *Serpianosaurus* - *Neusticosaurus* clade. The confusion may be entirely our own. However, after carefully reviewing all three comprehensive descriptions of this area (*i.e*. [CG85], [R89], and [S89]), we still don't see exactly how matters are arranged. We add this querulous note because we tried -- but failed -- to understand this tricky region enough to supply the usual colored images. Because we failed, our images of this region are inconsistent and unreliable. We supply the blow-up of an image from Rieppel's [R89] description of *Serpianosaurus* by way of illustrating the problem.

This image shows the jaw articulation in a sort of postero-latero-dorsal view. Most of the difficulty is related to the *retroarticular process*. Notice the vague labeling. Many published figures show the articular as making an appearance at the very tip of the retroarticular process, and, surely, the articular is also the surface of the lower jaw in direct contact with the quadrate. OK. Then what is the superficial bone separating the two exposures of the articular? Rieppel doesn't identify it. According to Sander [S89: fig. 4], it might be the surangular (in his fig. 4(a)), the angular (in 4(b)), or perhaps nothing (*i.e.* the articular exposures are not separated, as in his fig. 4(c)). Inspection of Carroll & Gaskill [CG85: fig. 14] suggests that the articular is covered distally (14e) or perhaps not (14a). If there are two separate exposures, the intervening surface may be by the surangular (14a, 14g), or perhaps the prearticular (14c).

Fitting In: For that matter, how exactly does the quadrate actually meet the articular? Unlike the first question, this one turns out to have a consistent answer. Sander [S89] provides a convincing illustration of three pits on the dorsal surface of the articular region, two sitting side-by side anteriorly, and a third just posterior to this pair. He identifies the anterior pair as receiving a double quadrate *condyle*, while the posterior receives the posterior process of the quadrate. This same process likely supported a tympanic membrane. [CG85] [R89]. All agree that the posterior process of the quadrate also tended to support the jaw while it was opening, and the anterior condyles carried the load during jaw closing.

Keeping a Stiff Upper Lip: This answers our question, but raises a slight additional difficulty: one that is unexplained, but probably not inexplicable. The medial part of the quadrate is also supposed to have formed a more or less rigid articulation with the recessed *quadrate ramus* of the pterygoid. The posterior part is supposed to have carried a tympanic membrane, as mentioned. What happened to these articulations in life? Note that water pressures would be fluctuating up and down on the tympanic membrane as a function of depth, while mechanical strains on the quadrate shifted back and forth between the three supports as a function of jaw position. The whole arrangement looks suspiciously awkward when looked at from this point of view.

Perhaps it *was* awkward, but we are simply overlooking a strong functional reason to maintain this complex arrangement. One of the peculiar things about pachypleurosaurs is the conflict between their anatomy and their *taphonomy*. Pachypleurosaurs had an inflexible quadrate with a tympanum. The usual inference from this anatomy is that they lived and hunted in very shallow seas, since their ability to dive would have been extremely limited [CG85] [R89]. However, the remains of pachypleurosaurs are actually found in conditions suggesting unusually deep, quiet waters with little postmortem transport [S89]. Sander points out, in particular, that even the gastralia and tail are often preserved in articulation. This implies that water pressure was high enough to prevent disarticulation from the usual prolonged floating and "blow-out" caused by the accumulation of decomposition gasses in the gut. Any number of odd circumstances could explain this disparity; but our favorite, among equally unsupported speculations, is that the funny-looking jaw articulation sustained a pressure-relief system for the middle ear.

Life reconstruction of *Serpianosaurus mirigiolensis*.
Artwork by Smokeybjb. Wikipedia, GNU Free Documentation/Creative Commons Attribution.

Other Pressure Points: In addition to (possibly) dealing with changes in external pressures of a physical nature, the jaw articulation is also trying to tell us part of a bigger story about evolutionary pressures. As we mentioned on a previous page, this is paleohistory in the style of William Faulkner or Günter Grass. That is, the tale has lots of interesting characters and memorable vignettes; but it's hard to say what the plot is. We can't even reconstruct the exact order in which events occurred. However -- in addition to providing the reader with this gold-plated example of utterly pointless literary name-dropping -- we will list a few evolutionary issues in the pertinent Middle Triassic phylospace:

1. Shift of the main jaw articulation to the posterior process of the quadrate in other Nothosauria, but not pachypleurosaurs. Rieppel [R89] provides a very satisfactory functional explanation of this phenomenon.

2. Gradual posterior shift of the jaw articulation to a point behind the *occipital condyle* -- probably related to #1; except that pachpleurosaurs seem to have moved in the opposite direction.

3. Lengthening of the dentary tooth row, *without* a corresponding expansion of the upper jaw dentition.

4. Increase in the size of the quadratojugal and a trend towards covering the quadrate in lateral view.

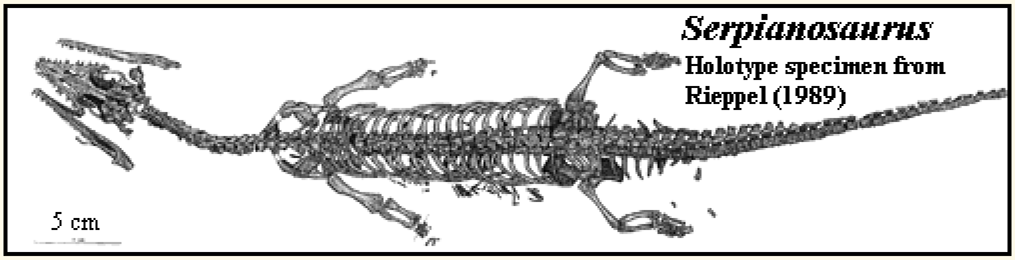
5. Gradual loss of the *coronoid process*, but (usually) retention of the coronoid bone.

6. Increase in stiffness and consolidation of the lower jaw, the palate -- and almost everything else.

ATW070103

Descriptions

Serpianosaurus**:** Rieppel [R89]. *S. mirigiolensis* Rieppel [R89]. The type was previously included in *Neusticosaurus ("Pachypleurosaurus") edwardsii* by Peyer 1932 and Zangerl 1935 [R89]. The type was also "informally referred" to *"Phygosaurus"* Arthaber 1924. [R89] argues that *"Phygosaurus"* is a *nomen dubium*, *i.e.*, the type has been lost and the descriptions are not diagnostic to genus [R89]. *S. zinae?* (may be a *nomen nudum*).

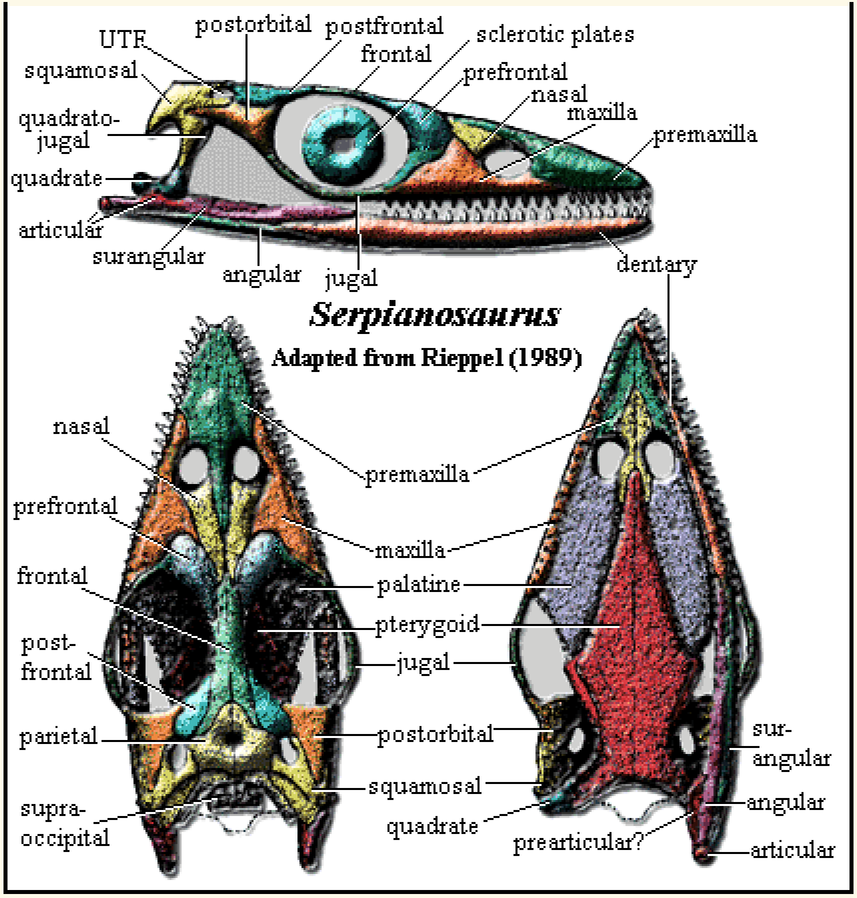


Range: Middle Triassic (Anisian/Ladinian boundary -- probably restricted to earliest Ladinian) of Europe (Switzerland) [R89] [S89] [R95].

Phylogeny: Pachypleurosauridae ::: *Neusticosaurus* + *.

Characters: medium-sized, with glenoid-acetabulum length up to 19 cm [R89];

dermal skull: **[1]** skull relatively long [R89];



Serpianosaurus

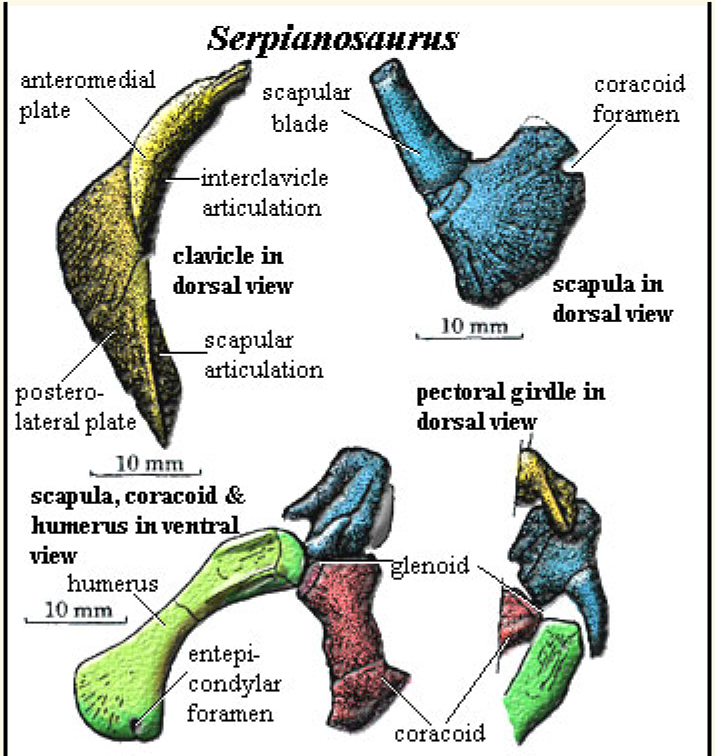
Adapted from Rieppel (1989)

premaxilla broad, meeting maxilla broadly along suture from anteroventral naris, anteroventrally to edge of snout [R89]; anterior sides of snout straight (not convex) [R89]; maxilla long, low, forming ventral & posterior margin of naris [R89] maxilla with ascending process between naris and prefrontal [R89]; maxilla tapering posteroventral process underlying contact between anterior tip of jugal and prefrontal [R89]; strap-like nasal reaching naris, separating deep posterodorsal process of premaxilla and ascending process of maxilla [R89] frontals and premaxillae variably separate nasals, but never contact, so that nasals always have some medial suture in dorsal view [R89]; nasals without descending process [R89]; lacrimal absent [R89]; prefrontal curved, slightly inflated dorsally, forming anterior margin of orbit [R89]; prefrontal with flat process forming anteroventral margin of orbit [R89]; frontal with facet for posterodorsal process of prefrontal [R89]; frontals usually variably fused, forming dorsal orbital margins [R89]; frontal with deep posterolateral process partially separating parietal and postfrontal [R89]; frontal does not reach UTF [R89]; UTF small, bordered by squamosal, parietal, postfrontal & sometimes (narrowly) by postorbital [R89]; parietals not fused, enclosing large pineal foramen at mid-length [R89]; UTF small and sometimes triangular [R89]; transverse ridge above parietal & squamosal occipital flanges [R89]; anterior tip of jugal embedded in deep facet on posteroventral maxilla [R89]; jugal thin, curved, running between posteroventral tip of prefrontal and anteroventral tip of postorbital to form ventral and posteroventral orbit margins [R89]; postorbital triradiate [R89]; postorbital descending process receives posterior tip of jugal [R89]; postorbital posterior process deeply penetrates squamosal, but more ventrally than in *Neusticosaurus* [R89]; squamosal bordered medially by UTF and parietal [R89]; squamosal forms posterior part of temporal embayment [R89]; posterolateral process of squamosal covers dorsal head of quadrate in lateral view [R89]; quadratojugal relatively small, on lateral quadrate below squamosal [R89]; for articular region, see note; dorsal occiput deeply embayed with occipital flanges of squamosal and parietal [R89]; supraoccipital rectangular and "typically projects beyond the posterior margin of the parietal skull table" **[2]** [R89] supraoccipital with ossified ascending process (under parietals) [R89]

palate & braincase: anterior palate as in *Neusticosaurus* **[3]** [R89]; "the palatal shelf of the maxilla ... excludes the palatine bone from the lateral [but not posterior] margin of the internal naris **[4]** [R89]; vomers partially split premaxillary shelf and form medial margins of choanae [R89]; palatines very thin [R89]; pterygoids meet broadly along ventral midline, overlapping vomers & forming wide plate extending back to occiput & covering braincase [R89]; pterygoid with broad quadrate ramus meeting medial surface of quadrate [R89] quadrate ramus set off from palatal surface by curved ridge (possible origin of deep portion m. pterygoideus) [R89]; ectopterygoid probably absent [R89];

jaw& dentition: dentaries straight [R89]; dentaries weakly joined at *symphysis* [S89]; dentary extends to just behind a low *coronoid process* [R89]; angular covers ventral & lateral face of jaw [R89]; anteromedial dentary overlapped by splenial, extending almost to symphysis [R89]; articular covers ventral face of*retroarticular process* [R89]; but articular underlies mandibular joint [R89]; coronoid present, running anteriorly from apex of coronoid process [R89]; palatal dentition absent [R89]; teeth with *thecodont* implantation [R89]; 6-8 functional(??) premaxillary tooth positions [R89]; 15-16 maxillary tooth positions, with alternate replacement posteriorly [R89]; >30 dentary tooth positions, more closely spaced in middle portion [R89] **[5]**;

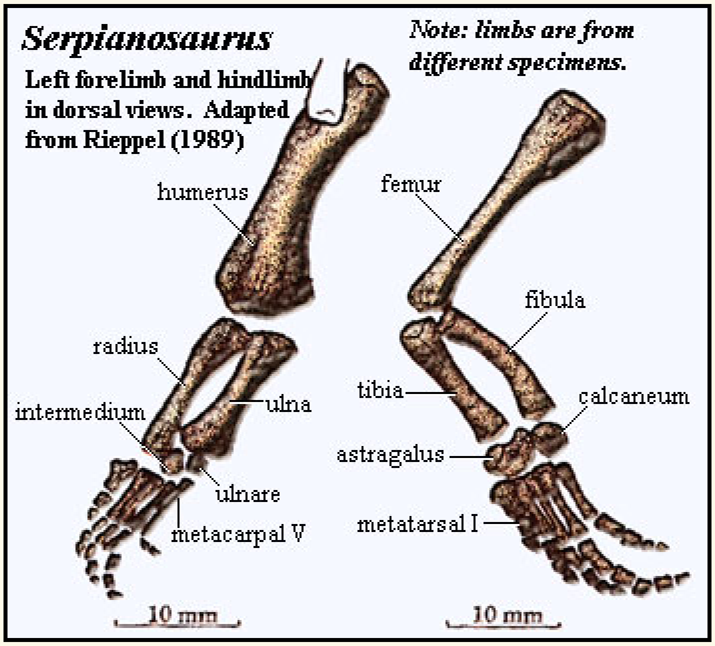
axial: long trunk (glenoid-acetabular distance 20 cm v. total length 75 cm) [CG85]; 35-38 presacral vertebrae [CG85] [R89]; centra *amphicoelous* [R89]; *neurocentral suture* present throughout [R89]; all vertebrae (except



Pectoral girdle elements. Adapted from Rieppel (1989).

posterior caudals) bearing accessory articulation as in *Neusticosaurus*, with unpaired anterior medial projection from base of neural arch articulating with facet between *postzygapophyses* of next anterior vertebra [R89] **[6]**; ribs with relatively little *pachyostosis* [CG85]; cervicals gradually increase length & breadth in dorsal view, [R89]; cervical spines low [R89]; cervicals with short transverse process bearing *diapophysis* [R89]; cervical *parapophysis* on centrum, just posteroventral to diapophysis [R89]; ribs increase in size & curvature to anterior dorsals, becoming shorter in posterior dorsals [R89]; cervical ribs with anterior process bridging gap to (i.e., possibly articulating with) next anterior rib [R89]; transition to single-headed dorsal ribs not as abrupt as in *Neusticosaurus*, involving *synapophysis* [R89]; dorsal vertebra without parapophysis and with increasingly prominent of diapophysis on arch, which moves to anterior position on arch, with increasing breadth of transverse process [R89]; dorsal centra with smooth ventral surface [R89]; dorsal centra with slight pachyostosis across *zygapophyses* [R89]; prezygapophyses appear as deep groove in lateral view, accommodating postzygapophyses of preceding vertebra so that articulation lies in transverse plane, restricting lateral bending [R89]; dorsal neural spines higher posteriorly [R89]; dorsal ribs without pachyostosis [R89]; gastralia with 5 elements [R89]; 3-4 sacrals [R89]; sacral ribs not *ankylosed* to centra, showing broad proximal head retaining "indications of the *dichocephalous* condition" [R89]; sacrals with extensive transverse processes, formed by both centra and arches [R89]; most anterior caudal ribs may bend anteriorly as if associated with pelvic girdle [R89]; 47-58 caudals [R89]; caudals with no pachyostosis [R89]; anterior caudals similar to sacrals, continuing increasing height of neural spines, peaking at caudals 3-5 [R89]; transverse processes and ribs persist in tail, but become smaller and shift ventrally on centrum [R89]; caudal neural spines with increasing posterior slant [R89]; caudal ribs disappear about caudal 11 [R89]; abrupt disappearance of neural spine at caudals 15-17 [R89]; hemal arches as in *Neusticosaurus*, but inexplicably absent in some well-preserved specimens [R89];

appendicular: interclavicle & clavicles form straight, solid transverse bar behind presacrals 15-18 [R89]; dermal pectoral girdle unlike *Neusticosaurus* in being much narrower and usually disarticulated [R89]; interclavicle entirely posteroventral and superficial to clavicle, sometimes with posteromedial extension [R89]; clavicle with anteromedial and a posterolateral plates at angle of ~120º [R89]; clavicle, posterolateral plate variably overlaps scapula [R89]; scapula with distinct ridge separating origins of dorsal & ventral pectoral muscles [R89]; scapula with narrow blade marked off by notch [R89]; scapular contribution to glenoid with strong ridge (compared to *Neusticosaurus*) [R89]; medial coracoid ossified (unlike *Neusticosaurus*) [R89]; coracoid anterolateral corner contributes to *glenoid* [R89]; coracoid meets ventral scapula in straight, transverse suture [R89]; humerus weakly curved [R89]; humerus distally expanded & flattened, with smooth convex or slightly *angulated* articulation (separating the radial & ulnar articulations) [R89]; humerus distal articulations not extending to ventral surface (so little flexion) [R89]; *ectepicondylar foramen* absent [R89]; humerus with strong sexual dimorphism [R89]; radius longer and projects beyond ulna [R89]; proximal radius and entire ulna shaft with concave facing surfaces [R89]; *olecranon* absent, allowing *epipodials* to project straight out from humerus [R89]; of carpals, only ulnare & intermedium ossified [R89]; metacarpal I shorter than others, & III longest [R89]; proximal metacarpals slightly overlap **[7]** [R89]; phalangeal count 2-3-4-4/5-3; ilium (see


Serpianosaurus

Left forelimb and hindlimb in dorsal views. Adapted from Rieppel (1989)

Note: limbs are from different specimens.

Neusticosaurus image for general scheme of pelvic girdle) small & dorsally constricted (= short anteroposteriorly?), broadening ventrally to contribute to *acetabulum* [R89]; pubis plate-like, with expanded ends, slightly angulated towards both ends [R89]; pubes & ischia contralateral bones at midline [R89]; ischium shaped very similar to pubis, with more constriction [R89]; pubis meets ischium only narrowly, to form ventral acetabulum [R89]; *obturator foramen* slit-like, may be completely in pubis in large specimens [R89]; femur shorter than humerus and less well-developed [R89] femoral shaft biconcave, flattened at ends, expanded proximally more than distally due to horizontal posterior extension possibly for insertion of *m. iliofemoralis* [R89]; fibula usually larger & longer, with much greater curvature than tibia [R89]; astragalus & calcaneum only ossified tarsals, articulating with tibia & fibula, respectively, with astragalus larger [R89]; metatarsal 1 short & broad, 4 longest [R89] phalangeal count 23454 [R89].

Links: The Plesiosaur Directory - Images; Saurier aus der Mitteltrias des Monte San Giorgio;

Notes:

[1] For general morphology, see images of *Neusticosaurus* skull and jaws.

[2] Nope. We have no idea what this means, either.

[3] In comparison with *Neusticosaurus*, the palate is very poorly known. The vomers appear to be considerably smaller in *Serpianosaurus* so that the anterior palate is dominated by the palatal shelf of the premaxillae. The braincase of *Serpianosaurus* is completely unknown.

[4] This is not at all clear in either the reconstruction or specimen drawings. Consequently, our images do not reflect this relationship.

[5] As Rieppel [R89] notes, more teeth on both jaws than *Neusticosaurus*.

[6] Rieppel [R89] does not find the second, more ventral, accessory articulation found in some *Neusticosaurus*.

[7] The implication is probably that they spread like a fan.

References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]; Rieppel (1995) [R95]; Sander (1989) [S89]. MAK991211, ATW061231, rev'd ATW080328.

Page Back | Unit Home | Page Top | Page Next

rev'd ATW080328

Sauropterygia: Pachypleurosauridae: *Neusticosaurus*

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Wumengosaurus
|  |--Pachypleurosauridae
|  |  |--Hanosaurus
|  |  `--+--+--Dactylosaurus
|  |     |  `--Anarosaurus
|  |     `--Serpianosaurus--Neusticosaurus--
pusillus--N. peyeri--N. edwardsii
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Taxa on This Page

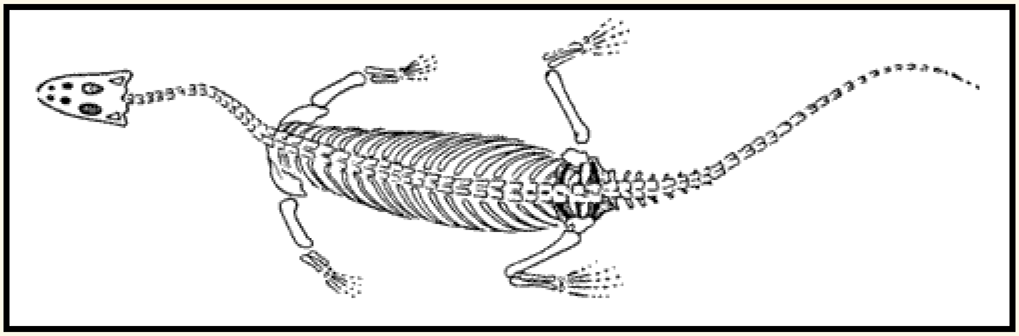
1. *Neusticosaurus* X

On discovering ancestors

Palaeos com, like other websites that take as their topic the evolutionary history of life, presents the relationship of life past and present in terms of tree like diagrams, called dendrograms. Each dendrogram is based on cladistic analyses and other studies; it represents an amalgamation of one or more phylogenetic hypotheses, represented in diagramatic form as cladograms (although dendrograms and cladograms are confused, most of what you read on the web that purports to be a cladogram is actually a dendrogram). Now, the whole thing about cladograms is that they are hypotheses for testing different phylogenies (geneologies of life so to speak). They don't actually tell you who the ancestors are, or even anything about those ancestors. All they do is provide statistical tests, on the basis of the data keyed in, on which species are most likely to be related to each other (these are called sister groups). This might seem a strange attitude to take, but the simple fact is that the fossil record, the trace of past life, is incomplete, and that the further back in deep time one goes, the more incomplete it becomes. Sometimes however things are fortuituous enough that we can get a glimpse of evolution in action, and see who the ancestors are. One such instance involves observation of a stratigraphic succession of pachypleurosaurs from the Middle Triassic of the Monte San Giorgio region, Switzerland (O'Keefe & Sander 1999). Deposition was continuous, and pachypleurosaurs common. Over a period of perhaps five million years (not long by geological standards, equivalent to Plio-Pleistocene or Quaternary time) these creatures lived and died and left their fossilised remains in the sediment. By comparing large numbers of specimens, it was possible to observe a single sequence of gradational evolution (this is called anagenesis), involving the series *Serpianosaurus mirigiolensis*, *Neusticosaurus pusillus*, *N. peyeri*, and finally *N. edwardsii*. The phylogeny was reconstructed using a combination of cladistic, phenetic, and stratigraphic (fossils and fossil sequences) information and methodologies. The result reveals the way that nature does not follow human laws and expectaions. As the authors say in their abstract "Phylogeny of the clade is interpreted from both (cladistic and, phenetic/stratigraphic) paradigms, and the interpretations are found to he inconsistent. Resolution of the phylogeny rests on the emphasis of one type of data over another. An interpretation of cladogenesis within the genus *Neusticosaurus* entails rejection of suggestive phenetic and stratigraphic data, whereas an anagenetic interpretation entails reversal of autapomorphies in ancestral taxa. Anagenesis is deemed to he the more probable interpretation, based on the strength of the stratigraphic and phenetic data relative to the character data. Implications of the test case results for phylogeny reconstruction in general are discussed, ending with a call for pluralism in approach" (O'Keefe & Sander 1999). The anagenetic hypothesis in this case is supported also by long bone microstructure, according to which *Serpianosaurus* has the more primitive, longitudinally orientated, vascularisation pattern, which is replaced by the more advanced, radially orientated, pattern of *Neusticosaurus edwardsii* (Hugi 2011)

For this reason, in the dendrograms at the top of the relevant pages here, instead of the usual branching pattern, the two general are connected by a single line (as *Serpianosaurus--Neusticosaurus*, and on this page all three species of *Neusticosaurus* are included. Strictly speaking of course the distinction between the two genera is quite arbitrary in any case, so *Serpianosaurus* could just as easily be included under *Neusticosaurus*. MAK111101

Descriptions

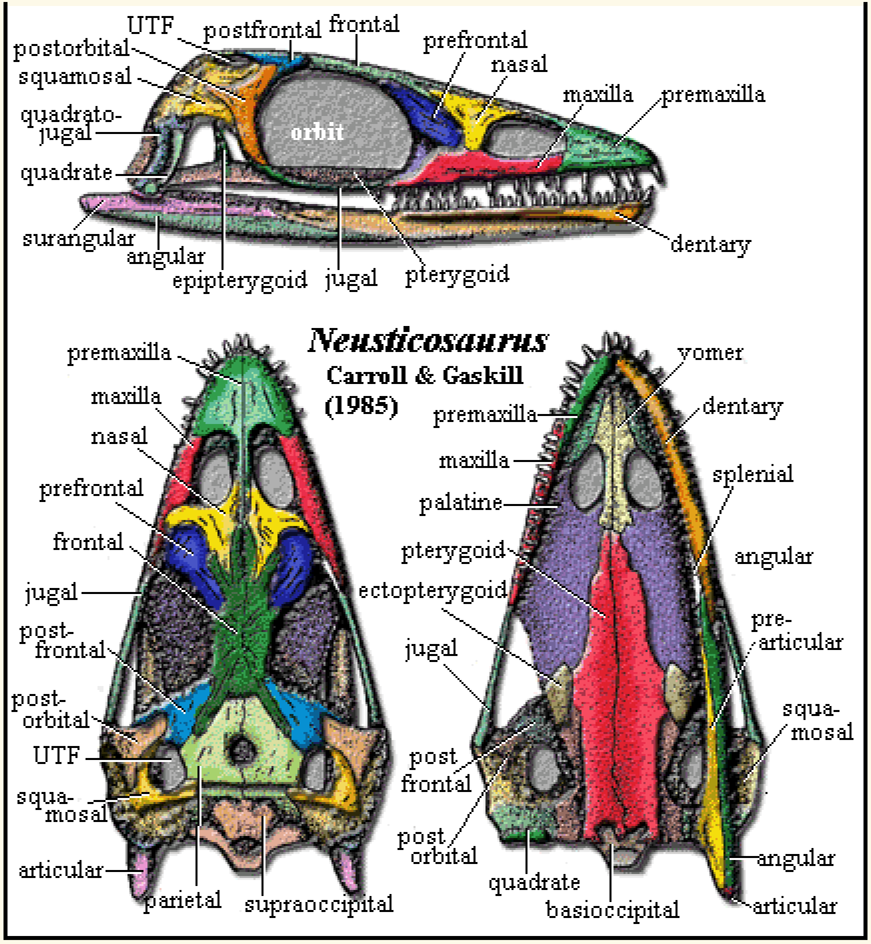


***Neusticosaurus*:** Seeley 1882. *N. ("Simosaurus") pusillus* Fraas 1881 (includes *N. "pygmaeus"* Fraas 1896 **[5]**); *N. ("Pachypleurus") edwardsii* Cornalia 1854; *N. peyeri* Sander 1988. *N. ("Psilotrachelosaurus") toeplitschi* Nopcsa, 1929 is questionable. *N. ("Pachypleurosaurus") "staubi"* Kuhn-Schnyder 1959 is a *nomen dubium*, not diagnostic to the species level, the material of which belongs to either *N. peyeri* or *N. pusillus* [CG85] [S89].

Range: Middle Triassic (Ladinian) to Late Triassic (early Carnian) of Europe (Northern Italy, SW Germany & Switzerland) [CG85] [S89].

Phylogeny: Pachypleurosauridae ::: *Serpianosaurus* + *.

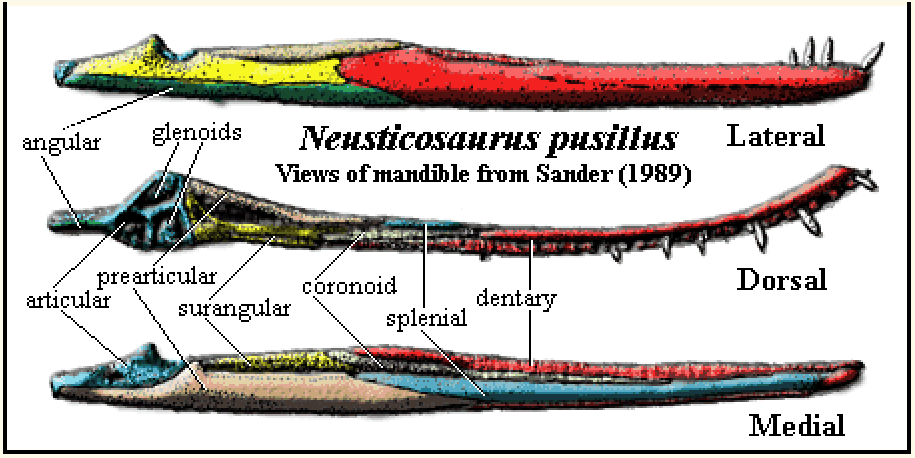
Characters: *dermal skull:* skull development with strong negative allometry, very small in large adults [CG85] [S89]; premaxillae broadly expanded across snout, with posterior process separating nares, nasals [CG85]; sides of snout



weakly convex [R89]; lacrimal probably absent in all species [S89]; maxilla with small or absent suborbital extension [CG85] [S89]; nasals large, may be separated at midline by frontals & premaxillae superficially (*peyeri*, *pusillus*) or completely (*edwardsii*) [CG85] [R89] [S89]; nasal with curving process to maxilla (in *edwardsii* only [S89]) [CG85]; nasal with anterior (to naris) and posterior processes [CG85]; nares formed by premaxilla, nasal and maxilla [S89]; frontals large, variably fused [CG85] [S89]; frontals form dorsal orbit [S89]; large pineal [R95] [S89]; parietal without median ventral flange [CG85]; parietal lappet onto occipital surface [CG85]; parietal (and squamosal [S89]) thickened medially to form transverse ridge dividing the skull table from occiput [CG85]; UTF small, bordered by squamosal, parietal, postfrontal & sometimes (narrowly) by postorbital [S89] [R89]; orbits large [CG85] [S89]; pre- & postfrontals massive, suggesting bulging eyeball [CG85]; prefrontal forming anterior orbit [S89]; sclerotic plates well-developed (14-20?) [CG85] [S89]; jugal extends anteriorly nearly to front of orbit. [CG85]; jugal forms ventral orbit [S89]; jugal slightly broadened below postorbital [CG85]; postorbital skull short & narrow [CG85] [S89]; postorbital triangular, covers squamosal anteriorly and almost bisects lateral exposure of squamosal [CG85]; postorbital with deep medial process into postfrontal [S89]; postorbital ventral process articulates with end of jugal [S89]; squamosal on lateral & posterior margin of small upper temporal fenestra [CG85] [R95]; squamosal also forms dorsal margin of lower temporal embayment [CG85]; squamosal with lappet onto occipital surface [CG85]; squamosal with notch to receive quadrate [CG85]; quadratojugal thin, but largely covering quadrate in lateral view [CG85]; supraoccipital arched, extending below, but not sutured to, parietals [CG85]; posttemporal fenestrae present [CG85]; exoccipitals very small [CG85]; exoccipitals with single XII foramen and recessed for jugular foramen [CG85];

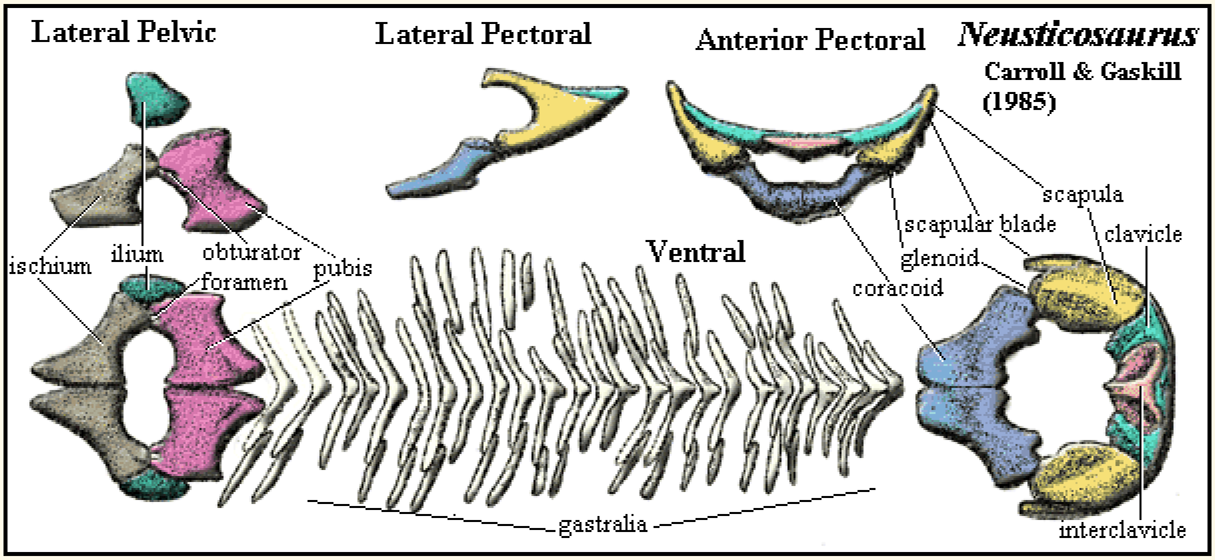
palate & braincase: quadrate not mobile [CG85]; quadrate posterior margin embayed as otic notch [CG85] [S89]; otic capsule forming stout rod extending toward top of cheek & supported by occipital flange of squamosal [CG85]; stapes short cylinder [CG85]; basipterygoid articulation present, but immobile [CG85]; epipterygoid thin, expanded at base [CG85]; sphenethmoid probably ossified in part [CG85]; premaxilla forming broad shelf separated posteriorly by vomers [CG85] [S89]; premaxillary shelf participated in choana and meets maxillary shelf [S89]; vomers narrow, meeting in weak suture [CG85]; choana large, round [CG85]; maxilla borders choana, supports palatine laterally [S89]; palatine large, flat, thin [CG85]; pterygoids long, flat, solidly attached to basioccipital [CG85]; pterygoid anterior process reaches vomer, but not choana [S89]; pterygoid transverse flange essentially absent [CG85]; pterygoid with parasagittal ridges medial to LTF (possibly pterygoideus muscle) [CG85]; interpterygoid & suborbital vacuities closed by pterygoids [CG85]; ectopterygoid small, triangular, not reaching cheek [CG85] (*contra* [S89]: pterygoid has thickened transverse flange, ectopterygoid absent);

jaw: mandible thin, weakly attached at symphysis [CG85] (*contra* [S89], who points out that the dentaries are almost always found together); dentary weakly convex [R89]; dentary with large lateral exposure, bearing long groove for external

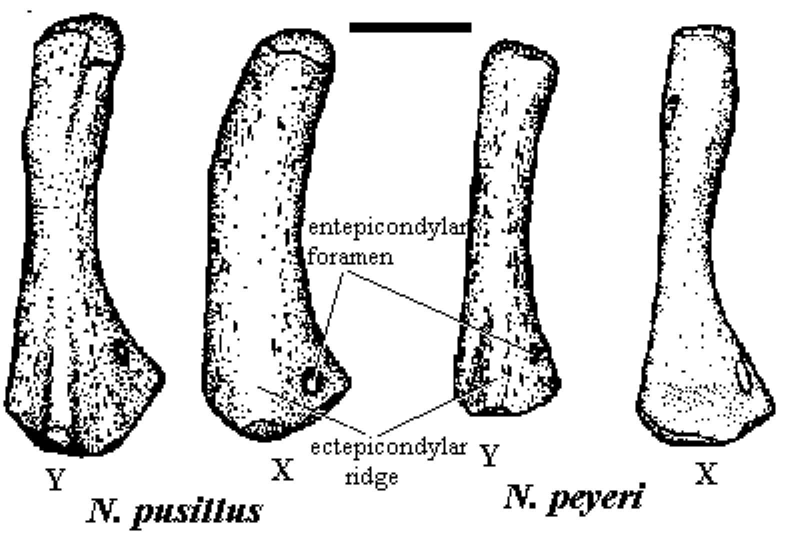


adductor muscle attachment [CG85] [S89]; angular extends about 50% of jaw length [CG85]; surangular with dorsolateral recess for jaw muscles [CG85]; surangular extends into strong retroarticular process [S89]; articular forms ventral surface of retroarticular process, with transverse groove as articulating surface [CG85]; thecodont dentition [CG85] [S89]; teeth small, conical, with longitudinal striations [S89]; teeth flattened laterally & convex medially, with longitudinal striations (no keels) [S89]; 4-6 premaxillary teeth, with long roots [CG85]; anterior teeth slightly procumbent [CG85]; anterior maxillary teeth somewhat larger and caniniform [S89]; 17-25 total upper teeth [S89] 24-28 teeth on lower jaw [S89]; lower tooth row reaches well back of maxillary row [S89];

axial: axial elements variably pachyostosed, with considerable inter- & intraspecific variation in degree and location [S89]; axis & atlas arches similar to other cervicals [CG85]; 15-20 cervicals, 34-44 presacrals [S89]; centra, attachment area for arch covers almost entire dorsal surface [CG85]; ribs on all presacrals [CG85]; neck long and at least laterally flexible [CG85]; cervical centra without adaptations for sharp bending [CG85]; cervical centra somewhat constricted medially, with longitudinal grooves [CG85]; cervical ribs double-headed [S89]; anterior cervicals short (50% length of posterior cervicals), narrow, with shorter spines [CG85]; anterior cervical zygapophyses with larger (~20º) angle [S89]; posterior cervicals with significant parapophyses [CG85]; anterior cervical ribs with distinct anterior processes [S89]; cervical ribs larger posteriorly, sharply pointed [CG85]; 19-24 dorsal vertebrae [S89]; anterior trunk probably stiffest region of spine [S89]; trunk centra length increases over first 7, then constant [CG85]; trunk centra swollen & "chubby" [CG85]; trunk zygapophyses broad, flat, angled 5-10º [CG85]; trunk centra with extra median dorsal & ventral articulations in some species [CG85] [S89] **[1]**; parapophyses abruptly absent in trunk [CG85]; trunk transverse processes from arch only except last two presacrals [CG85]; trunk spines tall, rhomboidal, slanted posteriorly, with rugose dorsal surface (interspinous ligament) [CG85] ([S89]: also in cervicals); trunk ribs single-headed and attached to anterior portion of arch [CG85] [S89]; ribs pachyostosed in adults [R95]; trunk ribs oriented laterally, abruptly changing to vertical, and ending bluntly [CG85] **[6]**; 22-28 gastralia of three elements each, with 2 gastralia to each corresponding vertebra [S89]; 3-4 sacrals [S89] **[7]**; sacrals with extensive transverse processes, formed by both centra and arches [R89]; tail length quite variable [CG85]; 40-60 caudals, 8-13 caudal ribs & 25-35 hemapophyses [S89]; caudal centra somewhat constricted medially, with longitudinal grooves [CG85]; caudal centra with arch attachment area quite narrow [CG85]; caudal zygapophyses 1-14 angled at ~20º [CG85]; large hemal arches from caudals 3/4 to 15, similar to neural arches, then shrink rapidly [CG85]; hemal arches with rugose ventral surface [CG85] **[2]**; last few caudal ribs articulate only with centrum, other wise with both arch & centrum [S89].



appendicular: **[3]** pectoral girdle elements strongly



Left humeri from both morphs of N. pusillus and N. peyeri showing probable sexual dimorphism. From Sander (1989). Scale bar = 5 mm.

bound, except coracoids [CG85]; pectoral fenestra always present (but variable size) [S89]; interclavicle thin, with short blade and rugose surface [CG85]; interclavicle with considerable variation in shape and size; scapular blade short, rather narrow, angled posteriorly at ~45º, with limited attachment surface [CG85] [S89] **[9]**; suprascapular cartilage probably absent [CG85]; glenoid formed between scapula & coracoid, but most cartilaginous [CG85]; coracoid flat, waisted [S89]; humerus with 50-60º of tortion [CG85]; humerus length & shape with strong (presumably sexual) dimorphism [S89]; humerus proximal end broadly oval, probably capped in cartilage [CG85]; deltopectoral crest present, but poorly developed [CG85]; humerus distally flattened, with single distal articulation [CG85]; distinct entepicondylar foramen [S89] **[8]**; ectepicondylar foramen restricted to a distal groove, lateral to ectepicondylar ridge [CG85]; radius & ulna preserved as extending straight from end of humerus [CG85]; ulna & radius about 50% length of femur, with ulna 80% length of radius [CG85]; ulna broader than radius [R95]; radius tapers 50% distally & extends beyond ulna [CG85]; forelimb with *spatium interosseum* [R95]; olecranon absent [CG85]; only carpals are ulnare, intermedium and (in *edwardsii*) a possible small lateral centrale [CG85] [S89]; ulnare circular [R95]; metacarpal I shorter than others, & III longest [R89]; metacarpals & phalanges very slender [CG85]; manus phalangeal count 1-2,2-3,3,3-4,2 with intraspecific variation in digits 3-5 [CG85]; pelvis mostly cartilaginous, with considerable variation between species [CG85] [S89]; ilium small, triangular & constricted dorsally, giving small sacral attachment area [CG85] [S89]; pubis & ischium relatively similar, plate-like, flat, waisted, and without specialized medial surface [CG85]; pubis separated from ischium by broad thyroid fenestra [CG85]; pubis with slit-like obturator foramen close to acetabulum [S89]; femur probably extended at 45º with lower limb directed posteriorly [CG85] **[4]**; femur longer than humerus [R95]; femur slightly curved [R95]; femur dorsoventrally flattened [CG85]; femur with expanded proximal end, including trochanter major (turtle term) possibly for iliofemoralis on posterior edge [CG85] [S89]; femur with "vaguely defined intertrochanteric fossa" [CG85]; femur distally flattened [S89]; distal articulating surface only, with no lateral development (as expected lower limb flexed much) [CG85]; no distinct tibial & fibular condyles [CG85]; tibia & fibula short, stocky [CG85]; tibia straight [R95]; medial edge of fibula strongly concave [CG85]; fibula distally expanded "in the plane of the tarsals but is quite thin in the opposite direction" [CG85]; fibula with distinct facets for astragalus & calcaneum [CG85]; astragalus & calcaneum only ossified tarsals [CG85] [S89]; calcaneum circular [CG85]; astragalus with crescentic indentation at articulation for tibia and fibula [CG85] [S89]; metatarsals broad, and probably overlapping [CG85]; pes phalangeal count 1-2,2-3,3-4,4-5,3 with intraspecific variation in digits 3-5 [CG85] [S89]; ungual phalanges wide, flattened & bluntly rounded, possibly clawed in life (digits 1-3) [CG85] [S89].

N. pusillus Ladinian of Germany and Italy [R95]; short-lived but most widespread species [R95]; often associated with *Lariosaurus*. Significantly smaller than *Serpianosaurus*. [ORS99]

N. peyeri: closely related to *N. pusillus* and about the same size.

N. edwardsii**:** considerably larger than *N. peyeri*. This species is the source of a unique and probably unprecedented taxonomical conundrum: it has been contended that the holotype is not, in fact, a member of the species [ORS99]. In theory this can't happen.

Notes: [1] As [CG85] note, all these articulating structures "would presumably have made rotation of the vertebrae around the long axis nearly impossible, and might also have restricted lateral flexion of the trunk. Except where the vertebrae have become disarticulated from one another, the trunk region appears ramrod straight in these specimens. It appears to have formed an almost rigid structure in the living animal." [CG85: 369]. *N. peyeri* seems to have lacked these extra articulations, at least in the trunk. Sander's [S89] comments on the tail are ambiguous. He states [S89: 609] that accessory articulations are absent from the trunk; but, later on the same page, he says that "Accessory articulations are also found in [the proximal] portion of the tail" -- with no further elaboration.

[2] In essence there are two tail regions. The proximal region is deep, laterally flexible, strong and heavily muscled, with ribs and neural spines. The distal region is (impliedly) stiffer, rod-like and without muscles, ribs, or neural spines. The transition was relatively abrupt, occurring over 2-4 vertebrae.

[3] for a general description of the pectoral girdle, see Nothosauria.

[4] [CG85] note that this is similar to the marine iguana and crocodiles, both of which do not use the rear limb for propulsion. They add that the foot is, however, broad and might have served for steering.

[5] Important explanatory note: although *N. pygmaeus* Fraas 1896 is the same as *N. pusillus* Fraas 1881, the Fraas who named *N. pusillus* (Oscar Fraas), is not the same as the Fraas who named *N. pygmaeus* (Eberhard Fraas). On the other hand Oscar Fraas (1824-1897) *is* the same Fraas who named Eberhard Fraas (1862-1915) -- which he had a perfect right to do because Eberhard was Oscar's son, even though both men turned out to be members of the same species.

[6] Sander [S89] speculates that the dorsal ribs articulated with a cartilaginous sternum.

[7] The last dorsal rib and/or the first 1-2 caudal ribs are bent at odd angles. They look somewhat like sacrals and may have articulated with cartilaginous expansions of the pelvic bones [S89].

[8] The entepicondylar foramen is on the distal end in immature specimens, and its distance from the distal end of the humerus is a good proxy for maturity. However, it is also a sexually dimorphic character (see figure).

[9] Sander [S89: 612] states of *N. peyeri* that the scapular blade "extends back over the glenoid fossa, thereby limiting the dorsal excursion of the humerus." This would probably be true of all species. Carroll & Gaskill [CG85] also remark on the limited mobility of the forelimb in their study of *N. edwardsii*.

References: Carroll & Gaskill (1985) [CG85]; O'Keefe *et al*. (1999) [ORS99]; Rieppel (1989) [R89]; Rieppel (1995) [R95]; Sander (1989) [S89]. MAK991210, ATW061224, rev'd ATW080328.

Comment: Comparison of long bone microstructure in various species of *Neusticosaurus* and in *Serpianosaurus* indicate different habitats, longevities and ages at sexual maturity. The bone histological data regarding *Serpianosaurus mirigiolensis* and *Neusticosaurus edwardsii* also may indicate climate-dependant reproductive seasons similar to Recent lacertilian squamates. Hugi et al 2011). MAK111103

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

ATW061231 revised ATW080328 checked ATW080127

Sauropterygia: Eusauropterygia

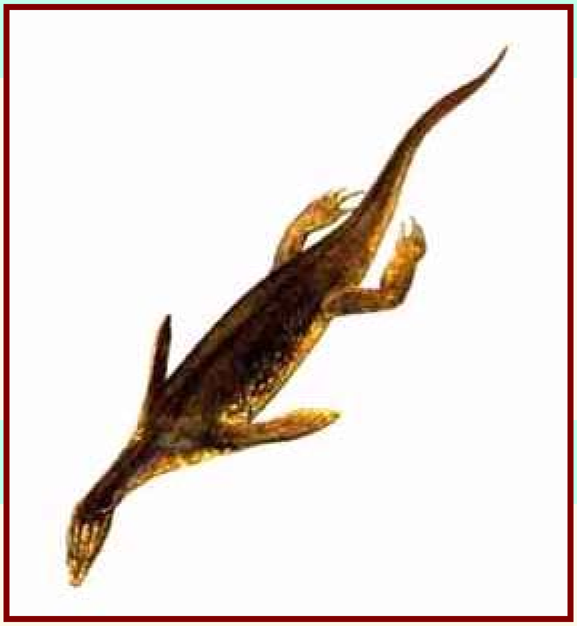
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Wumengosaurus
|  |--Pachypleurosauridae
|  `--Eusauropterygia
|     |--Corosaurus
|     `--+--Simosaurus
|        `--+--Nothosauridae
|           |  |--Nothosaurus
|           |  `--+--Lariosaurus
|           |     `--Ceresiosaurus
|           `--Plesiosauria
|              |--Pliosauroidea
|              `--Plesiosauroidea
|                 |--Elasmosauridae
|                 `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Taxa on This Page

1. *Ceresiosaurus* X
2. Eusauropterygia X
3. *Lariosaurus* X
4. Nothosauridae X
5. *Nothosaurus* X
6. *Simosaurus* X

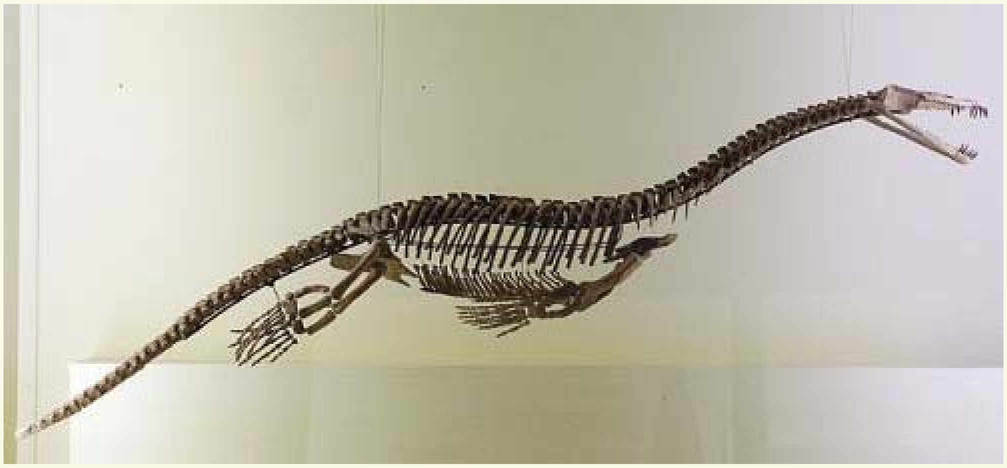


The Nothosauridae

The nothosaurids were fairly large reptiles, reaching 3 to 4 metres in length. *Lariosaurus*, shown at right, grew to 3 meters. They had long necks and long snouts, and probably could be thought of as a sort of cross between a crocodile and a seal. They were primarily aquatic, frequenting brackish lagoons and coastal marine environments. Most remains, such as those of *Lariosaurus*, have been found in Middle Triassic sediments of Switzerland and Germany (the Tethys Seaway). But the group is also known from China and elsewhere, and most probably had a world-wide tropical distribution. MAK991211.

Nothosaurs such as *Nothosaurus* and *Ceresiosaurus* have a more traditionally reptilian lamellar-zonal bone type similar to that of the pachypleurosaurs *Serpianosaurus*and *Neusticosaurus*. This is different from the fibrolamellar bone type of placodonts, pistosaurs, and some pachypleurosaurs, which implies a slower growth to maturity, and may or may not have a phylogenetic implications (Klein 2010, Hugi 2011). MAK111103

Descriptions



Eusauropterygia:

Range: Middle Triassic to Late Cretaceous

Phylogeny: Nothosauria : Pachypleurosauridae + * : (*Corosaurus* + (*Pistosaurus* + Plesiosauria)) + (*Simosaurus* + Nothosauridae)

Characters: skull flattened and elongated; elongation of jaws and mandibular symphysis; orbit small relative to skull length; relative size increase in the upper temporal fenestrae; **$** complex dual jaw adductor mechanism (related to rapid lateral snapping bite) to compensate for low temporal region, including separate anterior (anterodorsal force) and posterior (postero-dorsal force) adductors; loss of impedance-matching ear; strongly procumbent teeth on premaxilla and dentary; 5 premaxillary teeth; paired maxillary fangs; 5-6 sacral vertebrae; various adaptations for paraxial locomotion, i.e. rowing, rather than aguilliform motion; scapula small; . Overall trend is change from near-shore, possibly amphibious, adaptations to pelagic life.

Links: Fossil Room; Eusauropterygia after Rieppel, 1997 and Rieppel & Hagdorn, 1997.

References: Rieppel (1997). ATW020711.

Graphic: Skeleton of *Nothosaurus* in the *Berliner Museum für Naturkunde* (Berlin Museum of Natural History). Photo by Elke Wetzig, Wikipedia, GNU Free Documentation/Creative Commons Attribution

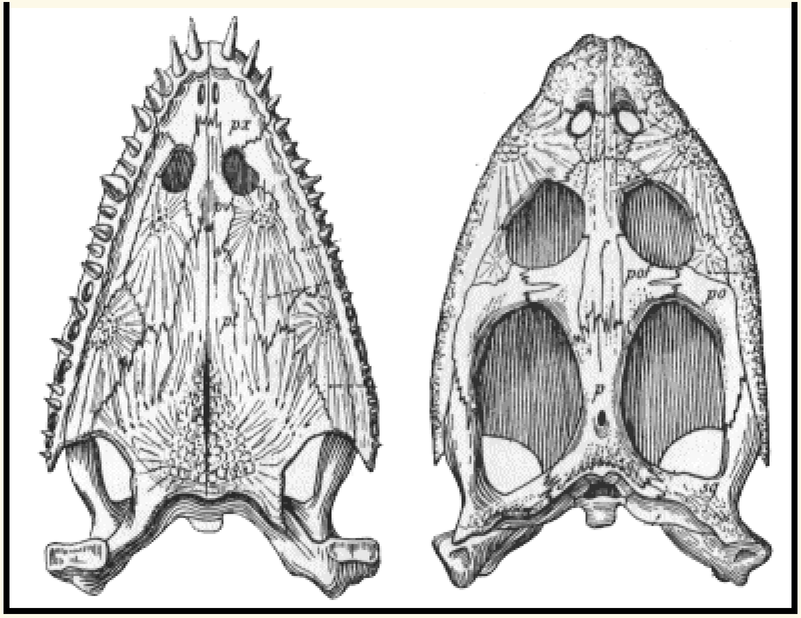
---

Simosaurus: *S. gaillardoti* von Meyer 1842, *S. guielmi* von Meyer 1855

Range: Middle Triassic to Late Triassic of Europe.

Phylogeny: Eusauropterygia **::** (Nothosauridae + (*Pistosaurus* + Plesiosauria)) + *.

Characters: medium-sized form; head broad and flattened; snout blunt; ectopterygoid extends to cheek & secures palate [CG85]; **[1]**; teeth short, bluntly conical or clavate, the crown strongly striated.



Links: Fossilien aus dem Muschelkalk des Kraichgaus (German, English); Simosaurus gaillardoti (French); The Plesiosaur Site - Species.

Notes: Known only from the Upper Muschelkalk and Lettenkohle (Early to Late Ladinian epoch) of central Europe (Germany). **[1]** Rieppel [R89: 60-63] does a wonderful reconstruction of the jaw muscles, in a paper otherwise unrelated to *Simosaurus*. We could only copy the whole thing, which would be risky, as well as boring. Thus, you'll have to get it yourself.

References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]. MAK990825; ATW061217.

Nothosauridae:

Range: Early Triassic to Late Triassic

Phylogeny: Eusauropterygia **:::** (*Pistosaurus* + Plesiosauria) + * **:** *Nothosaurus* + (*Lariosaurus* + *Ceresiosaurus*).

Characters: M-L (0.2-4.0m); typically >2m [CG85]; long snout, small, narrow head; pterygoid vacuities closed by extension of pterygoid; extreme dorsoventral flattening of temporal region with the development of occipital flange on the squamosal and parietal, allowing posterodorsal expansion of the jaw adductor musculature; upper temporal fenestra larger than orbit [CG85]; long neck; unique pectoral girdle: essentially circular in horizontal plane with large medial opening. Scapular blades greatly reduced and extend below clavicle. Distal limb elements reduced, humerus stout. Large coracoid with posterior extension (back stroke of anterior limbs?) . Pelvic girdle somewhat similar, but more primitive.

Links: Nothosaurus; Nothosaurus- Enchanted Learning Software; Nothosauridae; Untitled Document; some additions to Re: MOSASAURS AND PLIOSAURS; NOTHOSAURIA; Untitled Document; Kleiner Museumsrundgang (German).

References: Carroll & Gaskill (1985) [CG85]; Rieppel & Wild (1996). ATW061216.

Keichousaurus: *K. hui* Young 1958, *K. lusiensis* Gonzui 1978, *K. yuananensis* Young 1965.

Range: Middle Triassic (Anisian) of Xingyi, Guizhou province and Yuanan, Hubei

province, China.

Phylogeny: Pachypleurosauridae **:** (*Hanosaurus* + ((*Dactylosaurus* + *Anarosaurus*) + (*Serpianosaurus* + *Neusticosaurus*))) + *.

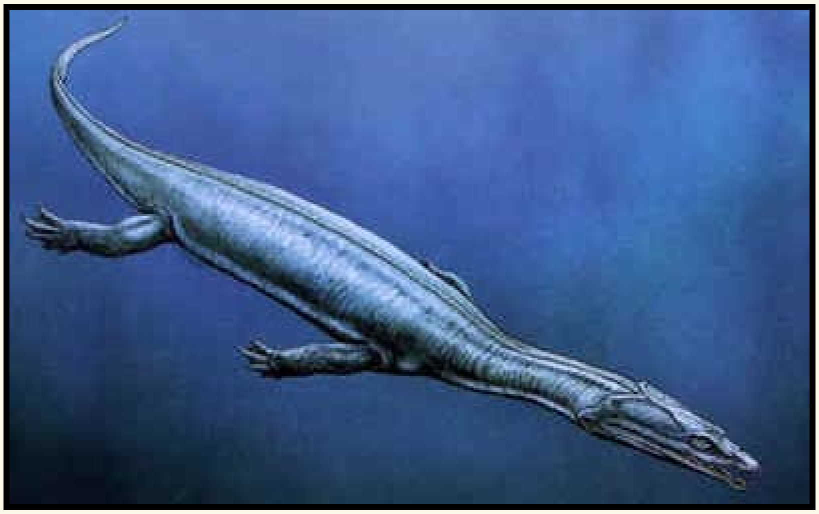
Characters: postorbital enters margin of UTF [R89]; 15-30 cm; neck long; limbs sturdy; ulna massive [CG95]; five-toed feet with long digits.

Comments: The best known and most abundant of the Chinese Triassic sauropterygia, represented by many complete skeletons, This is a small pachypleurosaur with very large orbits (eye sockets) and a pointed rostrum (snout), and unusally short and broad ulna (one of the two bones of the forearm, which in plesiosaurs are incorporated into the paddle) (Lucas, 2001, p.115), unlike those of any of the European genera. Originally shown by cladistic analysis to be a basal member of a monophyletic pachypleurosauridae (Rieppel 1998, see phylogeny above), a more recent analysis shows it as a basal nothosaur (Holmes et al 2008), the implication being pachypleurosaurs as conventionally defined are a paraphyletic grade. Known to have given birth to live young (Cheng et al 2004), Sauropterygia in general were primitively vipariaous. From the abstract of the afore-cited paper: "Here we report two gravid specimens of Keichousaurus hui Young from the Middle Triassic of China. These exquisitely preserved specimens not only provide the first unequivocal evidence of reproductive mode and sexual dimorphism in sauropterygians, but also indicate that viviparity could have been expedited by the evolution of a movable pelvis in pachypleurosaurs. By extension, this has implications for the reproductive pattern of other sauropterygians and Mesozoic marine reptiles that possessed a movable pelvis."

Links: Plesiosauria com Wikipedia, Paleontology and Geology Glossary: K; Triassica - Keichousaurus hui; Dinosaur facts - Keichousaurus; GEOCLASSICS - Keichosaurus; Paleozoic.org: Gallery of Fossil Images; Fossil Reptiles & Bird Fossils For Sale; Fossil aquatic reptile, Keichousaurus from China; Peripatus -Genus Keichousaurus MAK111126

References: Carroll & Gaskill (1985) [CG85]; Rieppel (1989) [R89]. Cheng et al 2004 ATW061231. MAK991209, 111126.

***Nothosaurus*:** Brinckmann 1994; *N. giganteus*, *N. mirabilis* Munster. *N. procerus* Schröder



Range: Early Triassic to Late Triassic of Europe, North Africa, Russia & China.

Phylogeny: Nothosauridae **:** (*Lariosaurus* + *Ceresiosaurus*) + *.

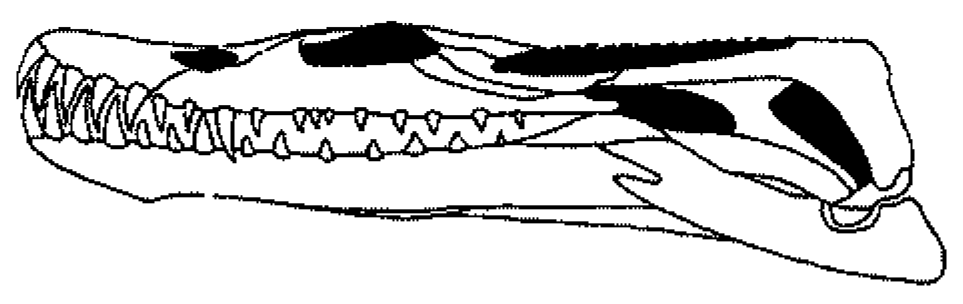
Characters: ~3m; ectopterygoid extends to cheek & secures palate [CG85]; epipterygoid rather massive [CG85]; laterally flattened tail with caudal "fin"; hindlimbs longer than forelimbs;

Comments: Fossil remains of *Nothosaurus* are common in the Muschelkalk (Anisian and early Ladinian) of Southern Germany. *Nothosaurus mirabilis* Munster is the typical and best-known species, attaining a length of 3 meters. Smaller species are found in the Buntsandstein and Lettenkohle (late Ladinian).

Links: Nothosaurus- Enchanted Learning Software; Nothosaurus sp. (note the elongated upper temporal fenestra, small orbits and wide occipital flange. Characteristic of secondarily aquatic reptiles, the vertebrae are disk-like and short, and the distal limb elements incompletely ossified); Untitled Document; Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; Fossils of the Upper Muschelkalk; Marine Reptiles: Nothosaur: Nothosaurus (test: this is a poor reconstruction. why?); Something about Pliosaurs (a completely different take on nothosaur phylogeny); Projekt \Naturkundemuseum\ (German); Nothosaurus mirabilis? Tanystropheus conspicius (Russian); Nothosaurus (basic information and speculation); Nothosaurus (Portuguese); NOTHOSAURUS MIRABILIS ? ??NYSTROPHEUS CONSPICIUS (Russian); PANGEA (Italian); Nothosaurus giganteus (German -- details of minimally-prepared fossils); muschelkalk lipperland; ?????? (Japanese models); Untitled Document; [노토사우루스류(Nothosaurs)] (Korean); vertabrates; Winterswijk; Nothosaurus (life reconstruction & a few factoids); Marine Reptiles- Nothosaur-Nothosaurus (same); Lexique dinosaures- Le Nothosaurus.Fiche descriptive.Images. (French: basic, but informative); Nothosaurus (detailed image of a single centrum); Natural History Museum Erfurt|Nothosaurus (German); Museum Wiesbaden - Naturwissenschaftliche Sammlung- Zeitreise (detailed image of a ?humerus); The Plesiosaur Site - Species; Saurier fordert Techniker heraus (lots of fossil images); The braincases of Simosaurus (abstract).

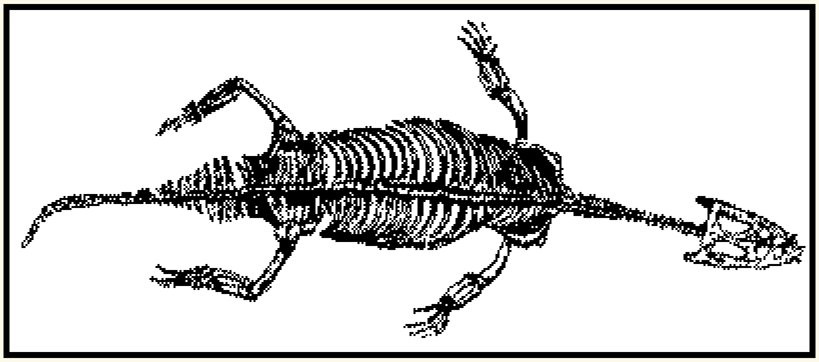
Image: from Fossils of the Upper Muschelkalk

References: Carroll & Gaskill (1985) [CG85]. ATW061217. MAK991211.



the skull of *Nothosaurus procerus parvus* Schröder
length 11.5 cm
Lower Muschelkalk (Anisian epoch)
of Rudersdorf, near Berlin

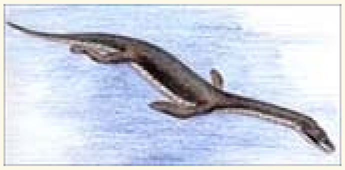
Lariosaurus: L. balsamii, *L. curoni*, *L. valcresii*.



Range: Middle Triassic of Europe (Upper Ladinian deposits).

Phylogeny: Nothosauridae :: *Ceresiosaurus* + *.

Characters: cranial: skull long & low; rostrum anteriorly constricted; very long postorbital region and elongate upper temporal fenestrae, which are larger than the orbits; Parietal and squamosal rise above the occiput to form occipital crest; palate with suborbital and infratemporal vacuities; anterior teeth are very long and fang-like, procumbent and interlocking with jaws closed; pterygoid with row of teeth; **axial:** 17-20 cervicals, relatively short neck; cervical ribs with distinct anterior process; cervical ribs small and double-headed; 20 dorsal vertebrae; dorsal ribs very robust & pachyostotic, but degree of pachyostosis is lower in *L. valceresii* holotype than in; *L. balsamii*; 5 sacral and at least 39 caudal vertebrae; caudal ribs shorten rapidly & do not extend beyond 15th or 16th caudal; tail forming about one-third the total length; **appendicular:** The pectoral girdle shows the typical sauropterygian morphology: it is stout ventrally but low, and the clavicle is placed on the anteromedial surface of the dorsal blade of the scapula. The anterior limb is much stouter than the posterior one, as in other *Lariosaurus* species. Probably the fore-limb played a major role in swimming as suggested for nothosaurs in contrast to pachypleurosaurs. The humerus is stout, but proportionally longer and more slender in *L. valceresii* holotype than in *L. balsami* specimens. The ulna is peculiar in *Lariosaurus*, as it is greatly broadened while the radius is much narrower. Between radius and ulna a wide *spatium interosseum* is enclosed. There are five or six ossified carpals followed by rod-like metacarpals; digits short (may have had some mobility on land); only some phalanges in each digit are preserved/ossified thus impossible to give phalangeal formula for the manus in *L. valceresiii*; two large proximal carpals and tarsals, the distal five each supporting a digit; phalangeal formula of hand, 23443; median longitudinal and two paired lateral series of abdominal ribs (gastralia?); pelvic girdle shows wide pubis and ischium and a tiny ilium with extremely reduced iliac blade; femur slender and approximately same length as humerus in *L. valceresii*, but somewhat longer than the humerus in *L. balsami*; tibia and fibula rod- like, enclosing rather wide *spatium interosseum* closed distally by wide astragalus,



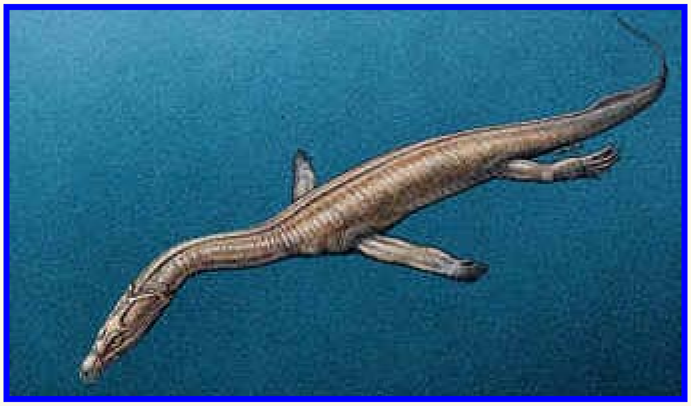
which is larger than calcaneum; In pes, only the first two toes are completely preserved in *L. valceresii* holotype (second toe with four phalanges, suggesting the presence of a slight hyperphalangy in this species); hind limb longer and stouter than forelimb, but otherwise very similar; pes phalangeal formula 23454.

Images: *Lariosaurus balsamii* Curioni, specimen just under a metre in length. Middle Triassic Perledo, Lake Como, Italy. Graphic and text from Zittel, Textbook of Paleontology, vol.II, p.289. Source of life reconstruction unknown.

Note: Our profound understanding of the anatomy of this part of the Sauropterygia results from the extensive work of Dr. Olivier Rieppel of the Field Museum in Chicago. Dr. Rieppel has contributed significantly to many areas of paleontology, but the nothosaurs are his real calling. It is likely that Dr. Rieppel and Dr. Philippe Janvier are our greatest living anatomists. With luck, these skills will not be lost. It is obvious that the next century will require that the traditional anatomy be alloyed with an increasing admixture of molecular genetics (*i.e.* genetic signal transduction), developmental biology, and brute force genomics. However, anyone who has read the attempts of molecular biologists and genomics masters to explain evolutionary events will immediately appreciate the problem. These disciplines do not merely lack the romance and beauty of organismal biology. The practitioners of these arts have little experience working with an entire organism, much less a species or an evolutionary biota, over geologically significant amounts of time. It is, of course, exceedingly important that organismal biologists also learn the cant and incantations of their molecular and silicon-based brethren -- if nothing else, this is the one of the true paths to adequate funding. However, it is equally important that we never forget the traditional arts of observation, dissection, anatomical description, histological preparation, and the like.

Links: Lariosaurus; Nuova pagina 1 (Italian); Nuova pagina 1 (Italian); Lariosaurus balsami. ATW020629, MAK991211.

***Ceresiosaurus*:** *C. calcagnii* Peyer 1931

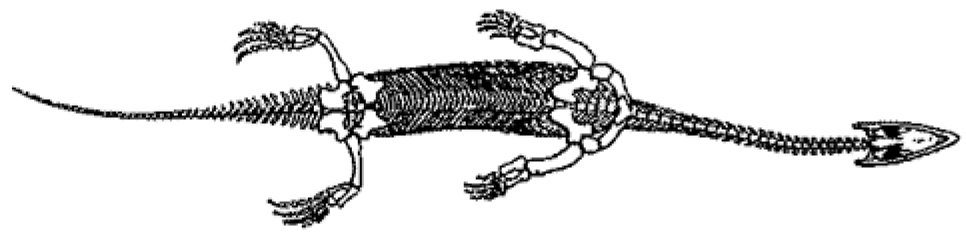


Range: Middle Triassic of Europe, Lower Muschelkalk of Tessin, Switzerland. (late Anisian or early Ladinian age).

Phylogeny: Nothosauridae ::: *Lariosaurus* + *.

Characters: 2-4 m; ball & socket glenoid for forelimbs; long digits with hyperphalangy

Note: **[1]** See skeletal image. This is an odd animal. It lacks, or rather minimizes, the cranial specializations which mark the Nothosauridae. The upper temporal fenestra is not strongly elongated. The external nares are well forward, and the occipital flanges are not strong. In fact, to judge by the skull alone, it looks more like a plesiosaur. The post-cranial skeleton is equally odd, although recognizably nothosaurid, The propulsive strength has been shifted to the hindlimbs. The short and proximally wide tail suggests that the *m. caudofemoralis* or equivalent muscle was highly developed. The femur is short, perhaps retained within the body wall, but the lower limb is long and powerful, with extensive polyphalangy. The pelvic girdle is simplified and very solid. The Web contains numerous references stating that *Ceresiosaurus* was an undulatory swimmer, but this must surely be one of those sourceless scientific myths propagated by mindless cut and paste. Despite its great length, this animal was clearly engineered to be a pursuit diver, perhaps along the lines of *Hesperornis*, although both slower and more agile. Given a diet consisting of pachypleurosaurs (see Geologia Insubrica - Rivista di Scienze della Terra), this method of propulsion seems entirely reasonable. **[2]** Despite these differences of proportion, Rieppel has suggested that *Ceresiosaurus* is congeneric with *Lariosaurus*. See Nuova pagina 1. Detailed photographs of a new specimen of *Lariosaurus* (see Nuova pagina 1) make this suggestion seem more reasonable than it would appear at first glance. ATW020629. **[3]** The two species, *C. calcagnii* and *C. lanzi* represent a stratigraphic series, with the earlier (Anisian-Ladinian boundary) *C.*



Ceresiosaurus in ventral view. Note the lack of typical nothosaur specializations in the skull, short & proximally thick tail, surprisingly frail-looking pectoral girdle, but stout pelvic area with marked hyperphalangy of hindlimbs.

calcagnii being successed by the stratigraphically younger (Ladinian) *C. lanzi* (= *Lariosaurus lanzi*?). The difference between the two as regards microstructure of the long bones is similar to that of the contemporary pachypleurosaurs *Serpianosaurus* and *Neusticosaurus* with which they shared their environment, and which have been shown to constitute an anagenetic series (O'Keefe & Sander1999, the difference being that the straigraphically earlier *C. calcagnii* most resembles the the stratigraphically youngest pachypleurosaurid *Neusticosaurus edwardsii*, both having a radially orientated vascularisation pattern, whereas the younger *C. lanzi* is more similar to *Serpianosaurus*, and also to young *Nothosaurus*, with a longitudinally orientated pattern. The different growth pattern might be linked to a different mode of life in the restricted lagoonal basin, which ties in with the morphological data that seems to shows two different locomotion types (Hugi 2011). If *Nothosaurus* constitutes a more primitive or ancestral condition then, unlike the pachypleurosaurs, this is not an anagenetic series (although it can still be a phylogenetic one), because the more primitive *C. lanzi* preceeds the more derived (histologically speaking) *C. calcagnii*. MAK111103

Links: Nothosaurus- Enchanted Learning Software; Ceresiosaurus; ichthyosaur.html; Kleiner Museumsrundgang (German); Saurier aus der Mitteltrias des Monte San Giorgio (German); The Plesiosaur Site - Species; Untitled Document; Título principal aqui (Spanish); evolution4. ATW020629, MAK 991211.

Page Back | Unit Home | Page Top | Page Next

Checked ATW050109

Sauropterygia: Pistosauridae

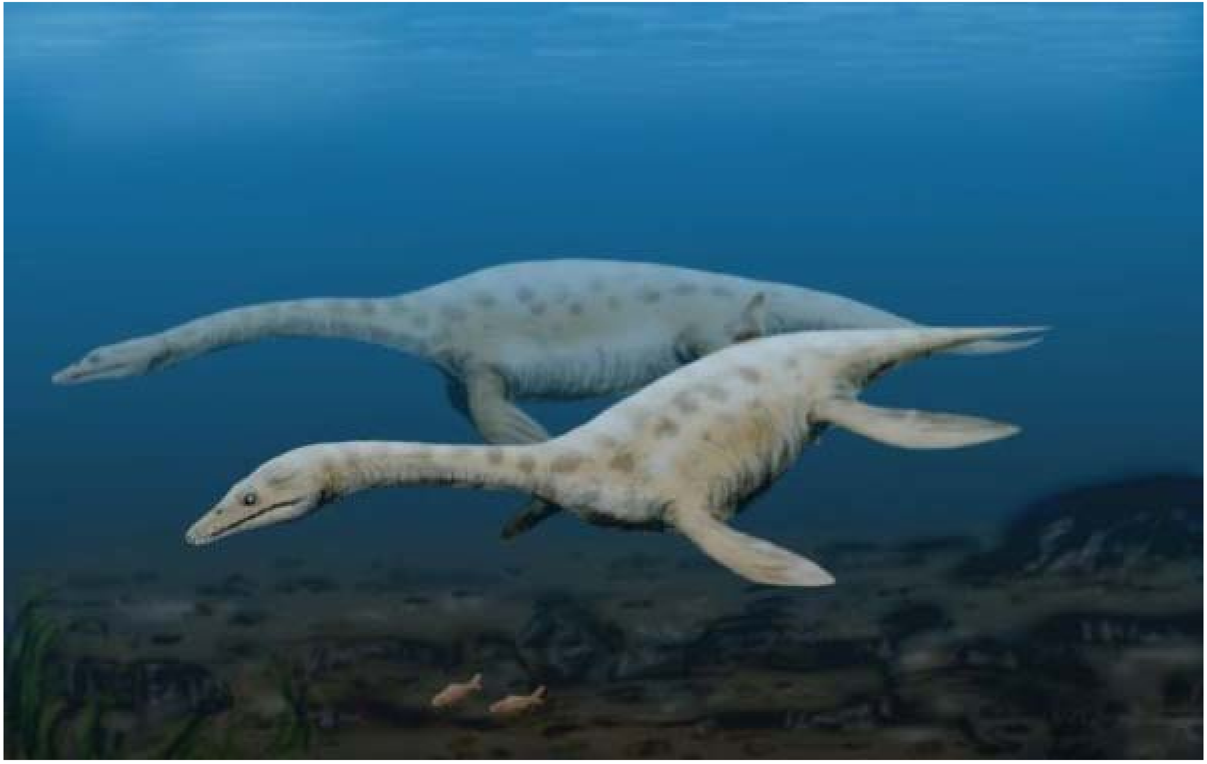
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Wumengosaurus
|  |==Pachypleurosauridae
|  `--+--Nothosauridae
|     `--+--Corosaurus     PISTOSAUROIDEA
|        `--+--Cymatosaurus
|           `--+--Pistosaurus
|              `--+--Yunguisaurus
|                 `--+--Augustasaurus
|                    `--+--Pliosauroidea
|                       `--Plesiosauroidea
|                          |--Elasmosauridae
|                          `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

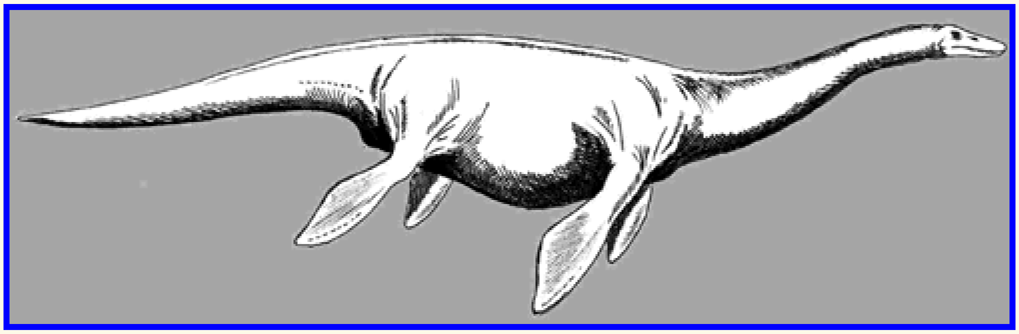
Contents

Taxa on This Page

1. *Augustasaurus* X
2. *Corosaurus* X
3. *Cymatosaurus* X
4. Pistosauroidea X
5. *Pistosaurus* X
6. *Yunguisaurus* X



Life reconstruction of *Augustasaurus hagdorni*, a pistosaur from the Middle Triassic of Nevada (West Pangaea). Artwork by Nobu Tamura, 2007. Wikipedia, GNU Free Documentation/Creative Commons Attribution



The Pistosaurs are morphologically intermediate between nothosaurs and the Plesiosauria proper. See image at right by J. Aragón from PLESIOSAURIOS. (The head may be proportionally too small in this picture; compare with skeletal recosntruction below). *Pistosaurus*, from the Middle Triassic (Ladinian epoch). Until recently, *Pistosaurus* was until recently the only genus in its family, but now we add the American *Augustasaurus*, the Chinese *Yunguisaurus* , and a number of other forms. At first interpreted cladistically as a monophyletictaxon (Rieppel et al 2002), the group is now considered a paraphyletic grade (Cheng et al 2006). We have retained the family ranked term Pistosauridae here for this assemblage because we don't believe anything can be gained by forcing Linnaean ranks to conform to Phylogenetic nomenclature (or vice versa). However, the (unoffical?) clade Pistosauroidea is used in this context.

Pistosaurus, as a typical (and eponymous) represetative of the pistosaurs, had a nothosaur-like body with a plesiosaur-like head. In Evolutionary systematics, it is variously classified under the Nothosauridae and the Plesiosauria, depending on what characteristics one uses to define membership of each group. Even if it is a nothosaur it is acknowledged to be closely related to the ancestors of plesiosaurs.

These may have been ocean going creatures. They are known from both sides of Pangea (Europe/Tethyan province and China, and North America) so they seem to have had a wide distribution. Nobody has as yet done an analysis on the way these animals moved so we do not know whether it swam like a crocodile (typical nothosaurid) or paddled like a turtle or sea lion (plesiosaurian). In view of the nothosaurid body it is likely that with Pistosaurus the characteristic plesiosaur locomotor pattern had not yet evolved.

Pistosaurs had fibrolamellar bone in contrast to the standard reptilian lamellar-zonal bone type of *Nothosaurus*. They may or may not have been descended directly from pachypleurosaurs like Anarosaurus; there is a contradiction here between histology and gross physiology, similar to the sorts of contradictions one encounters between morphology-blased cladistic studies and molecular sequenced phylogenies. It has been suggested that this indicates a superior metabolism which would have given them an advantage (faster growth, cold temeperture tolerance). In this way the group could became globally distributed, spreading to colder waters, and finally giving rise to the pelagic plesiosauria that dominated the post-Triassic oceans (Klein 2010 p.23). This does not have to have been the case though, because during the Triassic and indeed most of the Mesozoic, temperatures were warm and tropical worldwide, and global distribution is easily explained in terms of changes from pachypleurosaur and nothosaur to plesiosaur morphotype, sea-turtles for example, who are ectothermic also have a global distribution in warmer waters (the Quaternary environment being rather colder than the Mesozoic one). Fibrolamellar bone in sauropterygians is better explained in terms of rapid growth when young. Because small animals are more at risk from preditors, the less time spent small the greater the likelihood of overall survival. So it may have been their growth regime rather than overall metrabolism that gave sauropterygia the edge over their Triassic competitors. MAK991210, revised MAK111103

Descriptions

Pistosauroidea

Range: Middle Triassic to Late Cretaceous

Phylogeny: Eusauropterygia **:** (*Simosaurus* + Nothosauridae) + * **:** *Corosaurus* + (*Pistosaurus* + (Pliosauroidea + Plesiosauroidea)

Comments: Inclusive clade for *Corosaurus, Cymatosaurus, Augustasaurus, Pistosaurus* and Plesiosauria (Plesiosaur Directory) MAK111101

Links: Wikipedia

Corosaurus: *C. alcovensis* Case 1936a.

Range: Early Triassic to Late Triassic of North America

Phylogeny: Pistosauroidea **:** * + (*Cymatosaurus* + (*Pistosaurus* + (*Yunguisaurus* + (*Augustasaurus* + Plesiosauria))))

Links: The Journal of Vertebrate Paleontology; The Plesiosaur Site - Species.

Comment: Most primitive (basal) pistosaur (Rieppel 1997b)

References: Holmes *et al*. (2008) [HCW08]. ATW020627, rev'd ATW080330, MAK111125.

Cymatosaurus.

Range: Uppermost Buntsandstein and lower Muschelkalk (Early Middle Triassic - Early Anisian of Germany, Austria and Poland, possibly also Netherlands and Israel?

Phylogeny: Pistosauroidea **:** *Corosaurus* + ((*Pistosaurus* + (*Yunguisaurus* + (*Augustasaurus* + Plesiosauria)))+ *)

Comments: Small to large pistosaurs with moderately flattened skull, in cladistic analaysis comes out between *Corosaurus* and *Pistosaurus* (Rieppel 1997b). Known from cranial material, limb bones attributed to this genus may not belong with this taxon (Klein 2010) Ketchum and Benson, 2011 place this form in the Pistosauroidea but outside outside the Pistosauria

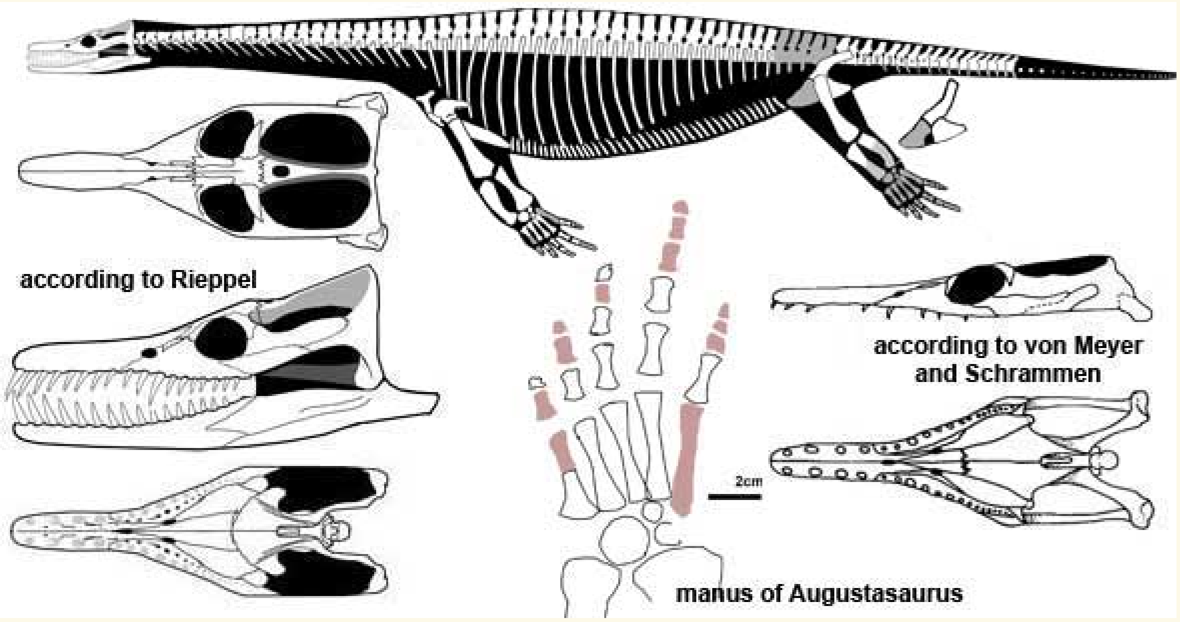
Links: Plesiosaur directory. MAK111103.

References: Rieppel 1997b

Pistosaurus: *P. grandaevus* von Meyer 1855, *P. longaevus* von Meyer 1839

Range: Middle Triassic of Europe & North America, Ladinian, Upper Muschelkalk

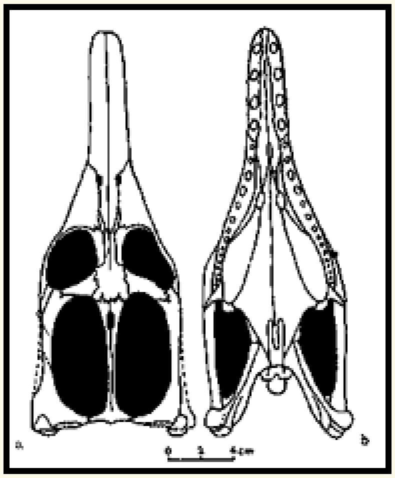
Phylogeny: Pistosauroidea **:** *Corosaurus* + (*Cymatosaurus* + ((*Yunguisaurus* + (*Augustasaurus* + Plesiosauria)) + *))



Characters: ~3m; vomeronasal organ present; very long neck; body form streamlined; more rigid spine as in plesiosaurs; gastralia present; limb girdles not strongly bound together as in Plesiosauria; limbs formed as paddle-shaped flippers.

Note: *Pistosaurus* is now the flagship genus of the Pistosauridae, the other member of the family being *Augustasaurus hagodorni* Sander, Rieppel & Bucher 1997. See The Journal of Vertebrate Paleontology. Since then additional genera have been added.

Links: Nothosaurus- Enchanted Learning Software; A Manual of the Anatomy of Vertebrated Animals (1881); Dinosaurios: Pistosaurus; PLESIOSAURIOS (Spanish J. Aragón); The Plesiosaur Site - Species; The Journal of Vertebrate Paleontology; pistosaurus.



References: Holmes *et al*. (2008) [HCW08]. ATW020630, rev'd ATW080330, MAK111101.

Image: David Peters - Reptile Evolution

Yunguisaurus: *Y. liae* Cheng et al 2006

Range: Late Triassic(Carnian) of southern China

Phylogeny: Pistosauroidea **:** *Corosaurus* + (*Cymatosaurus* + (*Pistosaurus* + ((*Augustasaurus* + Plesiosauria) + *)))

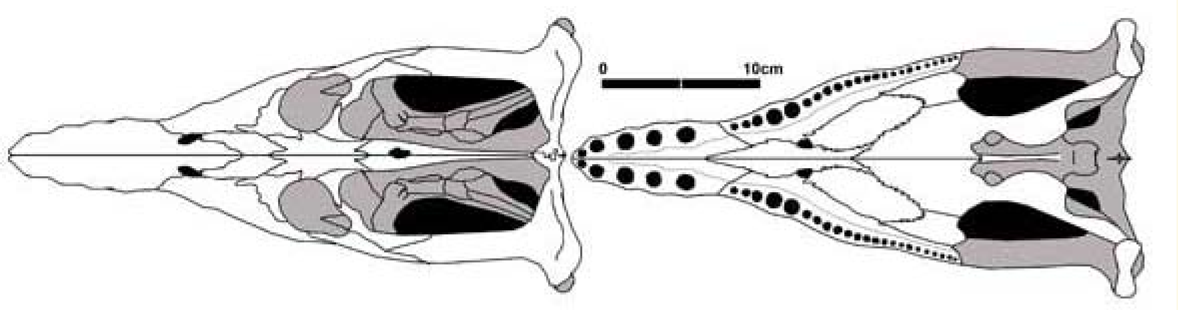
Size: preserved skeleton measures about 1.7 m from snout-tip to end of the incomplete tail; skull: length 12.6 cm, maximum width 6.3 cm

Comments: combination of primitive and derived traits, cladistic analysis places it between *Pistosaurus* and *Augustasaurus*

References: Cheng et al 2006 MAK111101

Augustasaurus: *A. hagdorni* Sander et al., 1997

Range: Middle Triassic (Late Anisian) of



Nevada,

Phylogeny:
Pistosauroidea **:** *Corosaurus* + (*Cymatosaurus* + (*Pistosaurus* + (*Yunguisaurus* + ((Pliosauroidea + Plesiosauroidea) + *))))

Comments: from Wikipedia "Augustasaurus' skull shares many general characteristics with its relative, Pistosaurus, such as tall, blade-like upper temporal arches.[1] The skull's elongated rostrum tapers to a dull point, the anterior premaxillary and maxillary teeth have been described as "fang-like", and the squamosal makes a box-like suspensorium. The dorsal neural spines of Augustasaurus are low with rugose tops. Its coracoids are large plates similar to those in other plesiosaurs. However, the coracoid foramen are missing from Agustasaurus, in a way similar to those in the plesiosaur Corosaurus.[5] Its cervical ribs have anterior process, and like most plesiosaurs, Augustasaurus' vertebrae have "thickened transverse processes" "

Comments: Originally included with *Pistosaurus* in a monophyletic Pistosauridae (Rieppel et al 2002); Cheng et al 2006 makes the Pistosauridae and places Augustasaurus as the sister group to all higher Plesiosauria

References: Sander et al 1997, Rieppel et al 2002 O'Keefe 2001) MAK111101

Image: David Peters - Reptile Evolution (redrawn from Rieppel et al 2002 fig.3)

Page Back | Unit Home | Page Top | Page Next

checked ATW050109, revised ATW080330

Sauropterygia: Plesiosauria

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Pachypleurosauridae
|  `--+--Nothosauridae
|     `--+--Corosaurus
|        `--+--Pistosaurus
|           `--Plesiosauria
|              |--Pliosauroidea
|              `--Plesiosauroidea
|                 |--Elasmosauridae
|                 `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

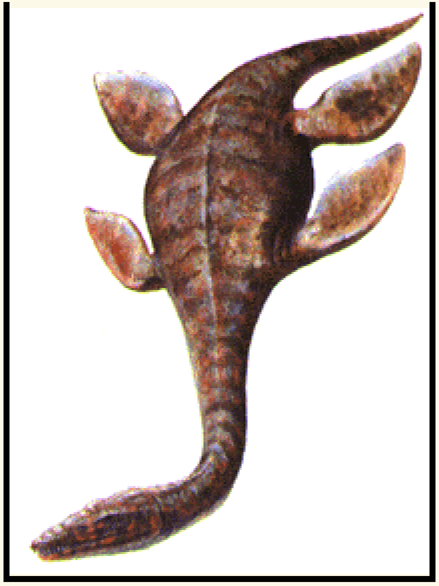
Contents

Taxa on This Page

1. Plesiosauria X

Plesiosauria: Introduction and History

Macroplata, in the figure at right, was a fairly typical Early Jurassic plesiosaur. The **Plesiosauria** (the name means "near lizards,") were an important order of Mesozoic marine reptiles, members of the superorder Sauropterygia. The Plesiosauria include both short and long-necked forms. The largest short-necked forms reached enormous sizes (lengths of over 10 meters, weight of 20 tonnes or more), while some of the later long-necked forms, although only marginally longer and not as heavily built, developed the greatest number of neck vertebrae



of any animal. Plesiosaurs evolved from animals related to pachypleurosaurs and nothosaurs during the Middle Triassic. They remained somewhat rare until the end of that period, when they underwent an amazing evolutionary radiation. These reptiles then dominated the seas throughout the Jurassic and Cretaceous periods, continuing to flourish right up until the end of the Mesozoic Era.

Plesiosaurs were among the earliest large prehistoric creatures to be described. Victorian British accounts are full of references to "antediluvian monsters". Most plesiosaur material was found and described in the Nineteenth Century, much of it located and prepared by an early paleontologist named Mary Anning (1799-1847). A life-long resident of Lyme Regis, England, Anning made a remarkable series of important discoveries in the Early Jurassic seaside cliffs and *limestone* quarries within walking distance of her home. Collectors quickly depleted these coastal exposures. Sadly, by about 1910 most limestone quarries had become mechanized, this severely limiting the collection of fossil material before it was destroyed. After this date very little new material was found, and paleontologists in this region were limited to re-classifying, redescribing, and reviewing old material.

Meanwhile, important discoveries were being made in North America, where sediments from the Late Cretaceous inland sea contain the remains of many large marine reptiles, including both long and short-necked plesiosaurs. This historical accident has led to the belief that plesiosaurs evolved and flourished in Europe during the Jurassic, and became rare there in the Cretaceous, spreading at that time to North America, and finally attaining world-wide distribution at the end of the period.

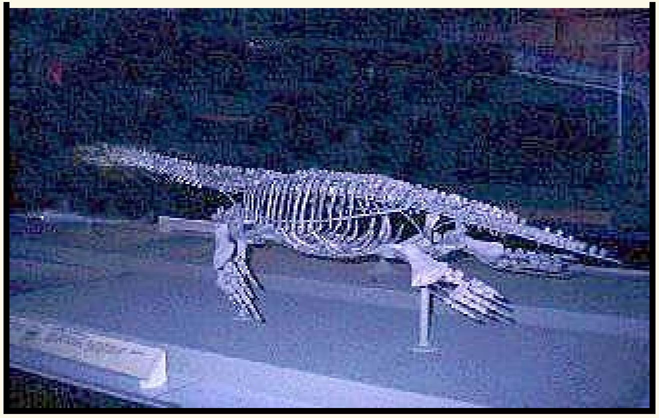
This opinion could not be more false. As with all large, ocean-going animals, there is no doubt that plesiosaurs had world-wide distribution virtually from the very start, even as early as the Triassic. Certainly Early Jurassic plesiosaurs are known from China, South America, and Australia as well as Europe. As with so much of paleobiology, it is misleading to make sweeping assumptions on the basis of patchy and incomplete geological preservation. MAK

Descriptions

Plesiosauria: plesiosaurs > nothosaurs.

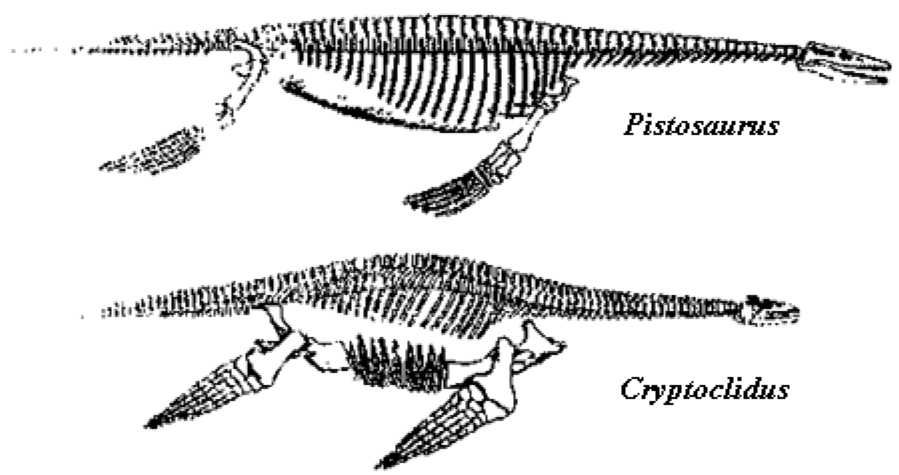
Range: Middle Triassic to Late Cretaceous

Phylogeny: depending on which cladistic node one wants to identify as Plesiosauria there is a choice of Eusauropterygia :Nothosauridae + * : *Corosaurus* + (*Pistosaurus* + (Pliosauroidea + Plesiosauroidea)) [HCW08] - for the stem-base definition (*Nothosaurus* &ltn; *Plesiosaurus*) *or* Eusauropterygia : Nothosauridae + (*Corosaurus* + (*Pistosaurus* + * : Pliosauroidea + Plesiosauroidea for the



node-base definition (common ancestor of *Pliosaurus brachydeirus* and *Plesiosaurus dolichodeirus* (or substitute preferred crown group taxa, this is just for the sake of example) and all their descendents). Both definitions are equally valid. Of course, this is nothing next to the problem of defining tetrapoda! MAK111103

Characters: Up to 13m; nostrils high, just preorbital; **$** nasals absent; large eyes located on sides of head; palate *less* specialized than nothosaurs; palate consists mainly of vomers, large palatines & pterygoids; ectopterygoid extends to cheek & secures palate [CG85]; interpterygoid vacuities retained, sharp, jagged teeth set in sockets at the edge of the jaw; heavy, rigid trunks; **$** presence of nutritive foramina in vertebral centra, on underside of cervical and caudal, on sides of dorsal centra, and on base of neural canal (either tubes joining neural canal to underside of spinal column, or openings into a space filled with some specialized tissue within the body of the centrum); single-headed ribs; **$** relatively short tail; **$** gastralia present and well-developed (ballast?); **$** both girdles elaborated ventrally, with massive ventral plates; space between girdles filled with thick gastralia, giving them almost continuous ventral bone surface; anterior and posterior limbs similar, **$** hyperphalangy; **$** illium does not contact pubis; presumed rowing or "flying" locomotion; propulsive stroke, but no dorsoventral control?



The Triassic Pistosaurus, compared with a typical Jurassic plesiosaur, Cryptoclidus. Both area about the same length (3 to 4 meters). But note the much finer and more conventional limbs, and the much smaller shoulder and pelvic girdles in Pistosaurus. Pistosaurus had not evolved the rigid body and powerful muscles and limbs posessed by the fully marine Plesiosauria.

Notes: There is still a school of thought that plesiosaurs laid eggs on land.

Image: (right) *Plesiosaurus* in the British Museum, modified from the former Donald Nute's Dinosaur Gallery site (former page), by permission.

Links: Plesiosauria Translation and Pronunciation Guide Introduction; Plesiosaur Skeleton; Marine Reptiles (NOT Dinosaurs); Plesiosaurs-Enchanted Learning Software; plesiosaurs; The UnMuseum - Sea Reptiles; List of fossils; Marine Reptiles II: Plesiosaurs - Suite101.com; PLESIOSAURIA; Untitled Document; plesiosauria (excellent, but rather incomplete site); Plesiosauria after O'Keefe, 2001 (Mikko's Phylogeny); The Plesiosaur Site (**Best on the Web** -- Richard has *finally* fixed up this site so that it really works, and the result is a very complete database); Nathis Fauna Reptilelen Mariene Reptielen; The CDM's Earth Sciences Resource Site- Elasmosauridae; Fauna (detailed image of vertebrae); The Journal of Vertebrate Paleontology (abstract).

References: Carroll & Gaskill (1985) [CG85]; Holmes *et al*. (2008) [HCW08]. ATW061217, rev'd ATW080330.

Continued on next page

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

checked ATW050109, revised ATW080330, MAK111103

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

Sauropterygia: More on Plesiosauria

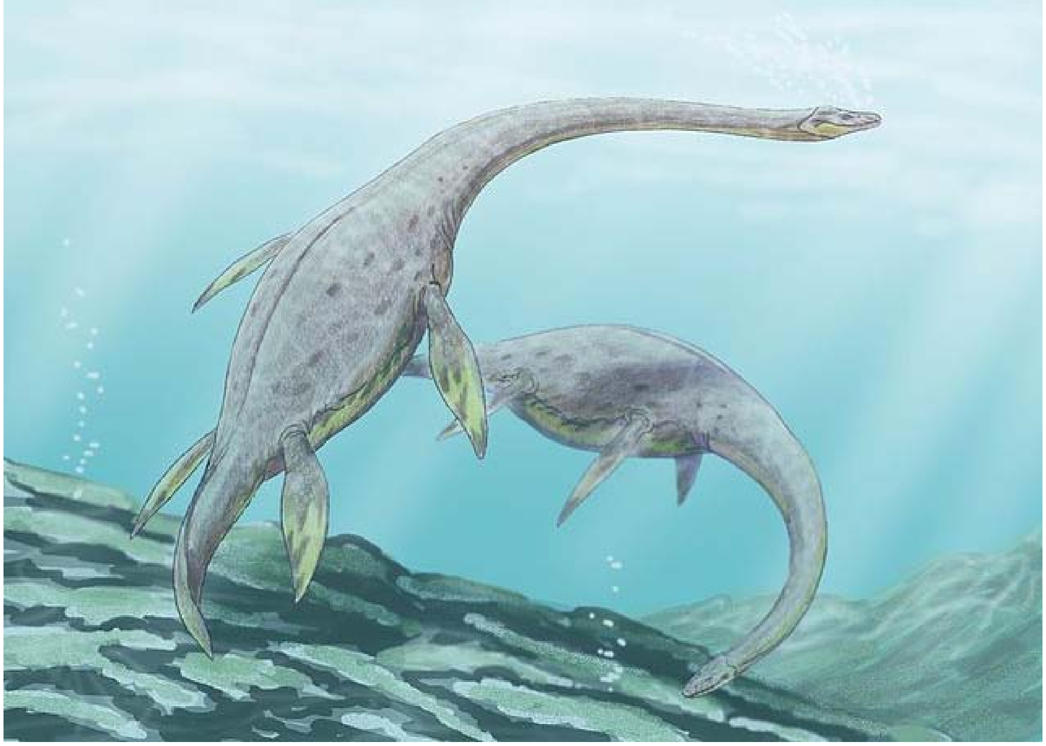
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

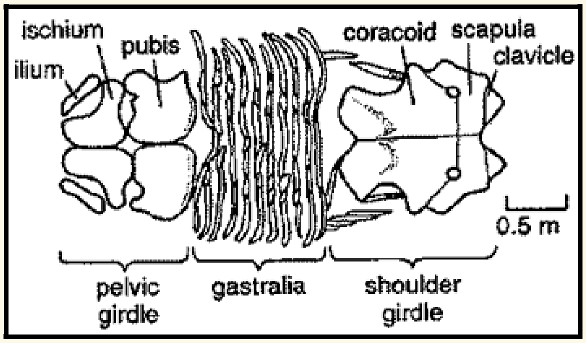
1. Plesiosauria X



Life reconstruction of the Early Jurassic necked plesiosaur *Plesiosaurus dolichodeirus* in underwater flight.
Drawing by Dr Adam Stuart Smith (Plesiosauria com), copied from Wikipedia, Creative Commons Attribution Share-Alike

Plesiosauria: Pectoral Girdle Anatomy

There is some controversy as to how these creatures moved, as no living sea animal propels itself with both pairs of flippers [with the possible exception of *Latimeria*, which has *five* flippers, including a highly modified anal fin]. The original notion was that plesiosaurs "rowed" like an ancient galley. Based on functional studies of plesiosaur limbs, Robinson (1975, 1977) argued that plesiosaurs swam using their paddles in an up-and-down in a "flying" motion to propel themselves through the water, as Recent marine turtles do. The paddles thus acted like hydrofoils generating thrust during the backstroke and also from lift during the recovery stroke. This hypothesis has since been modified, and the current view is that plesiosaur's swam much like modern sea lions. To appreciate the problem, we need a bit more understanding of the plesiosaur limb girdles.

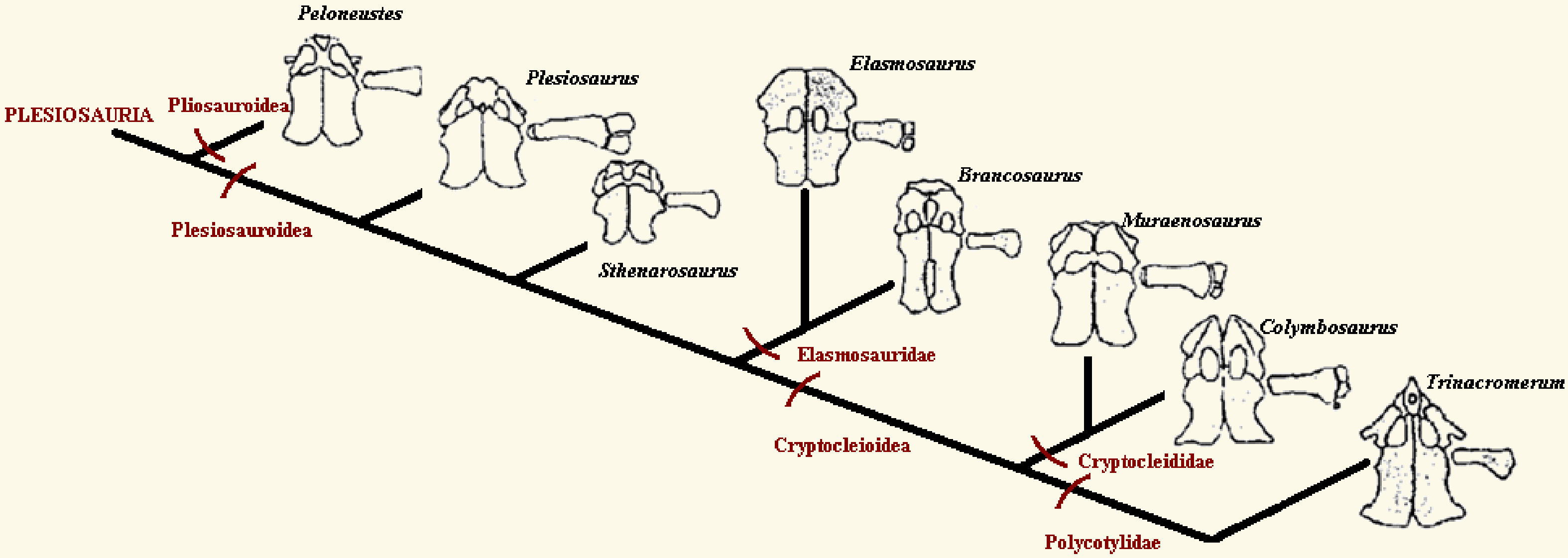


The basic scheme is shown in the figure at right, modified from Taylor (1981) **[1]**. The pelvic girdle is similar to the basal sauropterygian pattern. However, the shoulder girdle has been highly modified from the ancestral pattern discussed previously. Anteriorly, the clavicles are no longer the main support, and the plate-like scapulae are in broad contact along the midline. Carroll & Gaskill (1985) have examined growth series for *Plesiosaurus* and have shown that the juvenile arrangement is almost indistinguishable from the basal sauropterygian pattern. With increasing size, the scapulae grow towards each other. Eventually, they contact each, filling the space between the two sides.

Posteriorly, the coracoids are more massive and are elongated posteriorly to form a continuous ventral shield. During development, the coracoids both send strong midline processes forward until they meet the scapulae, splitting the vacuity at the center of the girdle. Ultimately, all that is left of the formerly large hole at the center of the pectoral girdle are two small coracoid foramina, as shown in the figure at right.

Because the shoulder and ventral girdles are so significant a part of plesiosaur anatomy, they are often very distinctive in different species, and are a useful way of identification and classification of this group. The evolution of shoulder girdle is shown against the overall scheme of plesiosaurian evolution in the figure below.

The gastralia, found in some pachypleurosaurs, are expanded in plesiosaurs to become a massive mesh of ventral ribs. These were presumably tightly linked to each other and to both sets of limb girdles by stout ligaments. Since all of the main limb girdle elements were in broad medial contact, they were no longer free to flex laterally or to rotate with respect to each other. Accordingly, a strong but flexible ventral "spring" was required to allow the animal to move at all. In essence, the shoulder and hip girdles were suspended within the ventral basket which was held under the vertebral column like the string in an archer's bow. This elastic suspension could absorb the up-and-down motion of the limb girdles at each beat of the limbs, while transmitting the propulsive force to the body. Robinson (1975, 1977).



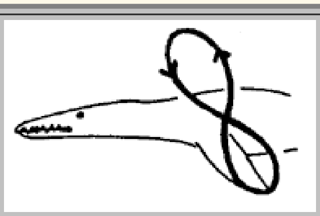
Plesiosaur Locomotion

Thus, we may model the shoulder and hip girdles of plesiosaurs as if they were broad, flat bony plates with limb joints on opposite edges. The main propulsive muscle masses lay on top and under the girdles, and their tendons attached to the dorsal and ventral surfaces of the limbs and swept them powerfully in the desired directions. Supplementary muscles controlled the trim of the flippers so that on both up- and down-stroke the hydrofoil surfaces of the limbs, moving in the vertical plane, generated a resultant thrust forwards. Effectively, therefore, each pair of limbs mounted on its girdle was a self-contained power unit producing a forwardly directed propulsive force.

These two power modules were supported within the domed body, by a distinctive 'ventral basket' made up from the two limb girdles bound together by ligaments running onto and between the gastralia, the splint-like bones of the middle abdominal floor. Robinson argues that this acted as a string to the 'archer's bow' formed by the vertebral column. The contraction of the muscles between the dorsal processes of the vertebrae bent the ends of the column upwards and pulled taut the ventral basket suspended from the vertebral column by its ligamentous attachments. With the ribs, this formed a remarkable suspension system restraining the girdles while allowing some elasticity to absorb the up-and-down motion of the girdles with each beat of the limbs. The ability to vary independently the action of each limb allowed rapid change of direction in the pursuit of prey. The arched vertebral column might even allow plesiosaurs to crawl up on land to breed without collapsing the lungs, like modern sea turtles and unlike Recent whales or the contemporary ichthyosaurs.

Although the functional anatomy of the plesiosaurs makes good sense overall, it is not as clear exactly how the plesiosaurs exploited the locomotor possibilities of their unique body plan. Their distinctively domed body, with its four large broad-bladed limbs, has no precise modern ecological counterpart. It is the old problem of trying to figure out the lifestyle of a creature that has been dead for tens of millions of years.

Unlike other marine reptiles, Plesiosaurs have relatively small tails, but large and powerful paddles, so it is assumed that the latter were used in creating thrust. Exactly how they did is the problem. Three possible hypotheses have been proposed. These are:

		
Rowing underwater like a duck, with an active power stroke backwards (bold line) then a recovery stroke forwards (dotted line). The plesiosaur's limb shape is particularly unsuited to such a movement.	**Flying underwater** like a turtle or penguin, with an up-and-down beat of the limbs; this movement would have been ideal for the limb shape but only the downstroke could have been really powerful.	**Swimming like a sea lion**, with a backwards power stroke and forwards recovery stroke, a movement combining elements of the other two modes

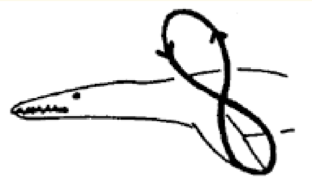
Possible mechanisms for swimming in Plesiosauria. The lines indicate the movement of the tip of the flipper

Rowing

For a long time scientists thought that plesiosaurs moved along by simply rowing their long limbs back and forth. This would seem the most obvious explanation. In rowing, the limb sweeps backwards, while its vertically aligned blade bites into the water and levers the animal forwards. The limb then returns forward to start another power stroke. A limb which is adapted to rowing therefore has to be rigid and oar shaped, broadening at the end, and moves in horizontal plane.

With plesiosaur paddles, this mode of locomotion would not work because the recovery stroke would create a counter-thrust which would oppose the forward motion to some extent, since the paddles could be feathered (i.e. tipped to the horizontal), but not removed from the water. If plesiosaurs really *had* rowed through the water, they should have had webbed folding feet like those of ducks. This is obviously not the case. As pointed out by Robinson, the limb of a plesiosaur is of a quite different design and has characteristic adaptations to undersea flight. Compare the limbs of *Ceresiosaurus*, which seem better designed for this duck-like locomotion.

Subaqueous Flight



Robinson (1975) argued that the plesiosaurs must have "flown" underwater, like sea turtles and penguins, because this movement was the most efficient use of their long hydrofoil-like limbs. She suggested that they swam by flapping both pairs of limbs up and down, producing lift force that propelled the animal forwards. The hydrofoil surfaces swept up and down producing lift forces which averaged out over the whole cycle to a forwardly directed propulsive resultant force

When we look at the plesiosaur limb, we see that it is flat with an aerofoil cross-section like a bird's wing. Or, more correctly, a hydrofoil, because we are speaking here about a "wing" that "flies" through the water.

The plesiosaur limb has a specific shape - it tapers towards its tip to reduce drag, unlike the oar-like shape of the rowing limb. The plesiosaur limb also has just enough flexibility to allow trimming and to damp out drag generating eddies. This arrangement is, again, quite unlike the rigid rowing limb which relies on its production of drag to bite into the water and gain leverage. In fact the limbs of plesiosaurs are similar to the forelimbs of marine turtles, sea lions and penguins, all of which all act as hydrofoils.

The cross-section is such that when it moves through the water with the plane of the limb edge-on to the direction of movement through the water it generates lift (it is the same principle as a bird or airplane wing generating lift in the air). This lift is perpendicular to the direction of movement of the limb. If such a paddle pushes down and backwards at an angle above the horizontal, it generates lift and forwards thrust. In the upstroke, the paddle is tipped the other way, and a further smaller forwards lift force is generated. The paddle tip describes a figure-of-eight pattern and each stage of the cycle produces forwards movement. The plesiosaur limb, in this hypothesis, has to move up and down in the vertical plane to produce horizontally forward directed propulsive force

Criticism of the Underwater Flight hypothesis

In 1982 Tarsitano & Riess suggested a modification to Robinson's underwater flight hypothesis. Although agreeing that plesiosaurs must have used their limbs to fly underwater, they noted that the simplest and apparently most effective up-and-down action was anatomically impossible. The bones of the shoulder joints would block movement of the forelimbs above the horizontal plane. Moreover, plesiosaurs do not seem to have had an equivalent to the avian *triosseal canal* which would allow muscles located in the trunk to pull the flipper above the muscle's own horizontal level.

In the same year Frey & Riess proposed that the 'wings' had an active downstroke, and a comparatively passive upstroke as they returned to the starting point. They suggested that the two pairs of limbs beat out of phase: one pair propelling the animal during its down stroke while the other was brought back to the start of its own power stroke. This limb action would be relatively inefficient compared with that of modern animals such as penguins, whose wings produce propulsive force throughout virtually the whole of the upstroke and downstroke.

The Sea lion theory

Two years later, Godfrey (1984) suggested a different modern analogy for plesiosaur locomotion: sea lions. The sea lion swims by beating its forelimbs forcefully downwards and then relatively passively upwards, while always moving them backwards. Once fully retracted, the limbs can then be feathered and brought forwards during a recovery stroke. In this modified version of the flying model, the paddle tip describes a crescent-shaped path as in the sea lion.

His argument is based on the anatomy of the plesiosaur skeleton. Plesiosaurs could not have moved their paddles up and down in a figure-of-eight because the pectoral and pelvic girdles are both flattened heavy units of bone that form an immovable ventral bony plate. The gastralia between the girdles are too weak for strong vertical movements. Evidence does however point to the plesiosaurian shoulder and hip girdles having the massive muscles needed for the limb action characteristic of sea lions.

Interestingly, sea lion swimming combines elements of both underwater flight (up-and-down action) with rowing (backwards and forwards movement). This appears to be the most plausible explanation for plesiosaur swimming. MAK990911, ATW020630

---

[1] In the original figure, the labels for scapula and coracoid appear to be reversed. This has been "corrected" here, but the reader is warned to be cautious.

Page Back | Unit Home | Page Top | Page Next

checked ATW050109, revised MAK111126

Sauropterygia: Pliosauroidea

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        |  |--Bishanopliosaurus
   |        |  |--Thalassiodracon
   |        |  `--+--Archaeonectrus
   |        |     |--Eurycleidus
   |        |     `--+--Rhomaleosauridae
   |        |        `--Pliosauridae
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

1. *Archaeonectrus* X
2. *Bishanopliosaurus* X
3. *Eurycleidus* X
4. Pliosauroidea X
5. *Thalassiodracon* X

The proto-pliosaur *Thalassiodracon hawkinsi* investigates an ammonite. At this early stage in plesiosaurian evolution, there was very little to distinguish pliosaurs from plesiosaurs; the traditional distinction of short versus long neck, and big versus small head, only appears in the Mid Jurassic. Latest Triassic and Earliest Jurassic of England (north-central Laurasia).
Artwork by Nobu Tamura. Wikipedia, GNU Free Documentation/Creative Commons Attribution.

Descriptions

Pliosauroidea:

Range: Late Triassic (Early Jurassic?) to Late Cretaceous.

Phylogeny: Plesiosauria ::: Plesiosauroidea + *: *Bishanopliosaurus* + *Thalassiodracon* + (*Archaeonectrus* + *Eurycleidus* + (Rhomaleosauridae + Pliosauridae)).

Characters: 3 to 12 m; Large head, skull and snout heavy and elongated; occipital condyle from basioccipital only; conical teeth with numerous vertical ridges, frequently showing wear at the tip; teeth may have keels; premaxillae with 5 tooth pairs; dentaries with 25-40 tooth pairs; neck short and thick, ~13 cervical vertebrae; 23-24 dorsal vertebrae; centra short; propodials long, with femur longer than humerus; hyperphalangy with up to 16 segments in longest digit; ischia long; adapted for streamlining and larger paddles, (seal-like pursuit hunter?).

Links: Walking with Dinosaurs - Chronology: 149 million years ago; Marine Reptiles (NOT Dinosaurs); Plesiosauria Translation and Pronunciation Guide; Pliosauroidea; saf4029-01.html; p3 - pliosaur2.jpg (?); 2_88_1.pdf; Kronosaurus (German).

References: Brown (1981). MAK990812, ATW011117.

Bishanopliosaurus: *B. youngi* Dong 1980.

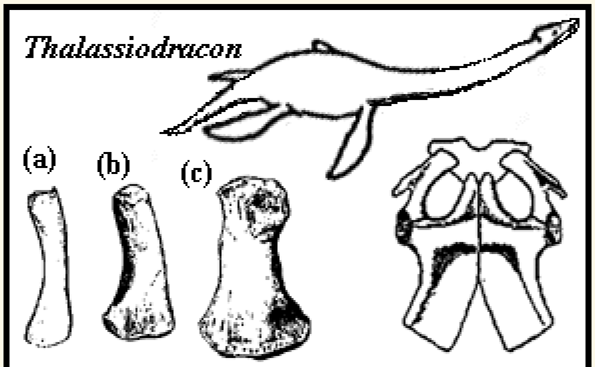
Range: Early Jurassic (Toarcian) of China (Sichuan).

Phylogeny: Pliosauroidea: *Thalassiodracon* + (*Archaeonectrus* + *Eurycleidus* + (Rhomaleosauridae + Pliosauridae)) + *.

Characters: ~4m; freshwater pliosaur.

Links: Plesiosauria Translation and Pronunciation Guide.

Note: may be a rhomaleosaurid. ATW020630.



Thalassiodracon: life reconstruction; pectoral girdle and (b) humerus, compared with humeri of Pistosaurus (a) and Muraenosaurus

Thalassiodracon: *T. hawkinsi* Storrs & Taylor 1996 (previously *Plesiosaurus hawkinsii* Owen 1838. The change in spelling of the specific name is apparently due to an error by Seeley, now perpetuated).

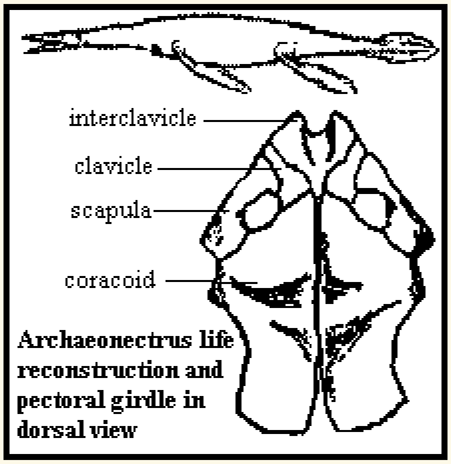
Range: Late Triassic (Rhaetian) to Early Jurassic (Hettangian) of Europe (England).

Phylogeny: Pliosauroidea: *Bishanopliosaurus* + (*Archaeonectrus* + *Eurycleidus* + (Rhomaleosauridae + Pliosauridae)) + *.

Characters: Small form rarely up to 2m; head small (10% total length, but proportionately larger than *Plesiosaurus*); skull of light construction; rostrum short & pointed (but proportionately longer than *Plesiosaurus*); upper temporal fenestra small, jugal elongate; cheek deeply excavated; mandibular symphysis spatulate; neck of moderate relative length (40% total length & 31-32 vertebrae); ~21-23 dorsals; 3-4- sacrals; 35 caudals; propodials & without massive distal expansion; humerus relatively straight; ischium elongate; anterior face of pubes rounded; hindlimbs slightly longer than forelimbs in adult (*contra*, Plesiosauria Translation and Pronunciation Guide).

Note: more typically classified as a basal plesiosauroid, *Thalassiodracon* may seem an unlikely candidate for a basal pliosaur. However, the shape of the pubes and lower jaw, as well as the larger size of the hindlimbs, are pliosauroid. In any case, we will follow Pliosauroidea after O'Keefe, 2001 until we have a chance to follow up on this issue.

Links: The Plesiosaur Site - Species; Plesiosaur References - STORRS & TAYLOR 1996; Plesiosauria Translation and Pronunciation Guide. MAK990901, ATW030519.



Archaeonectrus life reconstruction and pectoral girdle in dorsal view

Archaeonectrus: *A. rostratus* Novozhilov 1964 (= *Plesiosaurus rostratus* Owen 1865)

Range: Early Jurassic (Sinemurian) of Europe (England) & possibly Russia.

Phylogeny: Pliosauroidea:: *Eurycleidus* + (Rhomaleosauridae + Pliosauridae) + *.

Characters: head large & elongated (compared to *Plesiosaurus*) (~15% total length); snout narrow; orbits round; teeth pointed, conical and recurved; neck relatively short (20-25% total length); cervical vertebrae (20) short; 27? dorsal vertebrae; 3? sacrals; 34 caudals; some caudal centra vertically compressed (Owen suspected a caudal "fin" of some kind); hindlimbs larger (= longer?) than forelimbs.

Note: remember that the image shows the pectoral girdle in *dorsal* view. Most of the other images here are *ventral* views.

Links: Plesiosauria Translation and Pronunciation Guide. MAK990903, ATW020630.

Eurycleidus: *E. arcuata* Andrews 1922 (= *Plesiosaurus arcuata* Owen 1840)

Range: Early Jurassic of Europe, *Psiloceras planorbe* ammonite zone, (early

Hettangian age) Bitton and Somerset, England.

Phylogeny: Pliosauroidea:: *Archaeonectrus* + (Rhomaleosauridae + Pliosauridae)) + *.

Characters: ~4m overall; skull large & broad; Jugal short, not underlying orbit; postorbital and cheek bar dorso-ventrally deep; quadrates overlap the quadrate rami of the pterygoids anterolaterally; occiput said to be plesiosaur-like; exoccipitals- opisthotics participate in occipital condyle; prootics bridging the basioccipital- basisphenoid gap; fenestra ovalis small; parasphenoid with reduced participation in floor of braincase; coronoid absent; prearticular small; crowns of teeth curved, with weakly developed carinae and variably developed ridge ornament; symphysis covers at least four tooth positions; at least 5 pairs of large procumbent teeth anteriorly (on premaxilla); teeth not diminishing in size immediately behind the premaxilla-maxilla suture; at least 22 sets of very small teeth posteriorly; neck stout; neck vertebrae elongate (plesiosauroid character); cervicals with notch between the pre- and postzygapophyses; interclavicle broader than long; coracoids long (pliosauroid character); humerus larger than femur (?); radius & ulna much longer than tibia & fibula.

Note: [1] *Eurycleidus* was previously included in the family Leptocleididae. However, it also appears to be closely related to *Rhomaleosaurus*. The Rhomaleosauridae are often grouped together with the leptocleidine pliosaurs. Since *Leptocleidus* is the only certain member of the Leptocleididae, we treat the rhomaleosaurs as the only relevant supergeneric taxon, in order to avoid pointless discussion of a monogeneric family. We also follow Rhomaleosauridae after O'Keefe, 2001 in placing *Eurycleidus* outside the Rhomaleosauridae altogether. However, there is substantial contrary authority. Cruickshank & Long (1997) make the comparison between *Eurycleidus* and *Leptocleidus* several times. Storrs & Taylor (1996) have even considered *Eurycleidus arcuata* to be the same animal as *Rhomaleosaurus megacephalus*. **[2]** Cruickshank (1994) asserts that the skull of this animal combines plesiosauroid and pliosauroid features.

Image: from Praveký svet

Links: Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site; Praveký svet (Slovak -- I think); a pair of Eurycleidus arcuatus (really good sketch).

References: Cruickshank (1994), Cruickshank & Long (1997), Storrs & Taylor (1996). MAK991206, ATW030411.

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

checked ATW050526

Sauropterygia: Pliosauroidea: Pliosauridae

Abbreviated Dendrogram

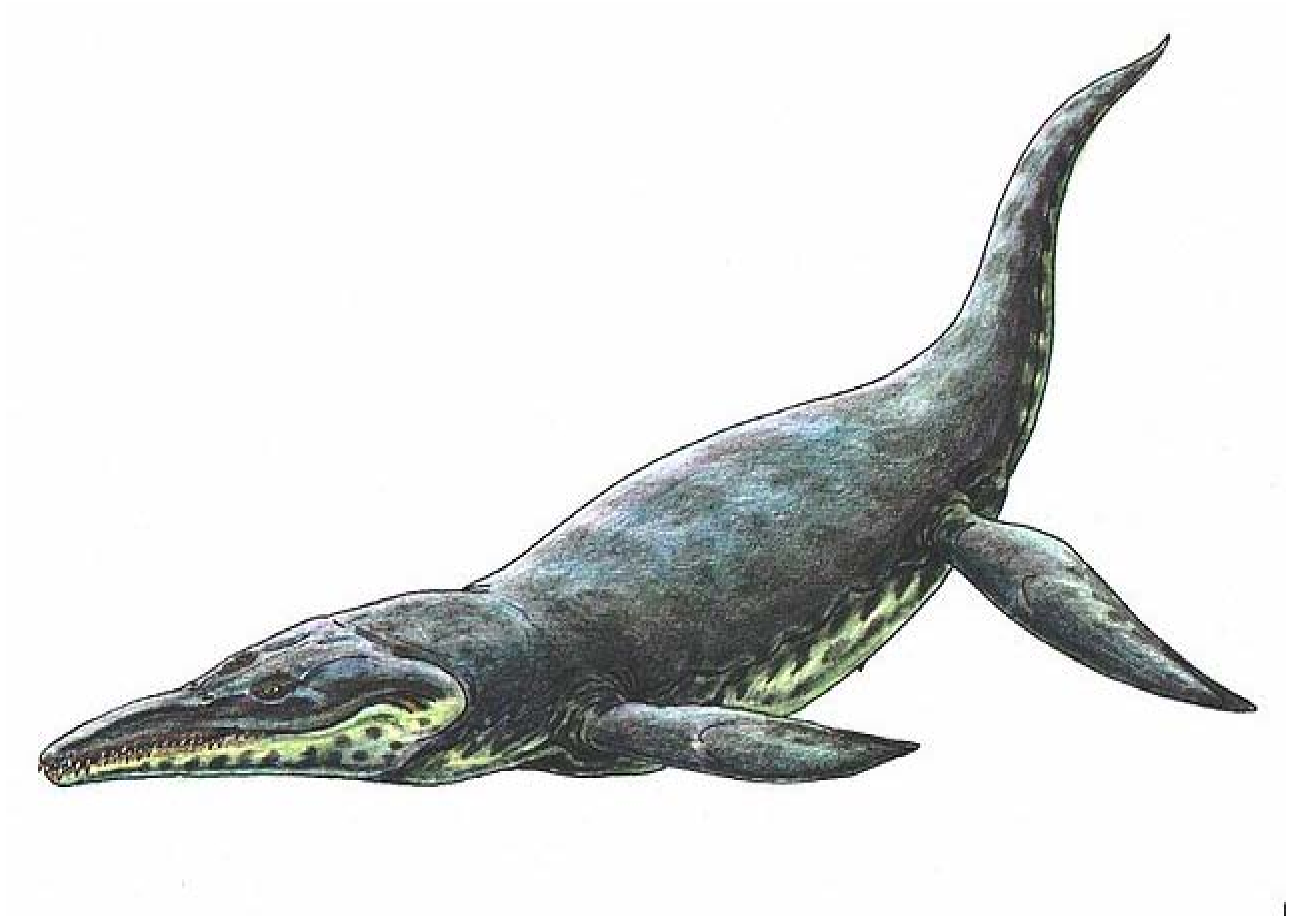
```
DIAPSIDA
|--ARCHOSAUROMORPHA

LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Pachypleurosauridae
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        |  |--Rhomaleosauridae
|        |  `--Pliosauridae
|        |     |--Maresaurus
|        |     |--Plesiopleurodon
|        |     |--Macroplata
|        |     `--+--Kronosaurus
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

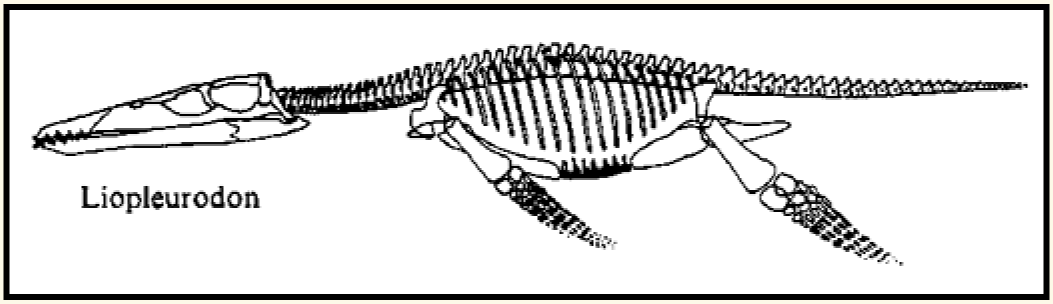
Taxa on This Page

1. *Kronosaurus* X
2. *Macroplata* X
3. *Maresaurus* X
4. Pliosauridae X



Life reconstruction of the giant (length to 10 meters) advanced pliosaurid *Kronosaurus queenslandicus*, from the Middle Cretaceous (Aptian-Albian) of Queensland (south-central Gondwana).
Artwork by Dmitry Bogdanov. Wikipedia, Public Domain

Pliosauridae



It is often said that the short-necked **Pliosauridae** were "the killer whales of the Mesozoic." In fact, the two groups have very little in common beyond a superficially similar body plan and -- perhaps -- a similar ecological niche. Like the killer whales, the pliosaurids were large marine tetrapods with huge skulls and relatively short necks (about 13 cervical vertebrae). It seems they also had a small vertical tail fin. Their sizes ranged from 3 to 12 or possibly even more in length. The head alone was 3 meters or more in length in the larger forms. Examples of pliosaurids are *Pliosaurus*, *Peloneustes*, and *Liopleurodon*. The relationship of the pliosauroid ***Kronosaurus*** is uncertain, although it is treated here as a pliosaurid.

Among Jurassic forms, *Pliosaurus* and *Liopleurodon* were were the giants of the oceans, around 7 to 12 metres in length; although large forms may have been even bigger. The skull and snout were heavy and elongated. The conical teeth bore numerous vertical ridges. The neck short and thick, and the body streamlined. There were about 23 cervical and 24 dorsal vertebrae. MAK990814, ATW020704.

Pliosauridae: *Pliosaurus* > *Rhomaleosaurus*. Plesiosauria Translation and Pronunciation Guide

Range: Middle Jurassic to Late Cretaceous

Phylogeny: Pliosauroidea::: Rhomaleosauridae + *: *Maresaurus* + *Plesiopleurodon* + *Macroplata* + (*Kronosaurus* + (*Peloneustes* + (*Liopleurodon* + (*Pliosaurus* + *Brachauchenius*)))).

Characters: very large skulls (on the order of 25-30% total length); 13 cervical vertebrae in derived forms.

Image: *Macroplata*. Image by Steve Kirk, from Cox *et al.* (1988)

Links: Pliosauridae after O'Keefe, 2001; IL Geo Survey Past Dinosaur Questions; p3 - pliosaur2.jpg (teeth); Plesiosauria Translation and Pronunciation Guide; Re: Megalneusaurus rex (fwd). ATW020704.

Maresaurus: *M. coccai* Gasparini 1997.

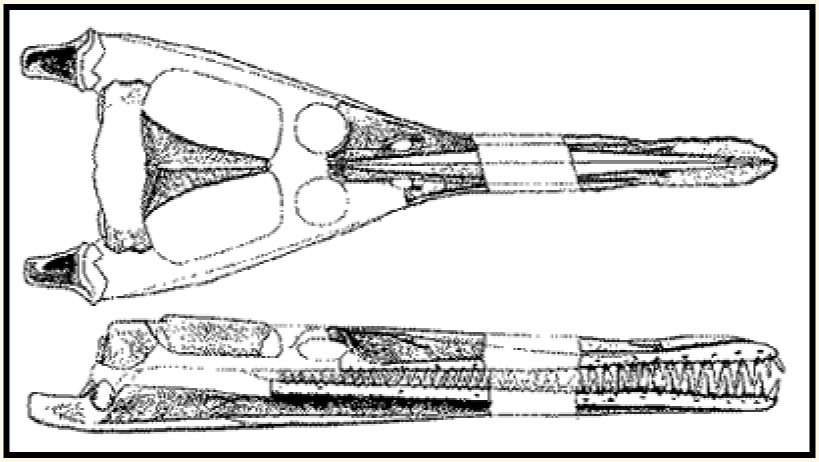
Range: Middle Jurassic (Bajocian) of South America

Phylogeny: Pliosauridae: *Plesiopleurodon* + *Macroplata* + (*Kronosaurus* + (*Peloneustes* + (*Liopleurodon* + (*Pliosaurus* + *Brachauchenius*)))) + *.

Characters: medium-length spatulate snout (convergent on rhomaleosaurids?).

Links: Plesiosauria Translation and Pronunciation Guide. ATW020705

Macroplata: Swinton 1930; *M. longirostris* (= *Plesiosaurus longirostris*) Blake 1876.



Range: Early Jurassic (Hettangian to Toarcian) of Europe.

Phylogeny: Pliosauridae: *Maresaurus* + *Plesiopleurodon* + (*Kronosaurus* + (*Peloneustes* + (*Liopleurodon* + (*Pliosaurus* + *Brachauchenius*)))) + *.

Characters: overall length 4.5-5.0 m; large skull (60-70 cm); relatively long neck with 29 short cervical vertebrae (twice length of skull); cervical vertebrae flattened; shoulder girdle modified to form bony ventral plates; coracoids narrow and much larger than scapulae; hindlimbs longer than forelimbs.

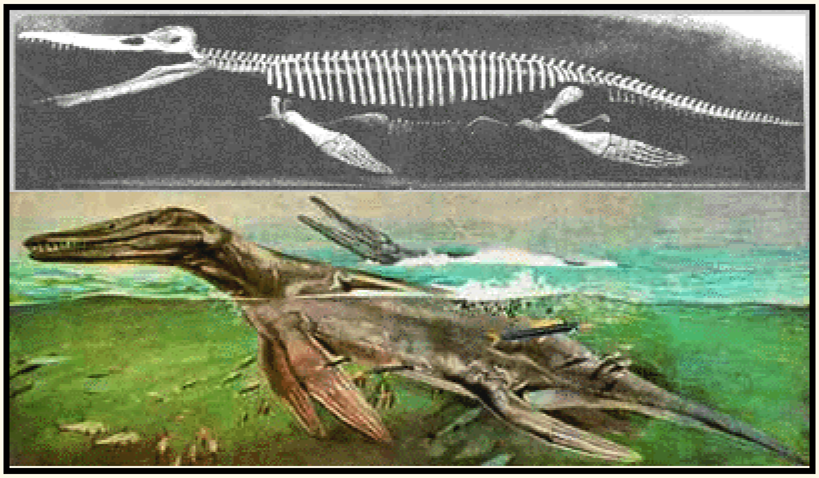
M. tenuiceps: from the Early Jurassic (Hettangian) of Warwickshire, England had a neck about twice the length of the crocodile-like head, with 29 shortened cervical (neck) vertebrae. *M. tenuiceps* had a shoulder girdle with coracoids that were proportionately much larger than the scapulae, indicating a powerful forward stroke for fast swimming. Length of this species 4.5 meters, skull: 58 cm long.

M. longirostris: from the Upper Lias *Ammonites serpentinus* subzone (Toarcian) of Whitby, Yorkshire, England had an even more elongate skull, 72 cm in length. It is not certain how much of the associated skeleton is from the same animal as the skull, or even whether the species belongs in the genus *Macroplata*. (It has been suggested that it might be a type of *Rhomaleosaurus*). If it is a *Macroplata* it shows the

evolutionary succession of this lineage over some fifteen million years. Overall length 5 meters long; skull 70 cm long.

Image: Right: *M. longirostris* skull from White (1940).

Links: DinoData Marine Reptiles Pliosauroidae; Plesiosauria Translation and Pronunciation Guide; Dinosaurios (Spanish); Mr. Fred Meyer's Macroplata QTVR Object; Rettili del mare (Italian: very brief); JURÁSSICO (Spanish); ERA MESOZÓICA plessiossauros (Portuguese); Lexique Dinosaures. Le Macroplata.Fiche.Images.(French: succinct encyclopedia-type entry); Paleontology and Geology Glossary- Ma. ATW031212, MAK990830.



***Kronosaurus*:** *K. queenslandicus* Longman, *K. boyacensis* Hampe 1992.

Range: Early Cretaceous (Albian) of Australia & South America

Phylogeny: Pliosauridae:: (*Peloneustes* + (*Liopleurodon* + (*Pliosaurus* + *Brachauchenius*))) + *.

Characters: said to be largest known pliosaur at 12-15m; skull ~3m long; neck short; 12 cervical vertebrae.

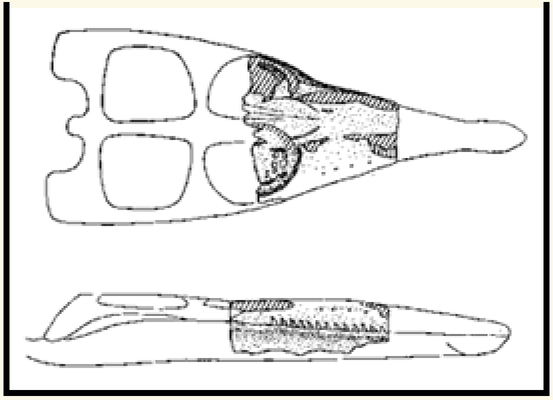
Note: During the middle Cretaceous period the role of giant marine predator was filled by the formidable *Kronosaurus*. Despite being a popular prehistoric marine reptile, featured in many paleontology text books and popular dinosaur books (as a sort of aquatic *T. rex*), *Kronosaurus* is a rather misunderstood genus. It has been variously included among the Pliosauridae and Polycotylidae. It may even belong in its own family. There seem to be at least three species:

Kronosaurus "queenslandicus" sp. This is the famous Harvard *Kronosaurus*. A Harvard expedition in 1931-1932 recovered two specimens of large pliosaurs from near Richmond, Queensland. Although identified with the type species *Kronosaurus queenslandicus* the skull is much higher as reconstructed, and the animal as a whole a little smaller. Wallumbilla Formation, Aptian age.

The famous vertebrate palaeontogist Alfred Sherwood Romer helped mount the giant skeleton in the Harvard Museum of Comparative Zoology in the 1950s, but much of material was badly eroded. Romer and his team were forced to fill in many details using plaster; in fact so much plaster that the specimen acquired the derisive nickname "Plasterosaurus" in some quarters. Romer gave the skeleton a whopping 30 dorsal vertebrae, stretching their *Kronosaurus* to 12.8 meters. Although the dimensions of the limb girdles are consistent with Romer's reconstruction, others have asserted that the actual length (when excess vertebrae are removed) is around 8 or 9 meters.

Kronosaurus boyacensis Hampe 1992 is a large pliosaur recently discovered in the Boyaca region of northern Columbia and dated to the late Aptian. The specimen included a fairly complete skull and much of the skeleton except the tail. It has 12 cervical, 3 pectoral, 19 dorsal, and 5 sacral vertebrae. The animal was probably about 9 meters (30 feet) long in life. It is unusual for its thickened ribs (not known in any other large pliosaur).

Kronosaurus queenslandicus Longman 1901 was actually erected on jaw fragments found near Hughenden, central-western Queensland,



Australia, in the 1920s. This creature had a flattened head very different from the Harvard specimen. It is from the Toolebuc Formation, Albian age (Early Cretaceous). A second partial skull from the same locality also differs from the Harvard specimen. The skull (illustrated at left) is very broad, low, and flat (the fragment is 87 cm across but only 13 cm high), with the large, upwardly directed orbits of an ambush predator. Matching those measurements with the above sketch, the total length of the skull would have been around 2.85 meters, far bigger than any theropod dinosaur skull. This species seems to be somewhat larger than the Harvard specimen, so perhaps in life it would have attained 10 meters or more in length - equal in size to the large Jurassic pliosaurs.

Links: Prehistoric animal - Kronosaurus - Cretaceous Reptile; Kronosaurus queenslandicus; varner06.jpg; Dino-Dispatches No. 1, 11/08/1998, Giant pliosaurs -- real and imaginary; Queensland Museum - Dinosaurs of Ancient Queensland - Dinosaurs! - Kronosaurus; Marine Reptiles (NOT Dinosaurs). MAK990813.

Page Back Unit Home Page Top Page Next

checked ATW060216

Sauropterygia: Pliosauroidea: Pliosauridae (2)

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        |  |--Rhomaleosauridae
   |        |  `--Pliosauridae
   |        |     |--Kronosaurus
   |        |     `--+--Peloneustes
   |        |        `--+--Liopleurodon
   |        |           `--+--Pliosaurus
   |        |              `--Brachauchenius
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

1. *Brachauchenius* X
2. *Liopleurodon* X
3. *Peloneustes* X
4. *Pliosaurus* X

Descriptions

Peloneustes: *P. philarchus* Seeley 1869

Range: Late Jurassic of Europe

Phylogeny: Pliosauridae::: (*Liopleurodon* + (*Pliosaurus* + *Brachauchenius*)) + *.

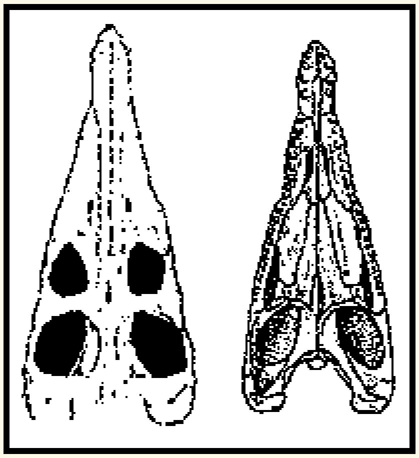
Characters: ~3m; lacrimal (usually absent in Plesiosauria) said to be present [C97]; Jacobson's Organ absent [C97]; relatively few teeth; 20-22 cervical vertebrae; ~20 dorsals; massive, apparently rigid ventral shield formed from limb girdles and gastralia.

Image: Right: apparently plantar view of forelimb from PLIOSAUR. Note extreme proximodistal compression of radius and ulna. Left: reconstruction in the Peterborough Museum (UK) from Senckenberg Fossile Wirbeltiere der Meere.

Note: stomach contents include cephalopods.

Links: Most links only contain a few basic pieces of information, with or without a life reconstruction, in a great variety of languages: for example, Dinosaurios: Peloneustes (Spanish), the Enchanted Learning page (more on their Plesiosaur page), Peloneustes (German), Prehistorics Illustrated, Praveký svet (?language), Dinooption (Korean), Rettili del mare (Italian), Nathis (Dutch). The most amusing of these is Multimedia Development and 3d Animation, which has a 3D animation. Dinodata goes a bit further, and the Bedford Museum site has a small, but detailed skeletal reconstruction. Reptilien has an image of a humerus, while PLIOSAUR has both the humerus and most of the rest of the forelimb (this is the image above). The Plesiosaur Site, as always, has gobs of specimen information and references for the working paleontologist, although it is less useful for us armchair types. ThePlesiosauria Translation and Pronunciation Guide is a better bet, but the entry is relatively short. Finally, a brief abstract (see p. 20) from Leslie Noè has some interesting information on dietary specialization.

References: Carpenter (1997) [C97]. ATW050808.



Liopleurodon: *L. ferox* Sauvage 1874a, *L. grossouveri* Sauvage 1874a, *L. macromerius* Tarlo 1989, *L. pachydeirus* Seeley 1869, *L. rossicus* Novozhilov 1948.

Range: Middle Jurassic (Callovian) to Late Jurassic (Tithonian) of South America, Europe

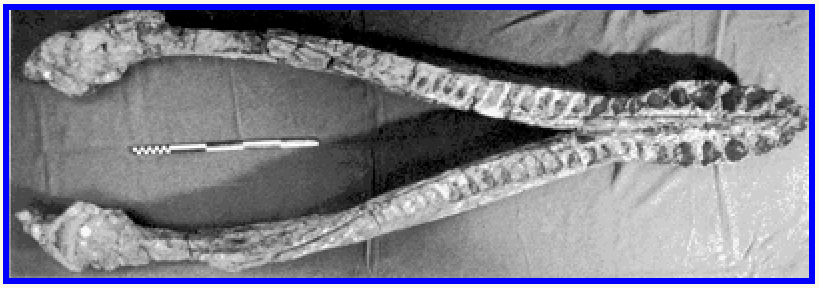
Phylogeny: Pliosauridae:::: (*Pliosaurus* + *Brachauchenius*) + *.

Characters: large individuals may have exceeded 15m; lacrimal (usually absent in Plesiosauria) said to be present [C97]; Jacobson's Organ absent [C97].

Links: Walking with Dinosaurs - Fact File: Liopleurodon (file, yes, but "fact"?); The UnMuseum - Sea Reptiles; Dino-Dispatches No. 1, 11/08/1998, Giant pliosaurs -- real and imaginary; Liopleurodon; geraths.htm (I really like this life reconstruction -- perhaps a bit thicker neck & more angle to the forelimbs?); The Plesiosaur Site - Species; Liopleurodon (pictures from WWD & Portuguese essay); Liopleurodon; Dinosaurios- Liopleurodon; Liopleurodon ferox- el terror de los mares; Liopleurodon (Danish); Descubierto el primer esqueleto completo de Liopleurodon ferox; Plesiosaur Directory - Research - Liopleurodon Skull by Adam ...; PANGEA; 巨型滑齿龙; SIC Online.

References: Carpenter (1997) [C97]. ATW030621.

Pliosaurus: Owen 1841a. *P. brachydeirus* Owen 1841a, *P. andrewsi* Tarlo 1960, *P. brachyspondylus* Owen 1839, *P. ferox* (may = *Liopleurodon ferox*), *P. macromerus* Phillips 1871.



Range: Middle Jurassic (Callovian) to Late Jurassic (Kimmeridgian) of Europe & South America.

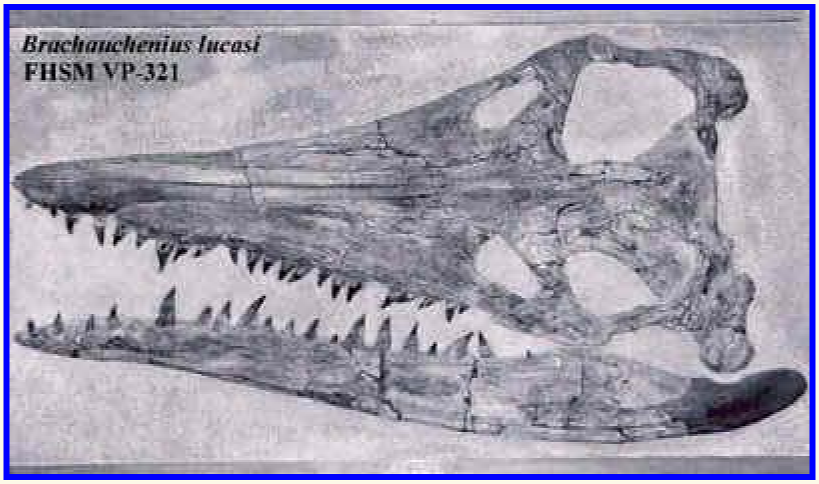
Phylogeny: Pliosauridae:::: *Brachauchenius* + *.

Characters: another candidate for largest pliosaur at ~12m; skull 1.5-2.0 m long & deep; rostrum long & blunt anterior to nares; mandible with a long symphysis; 10-12 pairs of symphysial teeth, with first 5-6 large & caniniform; 30-38 distal pairs of teeth; teeth trihedral (conical in*Liopleurodon*); 20 cervical vertebrae; cervical ribs double-headed.

Image: lower jaw of *P. ferox* from Pliosaurus ferox.

Links: Geology Field Trip Guide - Kimmeridge, Dorset - Kimmeridge Clay Fossils; Westbury pliosaur centrum; The Plesiosaur Site - Species; Ravin' Ray's Plesiosaur FAQ's; Pliosaurus (tooth); Pliosaurus ferox (French); plreptmar vsm.pdf (French); pliosaurus 3.jpg. ATW020705.

Brachauchenius: *B. lucasi* Williston 1903.



Range: Late Cretaceous (Cenomanian to Turonian) of North America (Kansas & Texas)

Phylogeny: Pliosauridae:::: *Pliosaurus* + *.

Characters: very large (~11 m); skull (1.5 m) broad and triangular; rostrum pointed; symphysis short; teeth striated, with striations branching near root; very short neck, with 13 short vertebrae; neck ~75% length of skull; cervical vertebrae without *nutritive foramina*; cervical vertebrae lack ventral or lateral keels; cervical ribs single-headed; 22 dorsals.

Image: one of many excellent pliosaur-related images at the Oceans of Kansas site. See also Dan Varner's image at the top of that page.

Links: Plesiosauria Translation and Pronunciation Guide; Dan Varner Paleo-Life Art; Paleontology and Geology Glossary: Br; Brachauchenius facts @ Prehistorics Illustrated; ?????? ???;

References: Welles (1962). MAK990903, ATW020706.

Page Back | Unit Home | Page Top | Page Next

checked ATW050804

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

Sauropterygia: Pliosauroidea: Rhomaleosauridae

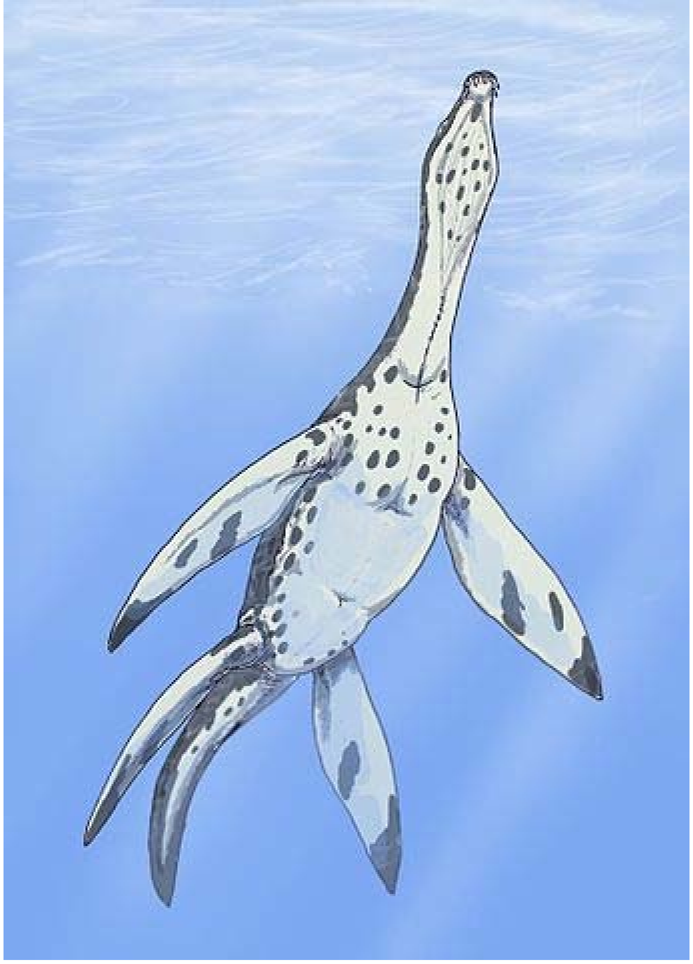
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        |  |--Rhomaleosauridae
   |        |  |  |--Yuzhoupliosaurus
   |        |  |  `--+--Rhomaleosaurus
   |        |  |     `--+--Simolestes
   |        |  |        `--Leptocleidus
   |        |  `--Pliosauridae
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

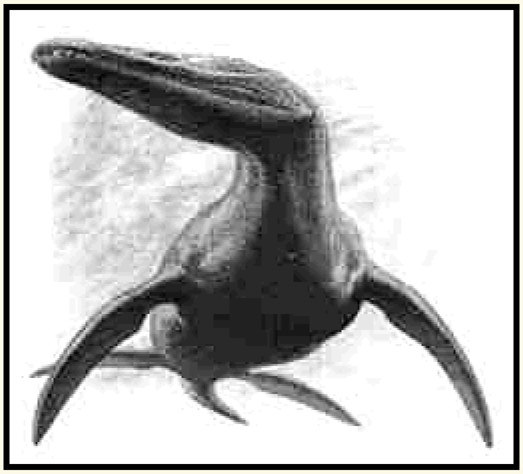
Taxa on This Page

1. *Leptocleidus* X
2. Rhomaleosauridae X
3. *Rhomaleosaurus* X
4. *Simolestes* X
5. *Yuzhoupliosaurus* X



Life reconstruction of the medium-sized (length 3.3 meters) Rhomaleosaur *Meyerasaurus victor* (Thaumatosaurus), from the Early Jurassic of Germany (north-central Laurasia). Artwork by Dmitry Bogdanov. Wikipedia, GNU Free Documentation/Creative Commons Attribution.

The Rhomaleosaurs



The **Rhomaleosauridae** were the earliest of the giant sauropterygian predators, rivaling the biggest ichthyosaurs in size. They are also relatively primitive pliosauroids. They differ from conventional pliosaurs in their longer neck and crocodile-like head. For some thirty or forty million years they were the top predators of the ocean, attaining 5 to 7 metres in length. Genera may include ***Rhomaleosaurus*** (=*Thaumatosaurus*), ***Yuzhoupliosaurus***, *Macroplata*, *Sthenarosaurus*, and ***Simolestes***, but it is not certain if any or all of these genera are actually related, or whether they are the result of evolutionary convergence due to similar lifestyle. Some species have previously been identified as species of *Plesiosaurus*. In certain respects the rhomaleosaurs seem to be intermediate between the plesiosauroid and pliosauroid lineages. The group may also include ***Leptocleidus***. However, the phylogenetic relationships of Early Jurassic Sauropterygia are poorly known, and the whole group is in need of study and revision.

In an email to one of us (MAK) on this subject (24 Aug 1999) Darren Naish says:

> As you know, plesiosaur affinities are a mess, and no one can say what the true picture was at present. I do suspect that rhomaleosaurs are primitive pliosauroids, and that pliosauroids are primitive plesiosaurs (i.e. they diverged before things like *Plesiosaurus*, cryptoclidids and

elasmosaurids), but I am not convinced that rhomaleosaurs are close to true pliosaurids like the *Liopleurodon* group and *Peloneustes*. However, I also believe that Leptocleidines are highly specialized rhomaleosaurs - both groups share the same pattern of premaxillary foramina and both have a peculiar trough on the inside of the lower jaw. This is exciting as it means that rhomaleosaurs lived on as miniaturized predators that invaded estuarine/ ?freshwater environments.

Image: Right; *Rhomaleosaurus*. Early Jurassic. Length 3.5 to 6 meters. Illustration by John Sibbick - in David Norman, **Prehistoric Life: the Rise of Vertebrates** Left: *Leptocleidus* from Brian Choo, donated to Classroom Clipart for educational use. MAK991206.

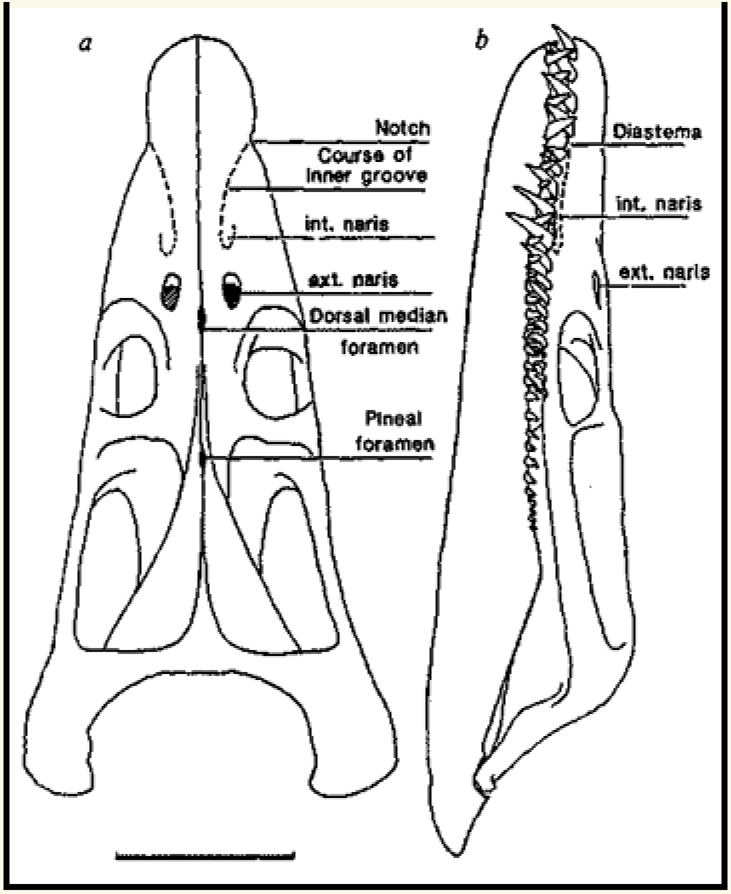
Rhomaleosaurus

This important genus includes a number of species, some of which grew quite large. These were powerfully built pliosaurs, with long toothy jaws which hunted both by site and smell and tore their prey apart with jerks of the head, much as a modern crocodile does. Think of a crocodile crossed with a modern killer whale.

Cruickshank *et al*. (1991), showed that the skull of this predator is designed in a way that the animal could swim with its mouth slightly open, enabling water to pass through scoop-shaped openings in the roof of the mouth, through a channel where the smell sensors were located (*Jacobson's organ*), then out external nostrils on the snout. This arrangement -- the reverse of what might be expected in a normal air-breathing animal, would have enabled *Rhomaleosaurus* to hunt its prey by smell, just sharks do.

The following material is taken from their short article in *Nature*, and shows how the skull of this marine carnivore was designed to allow water to flow in through the nostrils (nares), thus enabling it to smell the water:

> The dorsally placed external nostrils of plesiosaurs are usually regarded as an adaptation to breathing in those extinct marine reptiles. We suggest instead that the narial system was used in underwater olfaction. The internal nares are anterior to the external nares. Hydrodynamic pressure during swimming forced water into the mouth, along palatal grooves into the scoop-shaped internal nares and up short ducts, presumably lined with olfactory epithelia. Alternatively, or additionally, the so far unlocated Jacobson's organ detected particulate matter. The water was sucked out through the external nares by hydrodynamic pressure generated by fast flow over the convex upper surface of the head.



The internal nares strongly resembles the NACA Duct (National Advisory Committee for Aeronautics) design of air scoops on aircraft, whose opening is flush with the surface. This design deepens and widens in the direction of fluid flow and ends in a transverse scoop, suggesting that the internal nares acted as a ram scoop for water flowing backwards along the inner groove....

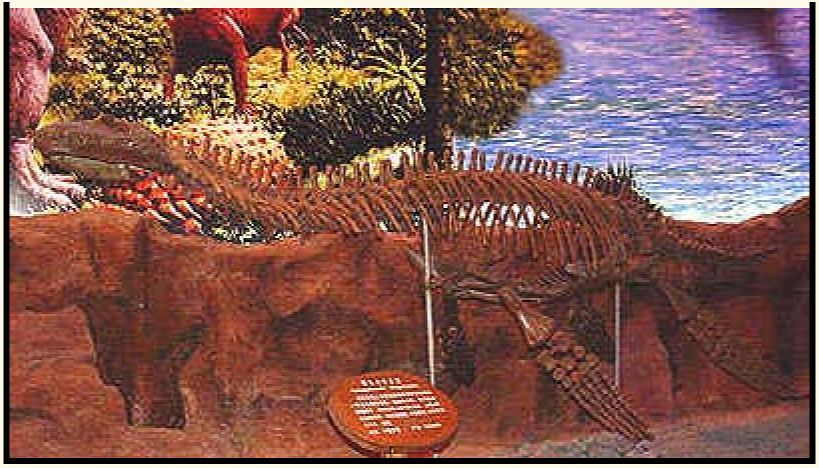
Were the nares used for respiration? Both internal and external nares would have been partly occluded by soft tissue and any measurement of the bony outlines will only give a maximum dimension. In the very similar *R. zetlandicus*, sculpture on the anterior external narial wall may indicate insertions for muscles and ligaments controlling a narial valve. In *R. megacephalus* each internal nares had a functionally clear area of 2.0 cm^2 or less, which seems disproportionately small for a 5-meter long *Rhomaleosaurus*. Also, the placement of the internal nares anterior to the external nares would have hindered respiratory air flow. We believe that *Rhomaleosaurus* breathed through its open mouth, contrary to the conventional view that all respiration occurs through the narial system. Water would have been excluded from the trachea during normal swimming and in heavy seas, by a glottal valve and a large muscular tongue. The reconstruction of anteriorly hinged nasal flaps on the external nares would presume automatic closure if inspiration were attempted through them. We therefore believe that the dorsal placement of the external nares is thus irrelevant for respiration, unlike in crocodilians and cetaceans, which have full secondary palates. In these two groups with secondary palates, respiration is associated with airborne olfaction, but in the case of this pliosaur we believe the adaptation to be for the sampling of water and not air.

Rhomaleosauridae:

Range: Early Jurassic to Middle Jurassic (middle Cretaceous?).

Phylogeny: Pliosauroidea::: Pliosauridae + *: *Yuzhoupliosaurus* + (*Rhomaleosaurus* + (*Simolestes* + *Leptocleidus*)).

Characters: skull relatively large (12-17% total

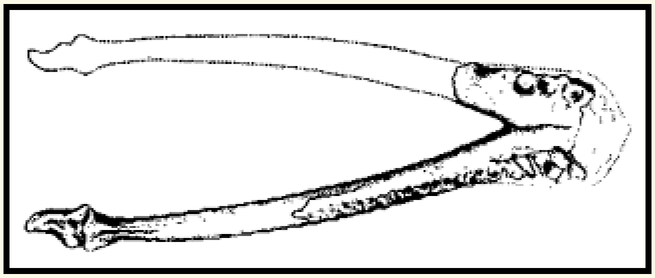


length); rostrum short-moderate length; rostrum distally expanded and spatulate; some large, caniniform teeth (perhaps associated with croc-like bight, twist & tear tactics); neck short (20-30% body length); cervical centra short & compact.

Note: **[1]** precisely because of the common requirements of a croc-style hunter, these features may be the result of convergence. **[2]** Since *Yuzhoupliosaurus* is known only in small part, the reconstruction shown here should be taken as that of a fair average sort of rhomaleosaur.

Links: The Plesiosaur Site - Species; Rhomaleosauridae after O'Keefe, 2001; Plesiosauria Translation and Pronunciation Guide. ATW020703.

Yuzhoupliosaurus**:** *Y. chengjiangensis* Zhang 1985.



Range: Middle Jurassic of China

Characters: ~4m?; lower jaw containing 5 pairs of large teeth; about 23 or 24 smaller teeth; cervical vertebrae high and short; anterior cervical ribs double-headed; posterior cervical ribs single-headed (a more derived form); scapula triradiate; coracoids elongated anteroposteriorly; clavicles well developed; believed to be freshwater form.

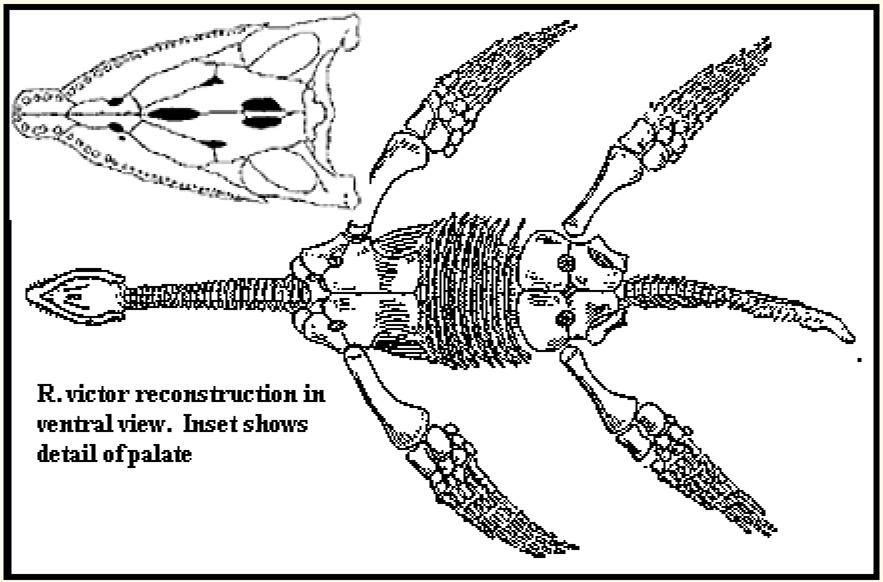
Phylogeny: Rhomaleosauridae: (*Rhomaleosaurus* + (*Simolestes* + *Leptocleidus*)) + *.

Note: known only from lower jaw, vertebrae & fragments of pectoral girdle.

Links: Plesiosauria Translation and Pronunciation Guide.

References: Zhang (1985)

Rhomaleosaurus**:** Seeley 1874.



R. victor reconstruction in ventral view. Inset shows detail of palate

Range: Early Jurassic (Hettangian to Toarcian)

Phylogeny: Rhomaleosauridae:: (*Simolestes* + *Leptocleidus*) + *.

Characters: neck short, with ~15. vertebrae; neural arches bases of (cervical? all?) vertebrae extending along entire length of centrum; ~25 dorsals; 4-5 sacrals; 2 pairs sacral ribs fused to ilium; humerus larger than femur.

Rhomaleosaurus megacephalus Stutchbury

1846: Hettangian of Somerset, England. This species represents the earliest species of *Rhomaleosaurus*. It averaged about 5 meters in length. The long crocodile-like skull alone was about 90 cm. This species was previously described as a species of *Eurycleidus*.

Rhomaleosaurus propinquus Blake 1876: from the Toarcian of Whitby, England, is similar in size and build to *R. victor* (below). It is characterized by a distinctive lower jaw.

Rhomaleosaurus victor Fraas 1910a: from the Toarcian of Germany and England, was 3 to 4 metres in length. This "gracile" species has also been identified as *Thaumatosaurus* ("miraculous lizard,") and *Eurycleidus*. This long-necked form is similar in proportions to *Plesiosaurus*, but with a somewhat shorter neck. It is distinguished from other rhomaleosaurs by its proportionately much larger paddles, smaller and broader head, and relatively longer neck. MAK991206 Update cladistic analysis shows *Rhomaleosaurus* to be a paraphyletic assemblage consisting of a number of distinct if closely related forms and sevral different lineages (Smith & Dyke 2008). In keeping with the current trend in phylogenetics this means that many of these taxa will have to be renamed [1]. It has since been given its own genus, *Meyerasaurus* (Smith & Vincent 2010); unfortunately the superb original name *Thaumatosaurus* ("miraculous reptile"), familar to generations of scientists and palaeo geeks (including yours truely) was an invalid taxon and could not be reinstated. MAK111031

Rhomaleosaurus zetlandicus Phillips 1854 is known from fossil remains the Toarcian of the Yorkshire coast (Whitby) England. This was a large predator, and the largest and heaviest known species of the Rhomaleosauridae. The holotype is an incomplete skeleton about 5.3 meters long. The head makes up 74 cm (14%) and the neck 1.3 meters (25%).

Rhomaleosaurus cramptoni Carte & Bailey 1863 and ***R. thorntoni*** Andrews, also both known from the Toarcian of England - are similar in size to the contemporary *R. zetlandicus*, reaching 5 to 7 meters. They are now considered junior synonyms of (the same species as) *R. zetlandicus*.

Links: Fossils of the Lias (Incredible photo near bottom of page); Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Imagese (beautiful photo of *R. victor*); The Plesiosaur Site - Species; The Plesiosaur Site - Home Page; ?????? ??? (Japanese); JURÁSSICO (Portuguese); wm851s.htm (detailed sketches of *R. propinquus*).

References: Taylor (1992). MAK991206, ATW020704

Simolestes: Andrews 1909. *S. indicus* Bardet *et al.* 1991 (= *Plesiosaurus indicus* Lydekker 1877), *S. keileni* Godefroit 1994, *S. vorax* Andrews 1909.

Range: Early Jurassic of Europe & India (*not* Africa -- this turned out to be a fragment from a teleosaurid). *S. vorax* is from the Callovian, Oxford Clay, Peterborough, England.

Phylogeny: Rhomaleosauridae::: *Leptocleidus* + *.

Characters: skull short & broad; rostrum not elongated; "rosette shaped symphysis" at end of lower jaw (probably an artifact) with 5-6 (pairs?) caniniform teeth; cervical vertebral centra (~20) with diameter twice length; 30-32 dorsals; 18+ caudals.

Links: NEW PLIOSAURIDS A-PLENTY; Plesiosauria Translation and Pronunciation Guide; Color Banding in Dinosaur Teeth - Reason? + plesiosaur repro.-Replies. ATW020704.

Leptocleidus: Andrews 1922. *L. capensis* Cruickshank 1997 (= *Plesiosaurus capensis* Andrews 1911), *L. clemai* Cruickshank & Long 1997, *L. superstes* Andrews 1922.

Range: Early Cretaceous to middle Cretaceous of Europe, South Africa & Australia

Phylogeny: Rhomaleosauridae:: *Simolestes* + *.

Characters: small-bodied (2-3 m); skull triangular; crest running from nasals posteriorly and merging with prominent sagittal crest; forwardly pointing expansion ('cockscomb') on the squamosal mid-line, at rear of parasagital crest, very similar to that seen in Late Cretaceous Polycotylidae; crest flanked by deep grooves or depressions which cause orbital rims to stand up from the general profile of the skull; constricted maxilla- premaxilla junction; spatulate mandibular symphysis; dorsomedially directed trough on prearticular & adjacent bones of lower jaw, similarto *Rhomaleosaurus*; 21 pairs of teeth in upper jaw (5 premaxillary + 16 maxillary), ~35 in lower; no vertebrae compressed; 13-24 cervical vertebrae; cervical ribs single-headed; cervical centra with deep central depression; scapulae small & widely separated; "thin clavicular arch" along the edge of the front limb girdle, composed of two "rather large" clavicles and a "transversely elongated" interclavicle (Plesiosauria Translation and Pronunciation Guide); humerus relatively straight, with symmetrical, fan-shaped distal end; freshwater or estuarine habit.

Images: Right: opalized remains from an Australian juvenile specimen at Fishing For Plesiosaur. Left: "*Leptocleidus*-type" cervical vertebra from The Plesiosaur Site.

Links: Plesiosauria Translation and Pronunciation Guide; Marine Reptiles (NOT Dinosaurs); NEW PLIOSAURIDS A-PLENTY; Crag's Lost Kingdom (?!); Image -- The Dinosauricon; Post forum2 3.pdf; Fishing For Plesiosaur; DinoWight- Leptocleidus, an Isle of Wight pliosaur; The Plesiosaur Site - Species (**Best on the Web**); evolution (beautifully preserved undescribed specimen from Canada); Leptocleidus.htm (Japanese); Eric, the pliosaur. ATW020704.

Notes:

[1] The present author (MAK) does not see the need for Linnaean binomials including generic names to conform to cladistic nomenclature. Given that these are two distinct systems, there should be nothing wrong with retaining genera as paraphyletic "grades"; however this sentiment is not shared by the majrority of systematists

---

Page Back | Unit Home | Page Top | Page Next

checked ATW031031

Sauropterygia: Plesiosauroidea

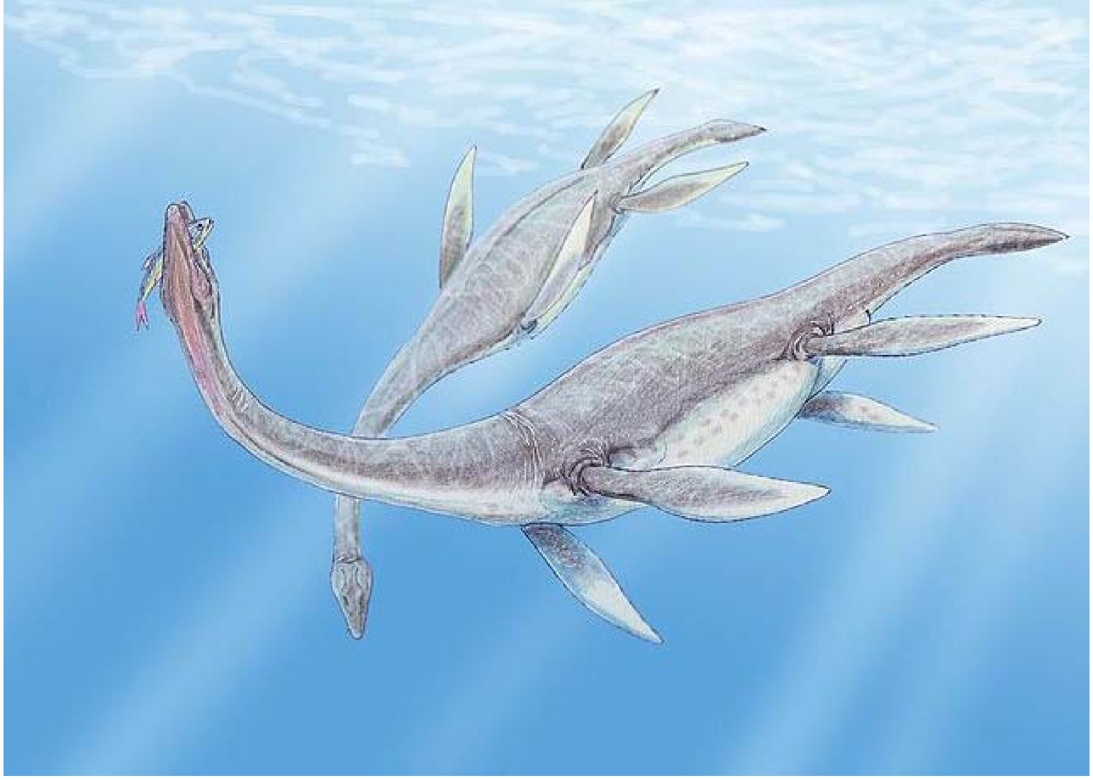
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Attenborosaurus
   |           `--+--Plesiosaurus
   |              |--Elasmosauridae
   |              `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

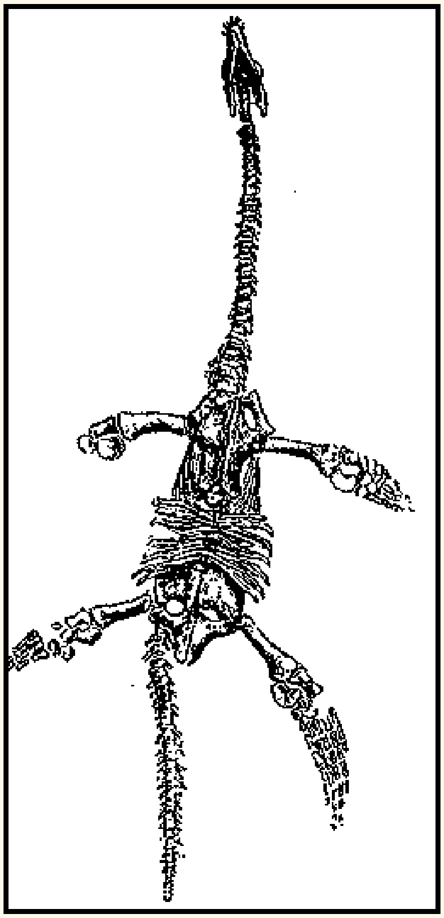
1. *Attenborosaurus* X
2. Plesiosauroidea X
3. *Plesiosaurus* X



Life reconstruction of the early long necked plesiosaur *Plesiosaurus dolichodeirus*, from the early Jurassic (Sinemurian) of England (north-central Laurasia), length about 5 meters.
Artwork by Dmitry Bogdanov. Wikipedia, GNU Free Documentation/Creative Commons Attribution

---

Plesiosauroidea



The plesiosauroids were sea-going reptiles with long neck and small heads filled with long sharp curved teeth. They had a flattened, barrel-shaped body and large paddle-shaped flippers. The two front flippers were always somewhat larger than the hind flippers. They ranged in size from 2.5 to 13 metres.

The plesiosauroids seem to have evolved during the Triassic, as supposed fragments occur in the Upper Keuper and Rhaetic of Europe. But it is only during the Early Jurassic that the group became well established. Beautiful skeletons are known from shallow marine deposits of Europe. Early Jurassic forms were generally quite small, about 3 meters in length, with a relatively short neck of about 32 vertebrae. As time progressed plesiosaurs developed longer necks and, by the middle Cretaceous, increased greatly in body size as well. The largest and most derived forms are known from the Late Cretaceous. These had long, snake-like necks and overall lengths of up to 13 meters. Ironically, the paddles are relatively smaller in these late forms then they were in the Jurassic types, indicating less emphasis on overall movement and more on capturing prey by stealth.

The long flexible necks enabled them to dart their small heads and catch fish in their toothy jaws. The neck became longer -- and perhaps more flexible with the addition of additional, shorter vertebrae -- as the group evolved through time. Plesiosauroids, unlike ichthyosaurs, used stomach stones for ballast to offset the buoyancy of their lungs. Plesiosauroids may have rested on the bottom, striking at prey with their long necks. Taylor (1981).

Plesiosaur classification has traditionally been a mess. One of the confounding factors has been the change in plesiosaur osteology during the course of development. As Brown (1981) notes:

> Examples are known of plesiosauroid individuals ranging from half-grown to full-grown. Differences of osteological structure of specimens of a single species, attributable entirely to ontogeny, have in the past been misinterpreted and used to produce taxonomic divisions. This, together with misinterpretation of other characters used in taxonomy, has led to the publication of a hyperabundance of generic and specific names, and a proliferation of schemes of classification based upon these. In order to facilitate description and the study of ontogeny, specimens are here allocated to one of three categories which represent growth stages, as follows:

(i) 'Juveniles', in which the neural arches of the vertebrae are not fused to the centra;
(ii) 'Adults', in which fusion of neural arches and centra has taken place, and
(iii) 'Old adults', in which the neural arches and centra are fused, and in addition further characters of advanced ossification are found.

Image: *Plesiosaurus dolichodeirus.* ATW020706

Descriptions

Plesiosauroidea:

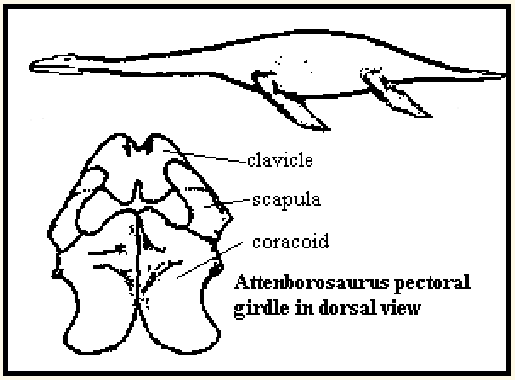
Range: Early Jurassic to Late Cretaceous.

Phylogeny: Plesiosauria **:::** Pliosauroidea + * **:** *Attenborosaurus* + (*Plesiosaurus* + (*Eretmosaurus* + *Sthenarosaurus* + (*Microcleidus* + (Elasmosauridae + Cryptocleidoidea)))).

Characters: skull small; neck long to extremely long (28-72 cervical vertebrae); individual cervical vertebrae may be moderately elongated; forelimbs larger than hindlimbs.

Links: PLESIOSAURIA; Plesiosauria Translation and Pronunciation Guide; Untitled; plesiosauroidea.

Attenborosaurus: Bakker 1993 *A. conybeari* (= *Plesiosaurus conybeari*) Sollas 1881.



Range: Early Jurassic (Sinemurian) of Europe

Phylogeny: Plesiosauroidea **:** (*Plesiosaurus* + (*Eretmosaurus* + *Sthenarosaurus* + (*Microcleidus* + (Elasmosauridae + Cryptocleidoidea)))) + *.

Characters: 5 m total length; skull 10% (45 cm); snout long, massive and evenly tapered; tooth crowns very large & conical; neck very long; 36 cervical vertebrae; ~23 dorsals; 4? sacrals; caudals not recovered but estimated to be ~30; scapulae not in contact, with anterior support of pectoral girdle from clavicles (as in nothosaurs); coracoids relatively short; pubes short with rounded anterior ends.

Note: **[1]** The holotype was destroyed in the same bombing (discussed at Sauropodomorpha) which destroyed the holotypes of *Thecodontosaurus* and *Ctenacanthus*, also housed in the Bristol City Museum. As in the case of *Thecodontosaurus*, a good cast was available. However, some information was irretrievably lost, as Sollas reported that some traces of integument were left on the fossil: the "thin brownish film...has nothing of the nature of scales and scutes, so far as we can see; it was a continuous membrane, not a collection of separate individual structures." However, small oblong bones were imbedded in the film in the pelvic region, and Sollas suggested "they may possibly be dermal plates." See Plesiosauria Translation and Pronunciation Guide.**[2]** The significance of this genus is that it has a relatively large, pliosaur-type skull, combined with a very long neck and a rather primitive pectoral girdle.

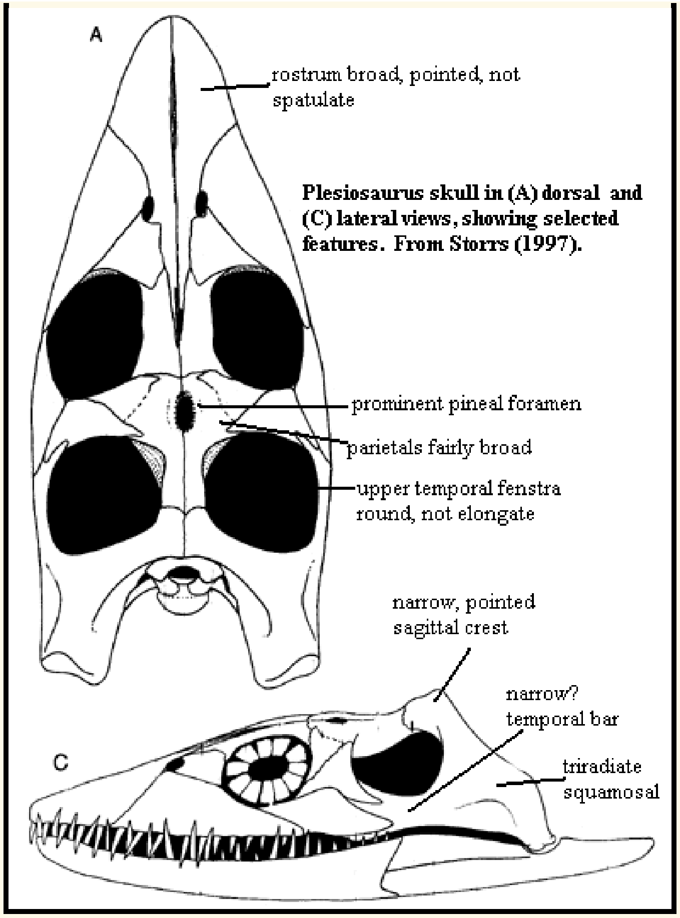
Links: Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Species. ATW020706

Plesiosaurus: dela Beche & Conybeare 1821. *P. dolichodeirus* Conybeare 1824, *P. guilelmiimperatoris* Dames 1895.

Range: Early Jurassic (Sinemurian, possibly Toarcian) of Europe. One specimen possibly Late Triassic.

Phylogeny: Plesiosauroidea **::** (*Eretmosaurus* + *Sthenarosaurus* + (*Microcleidus* + (Elasmosauridae + Cryptocleidoidea))) + *.

Characters: up to 3.5 m; head small; antorbital and temporal regions short; rostrum broad and pointed; pineal foramen prominent; parietals broad; sagittal crest present, sharp & narrow; jugal somewhat elongate; upper temporal fenestra circular; temporal bar narrow; cheek emargination weak; no real pterygoid flange; choanae placed almost directly below external nares; basicranium not covered by posterior expansion of pterygoids; mandibular symphysis not spatulate; 5 pairs of premaxillary teeth; ~24 pairs on dentary; teeth slender, pointed, homodont and without

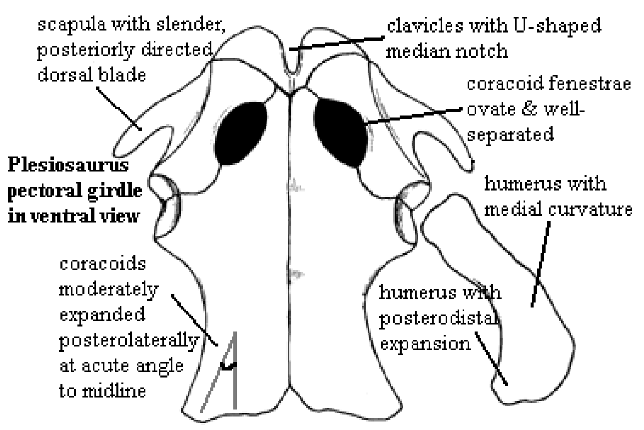


Plesiosaurus skull in (A) dorsal and (C) lateral views, showing selected features. From Storrs (1997).

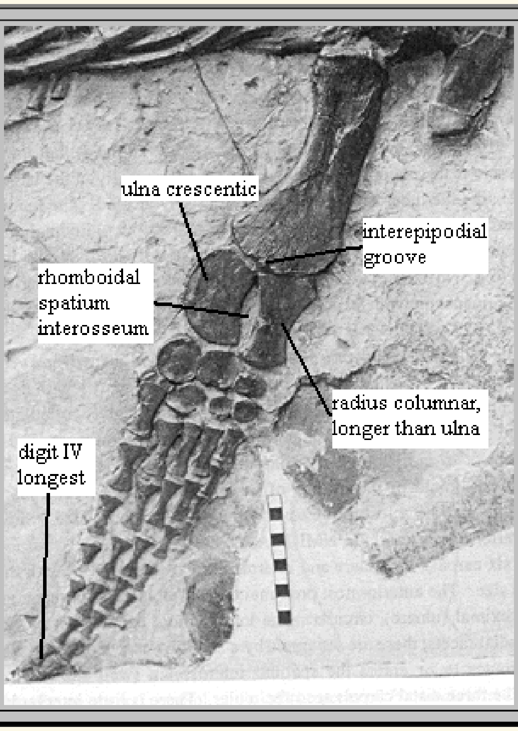
keels, round in cross-section; teeth ornamented with longitudinal ridges (?); neck long (150% body length) with ~40 cervical vertebrae; heads of cervical ribs separated by elongate longitudinal foramen (?); edges of centra articulations often rugose; prominent 'U'-shaped median notch at anterior of clavicular arch (for unossified interclavicle?); fenestrae (= coracoid foramina) of pectoral girdle are *ovate* and well-separated; scapula with a slender, posteriorly angled dorsal blade; coracoids moderately wide; "acute" (*i.e.* <45° from midline) angled posterolateral expansion of coracoids in adult; limbs narrow and very elongate; forelimbs slightly longer than hindlimbs (reversed in immature individuals); humerus with strong medial curvature in dorsal or ventral view; humerus with strong posterodistal expansion (entepicondyle?), but weak anterodistal corner (ectepicondyle?); humerus with interepipodial groove on distal end; robust, columnar anterior epipodials (radius & tibia) offset to extend beyond posterior epipodials (ulna & fibula); posterior epipodials crescentic; *spatia interossea* large and rhomboidal; 4 elements usually present in the proximal, 3 in the distal row of the carpus; 5 constricted metacarpals similar in form to phalanges; epipodials longer than broad; up to 9 phalanges in middle digit; digit IV longest; pubis large, slightly longer than ischium; pubis with generally convex anterior margin; puboischiadic fenestrae small, ovate to circular puboischiadic fenestra; pubis & ischium unfused across median bar; ilium with little twist to shaft; the fifth metapodial retained in the metapodial row.

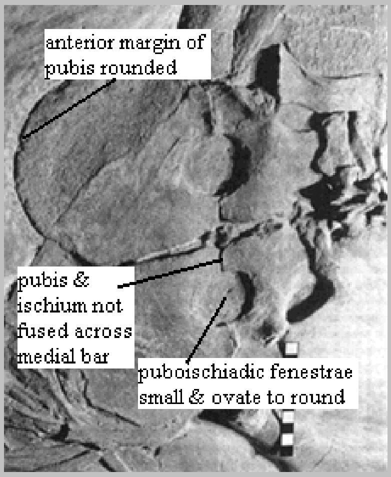
Images: all images modified from Storrs (1997). See also Plesiosaur Skull Anatomy.

Notes: The *Plesiosaurus*, along with the *Ichthyosaurus* and the Pterodactyl (*Dimorphodon*) were among the first Mesozoic reptiles to be recognized. Many beautiful specimens were unearthed along the cliffs of Lyme Regis by Mary Anning. Because this was one of the first prehistoric reptiles to be named, it ended up as something of a taxonomic wastebasket, and a great many other Plesiosaur remains were also identified as *Plesiosaurus*. Hence most "*Plesiosaurus*" species do not belong to this genus at all, and in fact belong to different families altogether (or are simply too incomplete to be properly identified). Valid species lived during the Early Jurassic only.



Plesiosaurus pectoral girdle in ventral view





Continued on Next Page ...

Page Back | Unit Home | Page Top | Page Next

checked ATW050804

Sauropterygia: Plesiosauroidea (2)

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Attenborosaurus
   |           `--+--Plesiosaurus
   |              `--+--Eretmosaurus
   |                 |--Sthenarosaurus
   |                 `--+--Microcleidus
   |                    `--+--Elasmosauridae
   |                       `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

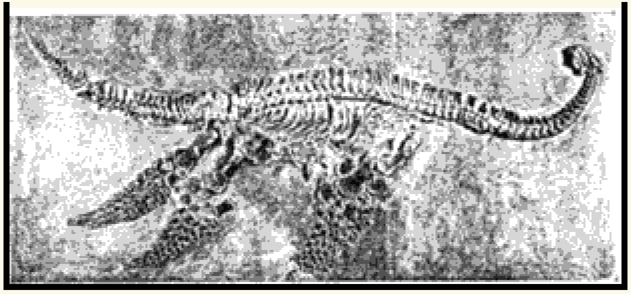
Taxa on This Page

1. *Eretmosaurus* X
2. *Microcleidus* X
3. *Sthenarosaurus* X

... *Plesiosaurus*, continued

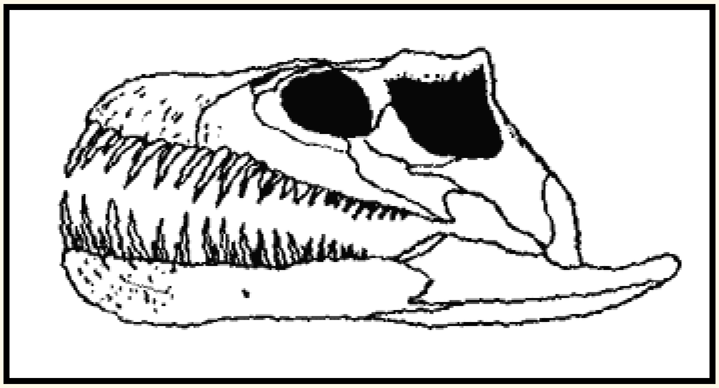
Since *Plesiosaurus* was for so long a garbage taxon, most references to *Plesiosaurus*, other than *P. dolichodeirus*, actually refer to something else. However there is another probably valid species, which goes by the awkward name of *P. guilelmiimperatoris*. In addition, *P. brachypterygius* is a probable junior synonym of *P. guilelmiimperatoris*.

P. guilelmiimperatoris Dames 1895 (originally called *Plesiosaurus guilelmi imperatoris)* is known from the later Toarcian or Epsilon Lias of Holzmaden, Würtemberg, southern Germany. According to Storrs (1997), it is distinguished from *P.*



dolichodeirus by a more delicate skull and a more robust, straighter humerus. Length 3.40 meters.

P. brachypterygius von Heune 1923 was also recovered from the epsilon Lias (Toarcian) of Holzmaden. Length 2.5 to 2.7 meters. Storrs (1997) considers this species a synonym of *P. guilelmiimperatoris*, while Robert Bakker asserts that it is an early elasmosaur, and transfers it to the genus *Microcleidus* (as *M. brachypterygius*). The skull, shown at left, does not appear to conform to the diagnosis of *Plesiosaurus*. Note the following features:

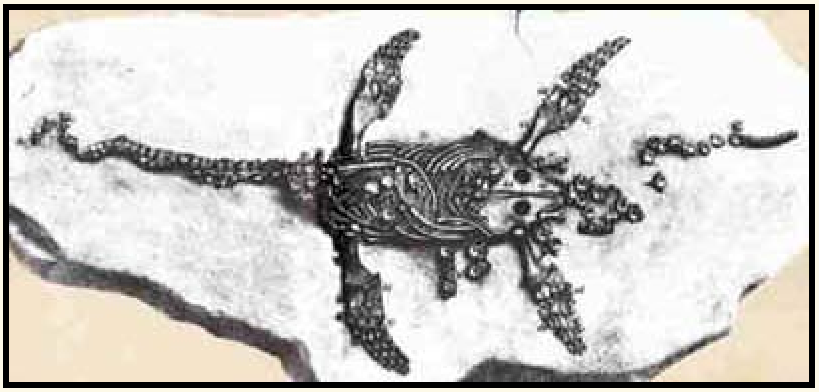


a) the cheek is strongly emarginated;
b) the upper temporal fenestra is not rounded;
c) the squamosal is not strongly triradiate -- at least the anterior process is weak; and
d) the temporal bar is robust.

On the other hand, the overall shape and proportions of the skull are similar to *Plesiosaurus dolichodeirus*. The dentition and postcranial skeleton are very similar.

References: Storrs (1997). ATW020706.

Eretmosaurus: Seeley 1874b. *E. rugosus* (= *Plesiosaurus rugosus*) Owen 1840b



Range: Late Triassic (Rhaetian) to Early Jurassic (Sinemurian) of Europe (UK).

Phylogeny: Plesiosauroidea ::: *Sthenarosaurus* + (*Microcleidus* + (Elasmosauridae + Cryptocleidoidea)) + *.

Characters: Length 4-5 m; 35+ cervical vertebrae; coracoids truncated anteriorly, not extending anterior to glenoid; scapulae extend ventromedially, fused to each other and coracoids on midline; "clavicular arch degenerate".

Note: *Eretmosaurus* is often placed among the Pliosauroidea, as was one of the earliest representatives of the group. It is known from isolated remains in the latest Triassic (Rhaetian) of England and possibly Scotland, and the earliest Jurassic (lower Lias) of England. A headless skeleton described by the famous paleontologist Sir Richard Owen, from the Sinemurian of England, forms the basis for this species. The head, although unknown, was clearly quite small, to fit on the end of the long neck. The general appearance very *Plesiosaurus*-like. Indeed for a long time this genus was included under the Plesiosauridae. It has recently been suggested, on the basis of the long neck, that *Eretmosaurus* is an elasmosaurid, the earliest known member of the family. However the individual neck vertebrae are not elongated as in later elasmosaurids, and it is just as, or more, likely, that the tendency towards increased neck length evolved simultaneously among a number of lineages of early Plesiosauria.

There is of course no guarantee that the poorly known chronologically earlier (by some eight or ten million years) specimens belong to the same species as the later, Sinemurian holotype. However, they may (even this is uncertain) belong to the same genus.

Links: The Plesiosaur Site - Species; Plesiosauria Translation and Pronunciation Guide;

References: Taylor & Cruickshank (1993)

Sthenarosaurus: Watson 1911? 1909?. *S. dawkins* Watson 1911? 1909?.

Range: Early Jurassic (Toarcian) of Europe (UK)

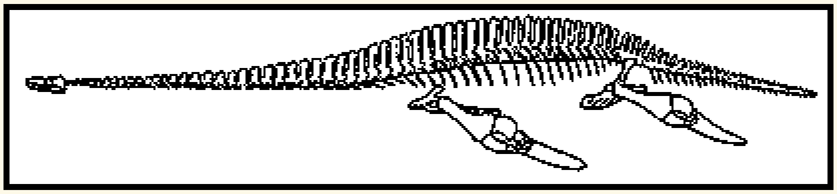
Phylogeny: Plesiosauroidea ::: *Eretmosaurus* + (*Microcleidus* + (Elasmosauridae + Cryptocleidoidea)) + *.

Characters: robust build; 2.8-3.0 m; 18 cervical vertebrae known, up to 28-32 possible; cervical vertebrae very strongly tapered (i.e. vertebrae at base of neck are much larger); coracoids short & thick; pelvis very broad & heavy.

Note: **[1]** This is another headless genus that has been placed almost everywhere except the Elasmosauridae. The cervical vertebrae show no trend to elongation. As a result, it has been estimated that there were 28 to 32 neck vertebrae. However, the vertebral column is also strongly tapered, to the extent that the smallest cervical, of the 18 known cervicals, is 1/8th the size of the largest. Extrapolating this trend over a further 12 vertebrae would likely result in a head the size of a cough drop. **[2]** On the basis of features of the pectoral (shoulder) girdle it resembles the *Plesiosaurus*. White (1940) although it has also been placed in the Pliosauroidea or related to *Attenborosaurus*. This genus is now considered *incertae sedis* (of uncertain relationships), but may perhaps possibly represent a transitional stage between the *Plesiosaurus* and the Cryptocleididae.

Links: The Plesiosaur Site - Species; Plesiosauria Translation and Pronunciation Guide. MAK990830, ATW020706.

Microcleidus: Watson 1909. *M.* ("*Plesiosaurus*") *homalospondylus* Owen 1865, *M.* ("*Plesiosaurus*") *macropterus* Seeley 1865b.



Range: Early Jurassic (Toarcian) of Europe (UK)

Phylogeny: Plesiosauroidea :::: (Elasmosauridae + Cryptocleidoidea) + *.

Characters: jugal excluded orbital margin by extended maxilla-postorbital contact; neck very long, with 40 cervical vertebrae; cervical ribs double-headed; cervical centra elongated; 22 dorsals; 3 sacrals; 28+ caudals; clavicles very small (hence the name); interclavicle absent.

Note: Note that the image lacks the heavy gastralia and ventral shield typical of plesiosauroids, has very short ribs, and very tall, robust neural spines. Whether this is an error, a taphonomic artifact, or the actual condition, we cannot say. It is certainly a strange animal. As with many other plesiosaurians, *Microcleidus* has led a full and varied taxonomic life, having bee variously referred to the Cryptocleididae (White, 1940), Elasmosauridae (Brown, 1981) and Plesiosauroidea *i.s.* The current tendency seems to be to place it among the cryptocleidid elasmosaurs, although we have not yet made this move.

Links: NEW SVP MARINE REPTILES; The Plesiosaur Site - Species; IV EUROPEAN WORKSHOP ON VERTEBRATE PALAEONTOLOGY (abstract on p. 29); Plesiosauria Translation and Pronunciation Guide (always a good source). MAK000218, ATW040712.

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

checked ATW050805

Sauropterygia: Elasmosauridae

Abbreviated Dendrogram

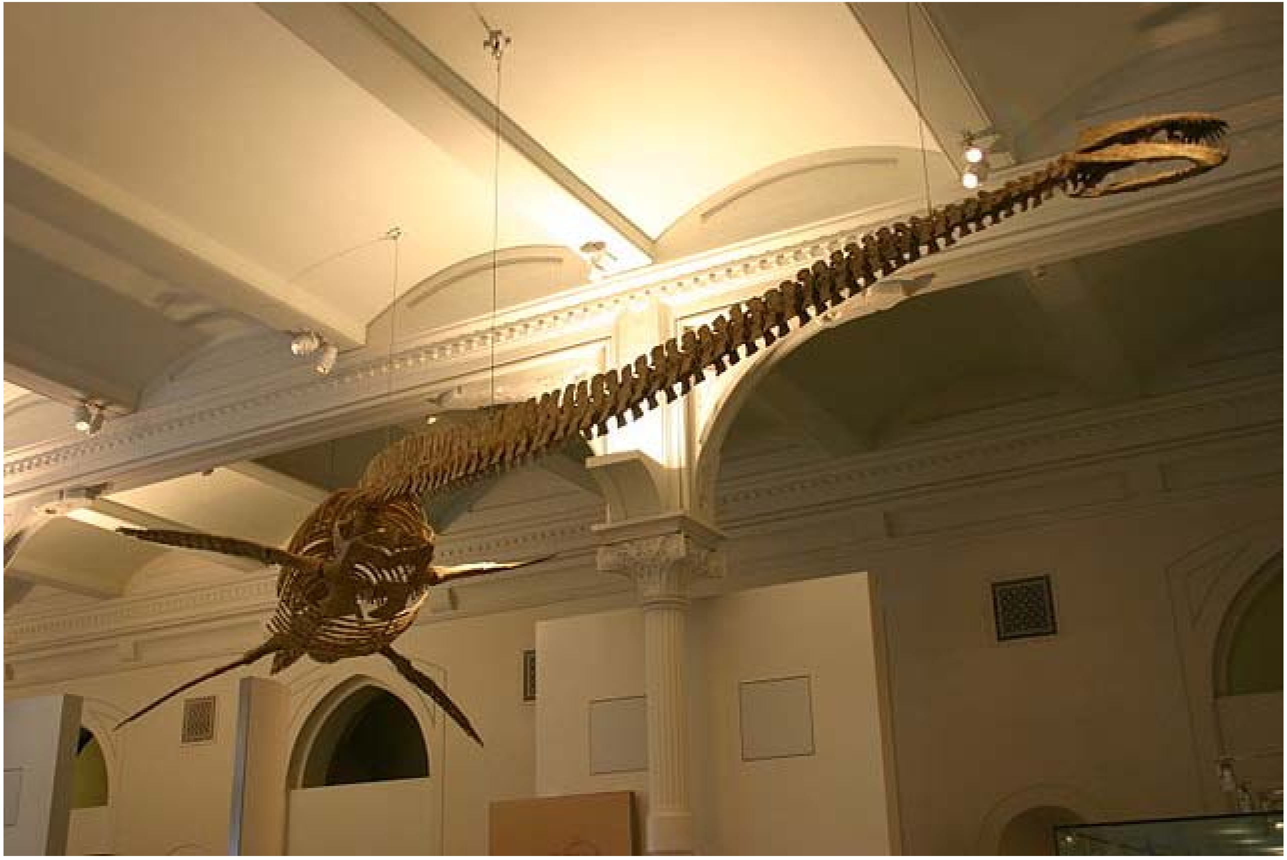
```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |==Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

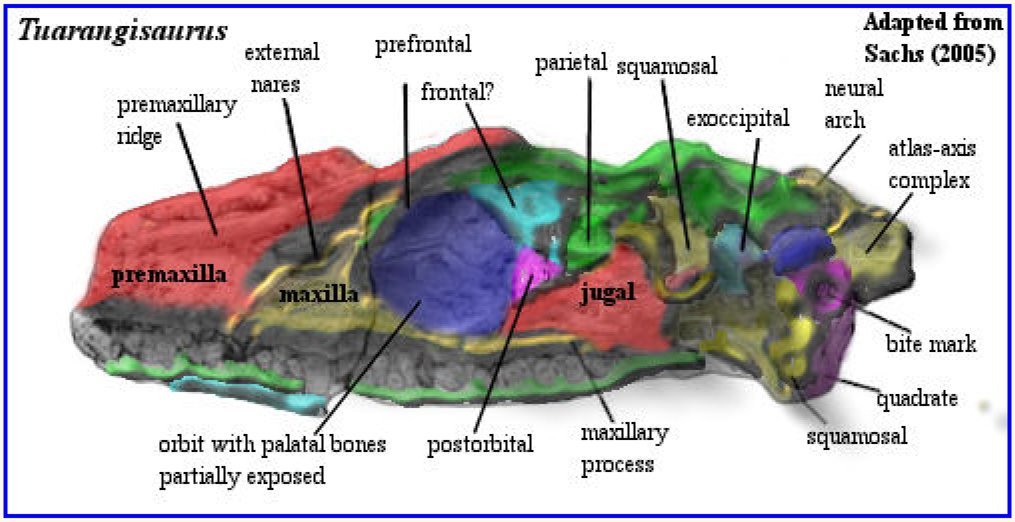
Taxa on This Page

1. Elasmosauridae X

The Elasmosaurids



Mounted skeleton of the advanced elasmosaur *Thalassomedon hanningtoni*, in the American Museum of Natural History; late Cretaceous (Cenomanian) of North America (western Laurasia), length about 12 meters.
Photo by Ryan Somma, Wikipedia, Creative Commons Attribution Share Alike



The Elasmosauridae were the largest most advanced of the long-necked plesiosaurs. The head is tiny in comparison to the rest of the body. The neck is extraordinarily long, with 32 to 71 cervical vertebrae, the number increasing in later species. The longer the neck the more flexible it is, thus giving a greater adaptive advantage in catching fish. It is known that these creatures swallowed stones for ballast. It is possible that they would rest on the bottom of shallow seas and wait for prey to come within reach.

Like the rest of the Plesiosauroidea, elasmosaurs had a barrel-shaped body with four paddle-shaped flippers. The two front flippers were always somewhat bigger than the hind flippers. There are up to 17 phalanges (finger bones) in each digit. The flippers are smaller in relation to the body then in other Plesiosaurus, indicating that these creatures were not fast swimmers.

Elasmosaurs have been found in North America, Europe, Australia and New Zealand. The group is diverse, and there is disagreement among different references over which genera to include in the family, but the current practice has both primitive Jurassic forms and advanced giant forms in the same family. In any case there are a number of distinct evolutionary trends in this group.

- an increase in neck length and number of vertebrae

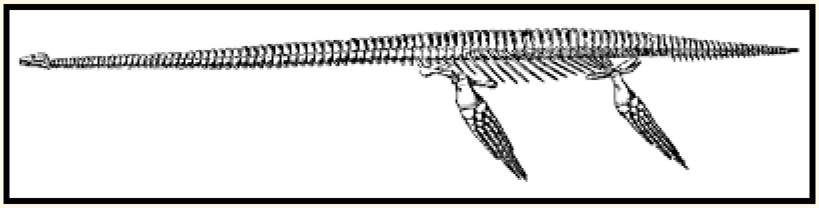
an increase in general body size
- a decrease in the number of teeth in the main part of the jaw
- changes in the structure of the flippers (perhaps to create a more efficient hydrofoil-like limb?)

The trends in the evolution of the elasmosaur skull, in particular, have been taken up cladistically by Sachs (2005). He finds that the posterior maxilla and retroarticular process expand. Presumably the overall picture is that the elasmosaurs were trading length of tooth row for increased mass and mechanical advantage of jaw muscle. The *axis centrum* becomes longer and lower. It is unclear what this means, but may signify relatively restricted motion of the head with respect to the neck. This is consistent with increased size and length of neck, as it would be unwise to have one's head flapping around loose at the end of a powerful, flexible, and fast-moving neck.

The ensemble of these features suggests specialization for small, fast-moving prey animals, which probably lived in groups. The elasmosaur would move slowly into the vicinity of a school. Then a rapid movement of its neck would bring the quick, but relatively small and weak, jaws close enough to trap a prey animal. We might speculate that even the slow speed of an elasmosaur, relative to its size, could easily keep it in contact with a shoal of small fish or squid, which, however quick in the sprint, cannot move long distances continuously.

Late Cretaceous species attained over 12 metres in length and possibly several tonnes in weight. Elasmosaurids were highly successful creatures, despite their ungainly appearance, and they persisted until the very end of the Mesozoic. MAK000218, ATW080302.

Descriptions



Elasmosauridae:

Range: Early Jurassic to Late Cretaceous.

Phylogeny: Plesiosauria ::::: Cryptocleidoidea + *.

Characters: Longest, largest and last plesiosaurs; overall length from about 3 m to 14 m; occipital condyle formed from the basioccipital only, usually ringed by constricting groove; maximum five pairs of premaxillary teeth; upper tooth row of derived forms with enlarged premaxillary & anterior maxillary teeth separated by smaller teeth around maxillo-premaxillary suture; dentary teeth primitively 24 pairs, reducing to a minimum of 14 pairs in Cretaceous species; teeth ornamented with numerous longitudinal ridges; primitively ~32 cervical vertebrae, reaching a maximum of over 70; except for some primitive forms, cervical centra relatively elongated; cervical ribs (primitively double-headed) are single-headed in Upper Jurassic and later species; ventral rami of the scapulae relatively broad and meeting in the ventral midline in 'adults'; Cretaceous species have strongly developed scapulae, permitting a strong backstroke and greater maneuverability; epipodials primitively longer than broad, becoming broader than long in later forms; 5th metapodial shifting proximally from the metapodial row in basal forms to the distal mesopodial row (see figure at *metapodial*); *hyperphalangy* of up to 17 phalanges in the longest digit.

Note: **[1]** the record for cervical vertebrae -- for any vertebrate -- appears to be held by the elasmosaurid *Elasmosaurus platyurus* at 76 cervicals. **[2]** because of the drag caused by the long neck, as well as the relatively small paddles and weak limb girdles, it is supposed that elasmosaurids were very slow swimmers. Possible lifestyles include browsing on slowly moving schools of cephalopods (belemnites & squid), and ambush predation using quick movements of the neck only. Note that an elasmosaur might not need to surface to breath if it chose its spot carefully and simply raised its head above the water. However, the head is so small, that one suspects that most gas exchange was handled over the surface of the paddles, through the cloaca or in some similar fashion. **[3]** from Plesiosauria Translation and Pronunciation Guide: "In Cretaceous elasmosaurs the right and left coracoids meet along the animal's midline then separate toward the back to form a scooped-out, roughly heart-shaped opening--Jurassic elasmosaurids and other types of plesiosaurs lack this rounded separation in the front limb girdle."

Image: *Hydrotherosaurus* - a giant elasmosaur (length over 12 meters) from the Late Cretaceous.

Links: Marine Reptiles (NOT Dinosaurs); Elasmosauridae after O'Keefe, 2001; Plesiosauria Translation and Pronunciation Guide; ????????? (Japanese). MAK000218, ATW020707.

Page Back | Unit Home | Page Top | Page Next

checked ATW080301

Sauropterygia: Cryptocleididae

Cryptoclidids

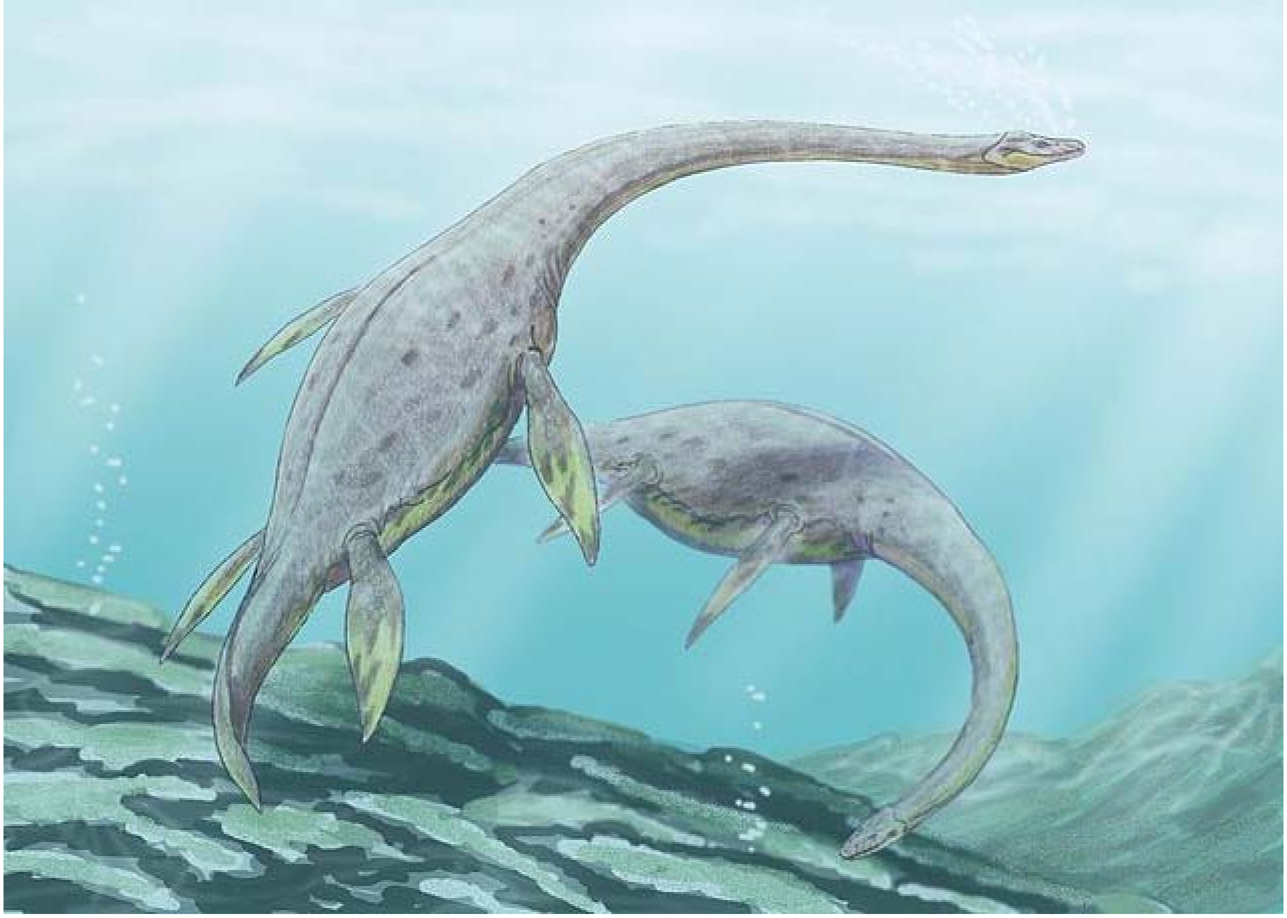
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   |              |--Cryptocleididae
   |              |  |--Colymbosaurus
   |              |  |--Cryptocleidus
   |              |  `--Muraenosaurus
   |              `--Tricleidia
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

1. *Colymbosaurus* X
2. Cryptocleidoidea X
3. Cryptocleididae X
4. *Cryptocleidus* X
5. *Muraenosaurus* X



Life reconstruction of the large (length over 5 meters) Cryptocleidid *Muraenosaurus leedsi*, from the late Jurassic of England (north-central Laurasia).
Artwork by Dmitry Bogdanov. Wikipedia, GNU Free Documentation/Creative Commons Attribution

---

Cryptocleidoidea: Presumably *Cryptocleidus* > *Elasmosaurus* -- not the best name or definition for the stem group, if the idea is to have a monophyletic Elasmosauridae on one side and all other derived plesiosauroids on the other. The problem is that *Cryptocleidus* may be on the elasmosaur side of that divide. Perhaps a better name would be "Polycotyloidea." Be that as it may, we will again follow Cryptoclidoidea after O'Keefe, 2001 for the present.

Range: Middle Jurassic to Late Cretaceous

Phylogeny: Plesiosauria **:::::** Elasmosauridae + * **:** Cryptocleididae + Tricleidia. ATW020707.

Cryptocleididae: *Apractocleidus, Aristonectes?, Kaiwhekea, Turneria*

Range: Middle Jurassic to Late Cretaceous, fl Late Jurassic.

Phylogeny: Cryptocleidoidea **:** Tricleidia + * **:** *Colymbosaurus* + *Cryptocleidus* + *Muraenosaurus*.

Cryptocleidus life reconstruction

Characters: primitively ~4 m; broad, short skulls; orbit large; narrow vertical jugal bar; deep ventral cheek excavation.occipital condyle formed by basioccipital & exoccipitals and not ringed by a constricting groove; teeth densely packed, thin, interlocking somewhat curved; dentition homodont, with size decreasing distally along tooth row; tooth ornament reduced or absent; premaxilla with at least 6 pairs of teeth (many more in derived forms); primitively 24 pairs of dentary teeth; neck relatively long (29-42 vertebrae); cervical centra not elongated; cervical ribs single-headed; ventral rami of the scapulae relatively broad and meeting in the ventral midline; epipodials broader than long; the fifth metapodial has shifted proximally into the distal mesopodial row; hyperphalangy of up to

15 phalanges in the longest digit.

Note: specialized for "filter- trap" feeding on small, soft-bodied prey (crustaceans, small fish) per Plesiosauria Translation and Pronunciation Guide. This would require some way of forcing the water out to trap the food items against the teeth -- tongue or palatal muscles?

Links: The Plesiosaur Site - Species; Plesiosauria Translation and Pronunciation Guide; Nathis Fauna Reptilelen Mariene Reptielen (Dutch); Scoop: New Species Of Ancient Marine Reptile Named; New papers--New exhibit in London; cryptoclididae; University of Otago Media Release 5 June 2002.

References: Brown (1981). ATW021104.

***Colymbosaurus*:** Seeley 1874. *C.* ("*Plesiosaurus*") *trochanterius* Owen 1840a.

Range: Middle Jurassic (Callovian) to Late Jurassic (Late Tithonian) of Europe (UK). Two incomplete skeletons, postcrania, and teeth from the Kimmeridge Clay (Kimmeridgian) of Dorset, Cambridgeshire, Cambridgeshire and Norfolk, England. Limb elements (juvenile) from the Portland Stone, Dorset, England (late Tithonian).

Phylogeny: Cryptocleididae **:** *Cryptocleidus* + *Muraenosaurus* + *.

Characters: 5-7 m; 42 cervical vertebrae; cervicals amphicoelous, shorter than tall; vertebrae similar in shape & proportions to *Cryptocleidus*; cervical centra not elongated; 28 dorsal vertebrae; 4 sacrals; 26? caudals; scapula ventral ramus relatively large & plate-like, with convex anterior margin; coracoids meet in the midline in adults; width across posterior cornua of coracoids slightly exceeds the distance across the body between the glenoids in adults; humerus and, to a lesser extent, femur expanded posterodistally, both forming three distinct articular facets (!); there are three epipodials in both manus and pes (!!);

Note: **[1]** The latest and largest of the Plesiosauroidea known from Jurassic England, it survived right until the very end of the Jurassic, avoiding the mid-Tithonian mass extinction that affected a large number of Jurassic dinosaurs, ichthyosaurs, plesiosaurs, and pterosaurs. **[2]** The skull and dermal elements of the pectoral girdle are unknown in *C. trochantericus*, the only decently known species.

Image: anterior and dorsal views of a cervical vertebra of *Colymbosaurus sp.* from Palaeo Jo's Reptile catalogue.

Links: Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Species.

References: Brown (1981). ATW020707, MAK000218.

***Cryptocleidus*:** Seeley 1892. *C. eurymerus* Phillips 1871.

Cryptocleidus

Range: Middle Jurassic to Late Jurassic of Europe (UK). Lower Oxford Clay (Callovian) of Oxfordshire and Peterborough, England. Also known from Russia, South America.

Phylogeny: Cryptocleididae **:** *Colymbosaurus* + *Muraenosaurus* + *.

Characters: ~4 m; skull relatively broad, rather lightly built; parietals form sagittal crest; orbits generally directed upward; paroccipital process moderately long; occipital condyle is not ringed by a groove, and extends onto the pedicles of exoccipitals; teeth densely packed, procumbent & intermeshing; tooth ornament reduced; dentary with 24 to 26 tooth pairs; premaxillae with six pairs, of which the first (most anterior) is small and the second to sixth are large; ~55 pre-sacral vertebrae, of which usually 32 are cervical; cervical vertebrae relatively amphicoelous; cervical centra length rarely exceeds height; 4 sacrals; 25 caudals; clavicles triangular & well developed, lie visceral to the ventral rami of the scapulae, and meet in the mid-line; interclavicle absent or rudimentary; coracoids meet scapulae on ventral mid-line in 'adults'; width across the posterior cornua of the coracoids exceeds the interglenoid width in 'adults' by up to 40%; elements of pectoral girdle tend to fuse in old individuals; normally only two epipodials in the manus; a foramen only appears between the epipodials showing advanced ossification; flippers very large.

***Cryptocleidus* pectoral girdle**

C. eurymerus Phillips 1871: teeth retain longitudinal ridges: two opposing axial ridges (mesial and distal) rise from the base of the crown and almost meet at the tip, and between them rise 4 to 7 lingual ridges which extend from the base to approximately one-third of the height of the crown; there are no buchal ridges; humerus greatly expanded distally by an anterior expansion of the portion bearing the radial facet; radius is enlarged by anterior expansion of the portion bearing the humeral facet, which may be up to twice as long as the facet for the radiale, so causing the anterior margin to describe a sigmoid curve; ulna is much wider than long. [this sounds like *Plesiosaurus*]

C. richardsoni: distal anterior portion of the humerus is not greatly expanded; the radius has a concave anterior border, and the humeral facet is only slightly longer than the facet for the radiale; the ulna is approximately square.

Note: **[1]** A common and well-known Jurassic form, with a relatively short neck with 32 vertebrae. *Cryptocleidus* is the earliest known member of a distinct line of Plesiosaurs that continue through the late Jurassic, and possibly right until the Maastrichtian (latest Cretaceous). They are never as varied or successful as their elasmosaurid cousins. The neck remains fairly short, similar in fact the early Jurassic plesiosaurs, and the tooth count in the lower jaw remains at 24 pairs (in the elasmosaurids it tends to be reduced), although tooth ornamentation is reduced or absent. **[2]** from the Plesiosauria Translation and Pronunciation Guide: *Cryptocleidus* probably fed on schools of soft-bodied cephalopods and small fish, using its many teeth as a filter or trap--its lightly built skull and jaws were not designed to resist strong twisting forces generated by biting or tearing prey. The small size of its external nasal openings and the forward position of the internal nares on the roof of its mouth have suggested to some researchers (Brown & Cruickshank 1994) that its nostrils were not used for breathing, but for "smelling" underwater -- *Cryptocleidus* would have passed water through the internal nares on the roof of its mouth, then up and out its nose to detect chemical traces of prey.

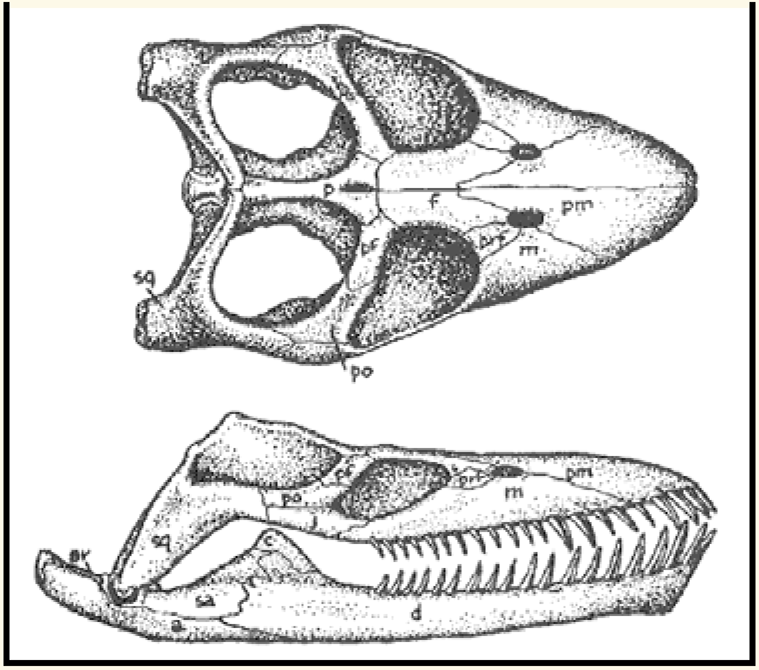
Links: The Plesiosaur Site - Species; BBC - Walking with Dinosaurs - Fact Files; Plesiosauria Translation and Pronunciation Guide; Cryptocleidus; CRYPTOCLIDUS Dinosaurs Poster; Geology Field Trip Guide - Kimmeridge, Dorset - Kimmeridge Clay Fossils; plesiosaures (French); evolution4; Cryptocleidus; Cat scan of Cryptocleidus centrum; Cryptocleidus; Cynodonte (Portuguese); Cryptocleidus oxoniensis; The Journal of Vertebrate Paleontology; Geology; Museum Laboratory for Geology Students; DinoData Marine Reptiles Plesiosauroidae; Cryptocleidus Printout- ZoomDinosaurs.com; ATW030517, MAK000218.

Muraenosaurus: Seeley 1874. *M. leedsi* Seeley 1874, *M. beloclis* Seeley 1892.

Range: Late Jurassic (Callovian) of Europe (UK & France), perhaps South America.

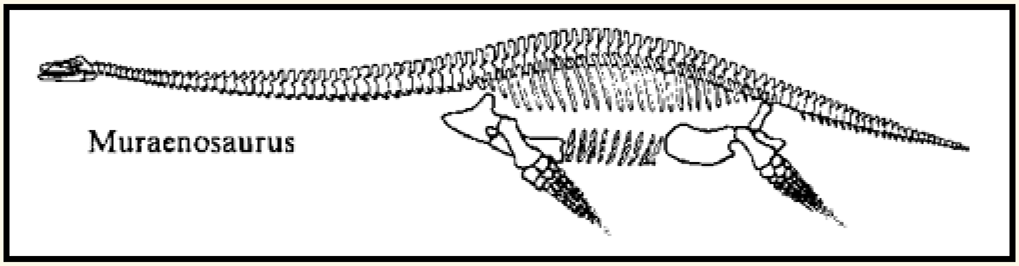
Phylogeny: Cryptocleididae : *Colymbosaurus* + *Cryptocleidus* + *.

Characters: ~5 m (*M. leedsi*); skull ~40 cm; snout fairly short; a rugose bump anterior to the orbits, dorsal to nares; external nares anterior to internal nares;



parietals form sagittal crest; quadrate overlaps quadrate ramus of pterygoid posteromedially; paroccipital process relatively long and slender; occipital condyle ringed by a groove, and is formed by basioccipital only; teeth ornamented with numerous longitudinal ridges; dentaries with 19 to 22 tooth pairs; premaxillae with 5 teeth each, 1st & 5th are small, and others large; anteriormost maxillary tooth (6th upper) small and 8th & 9th large; ~66 pre-sacral vertebrae, of which usually 44 are cervical; cervical vertebrae have relatively platycoelous centra, with length exceeding height in the anterior vertebrae, and >= height in posterior vertebrae; 22-23 dorsals; 4 sacral vertebrae; tail short (24 caudals); body wide; clavicles reduced or absent; interclavicle developed and may be plate-like or reduced and lanceolate; scapulae small compared to coracoids; coracoids meet scapulae at midline in 'adults'; width across posterior cornua of the coracoids is equal to or just in excess of interglenoid width in 'adults'; elements of pectoral girdle tend to fuse in old individuals; limbs short; there are normally only two epipodials in manus; a foramen is present between epipodials [between epipodials or between humeral condyles for the epipodials??] even in juveniles.

Muraenosaurus leedsi Seeley 1874, from the Lower Oxford Clay (Callovian), Peterborough, England ad Calvados area France. Two specimens known of overall length 4.65 and 6.20 m. A well-known Jurassic genus. The neck is very elongate relative to earlier forms like *Microcleidus*, and contains 44 cervical vertebrae. The head is very small relative to the body, and short and broad. The dentary is armed with 19 to 22 pairs of teeth. The forelimbs are slightly larger than the hindlimbs. Similar forms are known from Russia, Wyoming, and perhaps South America. It is likely that these ocean-going beasts had pretty much world-wide distribution.



Muraenosaurus beloclis Seeley 1892, from the Lower Oxford Clay (Callovian), Peterborough, England. This species is known from 4 incomplete skeletons. Its estimated overall length was 2.5 metres. This is a small species of *Muraenosaurus*, distinguished -- apart from much smaller size -- by a prominent flange on some of the anterior ribs, and details of the hand (manus) and interclavicle. The neck contains 40 short cervical vertebrae. It was previously known as *Picrocleidus*.

Note: [1] This genus was classically the flagship of a family including *Tricleidus* and *Colymbosaurus*. **[2]** See also image on **Overview page.**

Links: The Plesiosaur Site - Species; Digital \I\ Designs - Mesozoic Image - Somewhere Under Tethys (beautiful *and* technically accurate); Plesiosauria Translation and Pronunciation Guide; plesiosaures (French); forelasning7.pdf (Swedish); ???????? (Japanese and... odd); Dinosaurios- Muraenosaurus.

References: Brown (1981). ATW020708, MAK000218.

---

checked ATW050804

Sauropterygia: Cryptocleidoidea: Tricleidia

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   |              |--Cryptocleididae
   |              `--Tricleidia
   |                 |--Tricleidus
   |                 `--+--Cimoliasauridae
   |                    |  |--Kimmerosaurus
   |                    |  `--Cimoliasaurus
   |                    `--Polycotylidae
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

1. Cimoliasauridae X
2. *Cimoliasaurus* X
3. *Kimmerosaurus* X
4. Tricleidia X
5. *Tricleidus* X

Descriptions

Tricleidia:

Range: Late Jurassic

Phylogeny: Cryptocleidoidea **:** Cryptocleididae + * **:** *Tricleidus* + (Cimoliasauridae + Polycotylidae). ATW020709.

***Tricleidus*:** *T. seeleyi* Andrews 1909.

Range: Late Jurassic (Callovian) of Europe (Peterborough, UK).

Phylogeny: Tricleidia **:** (Cimoliasauridae + Polycotylidae) + *.

Characters: 2.5-3.0 m; skull 22 cm; rostrum shorter & skull table taller than in *Cryptocleidus*; parietals form sagittal crest; quadrate overlaps quadrate ramus of pterygoid posteromedially; paroccipital process relatively long and slender; occipital condyle ringed by a groove; occipital condyle formed from basioccipital only; pterygoid with articular process for basisphenoid; teeth with dense longitudinal ridges; dentaries with 17 tooth pairs; premaxillae with 5 teeth each, 1st and 5th small & 2nd to 4th large; anterior most maxillary tooth (6th upper) small and 8th & 9th uppers large; 26+ cervical vertebrae with relatively amphicoelous centra; cervical centra length only slightly exceeds height (but never the width) in most anterior vertebrae; pectoral girdle with "large interclavicle and a pair of well developed elongated clavicles"; clavicles are triangular, well-developed, and visceral to interclavicle which separates them in the midline; the interclavicle is well-developed and plate-like; the coracoids meet the scapulae in midline in 'adults'; width of posterior cornua of the coracoids exceeds interglenoid width in 'adults'; the humerus is not greatly expanded distally, and articulates with four epipodials; probable trap-feeder, but with fewer teeth than *Cryptocleidus*.

Note: supposed *Tricleidus* remains from Wyoming are now believed to be a distinct genus. SeeTate Geological Times.

Links: Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Species ATW020709

Cimoliasauridae: originally an unfashionable family based on scrappy materials and a vague definition, to wit: "A family in the Plesiosauroidea with neck relatively shorter than in the Plesiosauridae and the Elasmosauridae. Teeth of the general Plesiosaurian type (crowns high and slender). The height of at least the middle and posterior cervical centra approximately equal to the length, but the breadth of these centra considerably greater than the length; the end faces of the centra flat or slightly concave. Ribs single-headed." See Plesiosauria Translation and Pronunciation Guide. It has been resurrected as a clade, but remains an unfashionable family based on scrappy materials and a vague definition.

Range: Late Jurassic to Late Cretaceous of Europe, North America, Australia, & new Zealand

Phylogeny: Tricleidia **::** Polycotylidae + * **:** *Kimmerosaurus* + *Cimoliasaurus*.

Links: Plesiosauria Translation and Pronunciation Guide; plesiosarus (Swedish). ATW020709.

***Kimmerosaurus*:** *K. langhami* Brown 1981.

Range: Late Jurassic (Kimmeridgian) of Europe (Kimmeridge Clay, UK). Known from 3 partial skulls & several cervicals.

Phylogeny: Cimoliasauridae **:** *Cimoliasaurus* + *.

Characters: skull broad, but very lightly built and more elongated than in *Cryptocleidus*; no parietal sagittal crest; quadrate overlaps quadrate ramus of the pterygoid anterolaterally; paroccipital process relatively short & massive; occipital condyle is not ringed by a groove, and extends onto pedicles of exoccipitals; tooth ornament absent; teeth highly recurved, thin (laterally compressed), sharply pointed, with 36 dentary pairs & 6 premaxillary pairs.

Note: Postcranial skeleton is not known. Possible junior synonym of *Colymbosaurus*.

Links: Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Species; FILTER FEEDING REPTILES. ATW030114.

Cimoliasaurus: *C. maccoyi* Etheridge 1904, *C. planus*, numerous others, all *nomina dubia*.

Range: Early Cretaceous II (Aptian? Albian?) to Late Cretaceous of Australia, North America, Europe & New Zealand.

Phylogeny: Cimoliasauridae **:** *Kimmerosaurus* + *.

Characters: 3-8 m; and long, slender, recurved teeth; teeth conical, with oval cross section at base, becoming more flattened toward tip, somewhat flattened & without carinae; teeth coated with enamel, smooth, with some growth cracks, usually 2-5 cm long; relatively short neck, for holding fish **[1]**; centra dorsoventrally compressed and constricted in the middle, with oval articular surfaces and two large *nutritive foramina*; vertebrae morphologically similar, but decreasing in size from mid-dorsal toward sacrum;

Note: **[1]** This is odd, because we are also informed that no skull is known. **[2]** The Australian species, *C. maccoyi*, is said to differ from the others in lacking lateral ridges on the cervical centra. It is likely that this is a garbage taxon without diagnosable characters. **[3]** The following portion of a description of the vertebra from Leidy sounds interesting, but I can't quite make out what he means:

> The sides of the body of the vertebræ form, together with the sides of the vertebral arch and the upper part of the transverse processes, a nearly uniform slope, broken only by a slight elevation formed by the apparent sutural coossification of the transverse process with the body. The under part of the body between the transverse processes nearly forms a level surface, more or less elevated into a ridge between the venous foramina, and depressed along a line with the position of the latter.

Image: *Cimoliasaurus* vertebra from the Late Cretaceous of New Jersey. From D&D Fossils & Meteorites.

Links: Marine Reptiles (NOT Dinosaurs); Cope - Elasmosaurus2; Cope Additional Note; (these are where Cope explains how he managed to put the head on the wrong end of an elasmosaur!); Plesiosauria Translation and Pronunciation Guide; The Plesiosaur Site - Species; Cimoliasaurus vertebrae $45; Cretaceous Fossils: Cimoliasaurus magnus Page; Big Brook Plesiosaur Page (are these vertebrae from a plesiosaur?); Exponat mesice - Regionalni Muzeum v Teplicich (Czech); Leidy, 1865 (OOK: portions of Leidy's description. The OOK treatment is, of course **Best on the Web**); Plesiosaur History (OOK: the early papers); Big Brook Plesiosaur Page (very nice page with summary of anatomy, other information, and a rough life reconstruction).

References: Molnar (1991). ATW030708. MAK990821.

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

checked ATW040131

Sauropterygia: Cryptocleidoidea: Polycotylidae

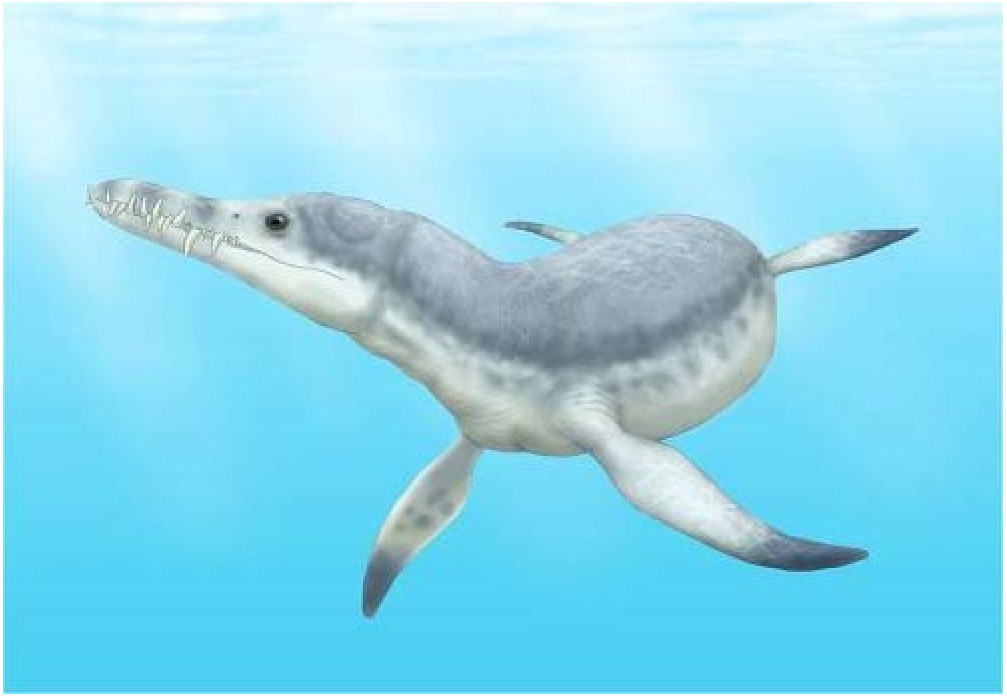
Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
   |--SAUROPTERYGIA
   |  |--Placodontia
   |  |--Pachypleurosauridae
   |  `--+--Nothosauridae
   |     `--Plesiosauria
   |        |--Pliosauroidea
   |        `--Plesiosauroidea
   |           |--Elasmosauridae
   |           `--Cryptocleidoidea
   |              |--Cryptocleididae
   |              `--Tricleidia
   |                 |--Tricleidus
   |                 `--+--Cimoliasauridae
   |                    `--Polycotylidae
   |                       |--Plesiopleurodon
   |                       `--+--Trinacromerum
   |                          `-
-Dolichorhynchops
   |                              |-
-Dolichorhynchops osborni
   |                              `-
-Dolichorhynchops bonneri
   `--Lepidosauriformes
      |--SPHENODONTIA
      `--SQUAMATA
```

Contents

Taxa on This Page

1. *Dolichorhynchops bonneri* X
2. *Dolichorhynchops osborni* X
3. *Dolichorhynchops* X
4. *Plesiopleurodon* X
5. Polycotylidae X
6. *Trinacromerum* X



Life reconstruction of the basal polycotylid *Edgarosaurus muddi.*, Early Cretaceous (late Albian) of Montana (Western Interior Seaway).
Artwork by Smokeybjb. Wikipedia, GNU Free Documentation/Creative Commons Attribution

Descriptions

Dolichorhynchops**:** *T. bonneri* (Adams 1997), *D. herschelensis* Sato 2005., *D. osborni* Williston 1903

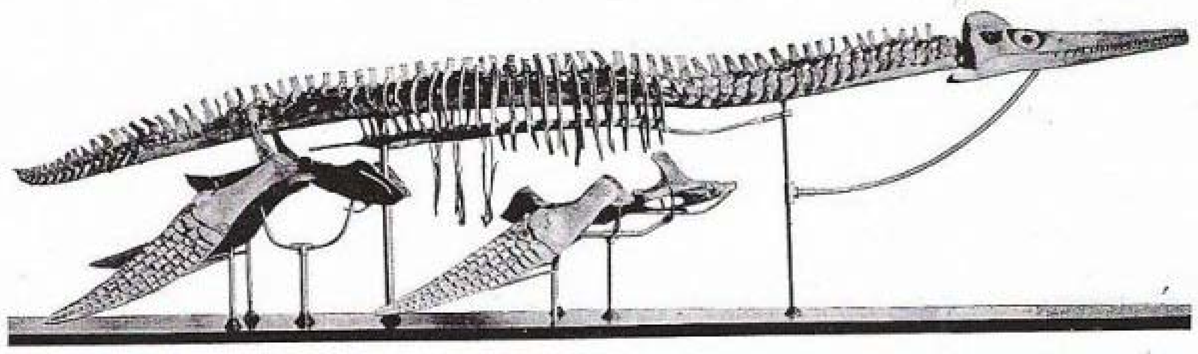
Range: Late Cretaceous (Santonian to Maastrichtian) of North America.

Phylogeny: Polycotylidae **:** *Plesiopleurodon* + (*Trinacromerum* + * **:** *Dolichorhynchops osborni* + *Dolichorhynchops bonneri*)

Characters: polycotylid plesiosaurs possessing 19 or 20 cervical vertebrae; 18-20 teeth in mandibular symphysis; short and very high sagittal crest; O'Keefe 2008

Links: Dolichorhynchops - Oceans of Kansas Paleobiology database; MAK111126

Dolichorhynchops osborni**:** Williston 1903 .



Range: *Hesperornis* zone, Smoky Hill Chalk Member, Niobrara Formation. Santonian-Campanian (Late Cretaceous) of North America.

Phylogeny: Dolichorhynchops **:** *Dolichorhynchops bonneri* + *

Comment: a relatively small polycotylid plesiosaur, (O'Keefe 2008) which lived slightly earlier than, but was otheriwsie very similatr to, *D. bonneri*. It is not impossible that this could be an ancestral species for the more advanced, later, larger and faster *D. bonneri*. If so, this would be an example of progressive evolution similar tpo that of the contemporary Tyrannosaurs on land, which likewise evolved into progressively larger and more formiable species during this same time period MAK111126

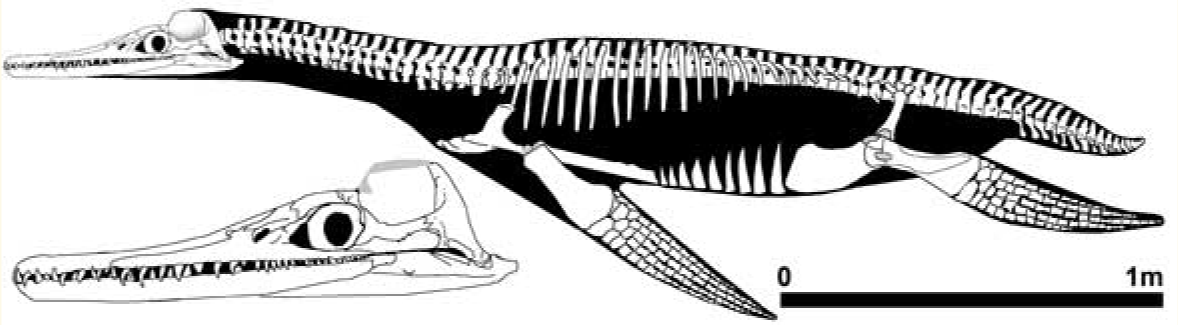
History of discovery: The following is from the Wikipedia entry on *Dolichorhynchops*: "The holotype specimen of Dolichorhynchops osborni was discovered in the upper Smoky Hill Chalk Logan County, Kansas, by George F. Sternberg, as a teenager, in around 1900. The remains were collected by him and his father, Charles H. Sternberg, and then sold to the University of Kansas (Lawrence, Kansas). KUVP 1300 was prepared and mounted by H.T. Martin under the supervision of Dr. Samuel Wendell Williston, who described and named it in1902. A more detailed description and photographs were provided by Williston 1903). The specimen has been on display in the KU Museum of Natural History since that time.

George Sternberg found a second, less complete specimen of *D.osborni* in 1926. In his effort to sell the specimen to a museum, Sternberg took detailed photographs of the skull. The specimen was eventually mounted in plaster and was acquired by the Harvard Museum of Comparative Zoology. MCZ 1064 was on display there until some time in the 1950s. This specimen was never completely described although the skull was figured by O'Keefe (2004). (See also Everhart, 2004)

The specimen of *D. osborni* on exhibit at the Sternberg, FHSM VP-404 was found by Marion Bonner near Russell Springs in Logan County in the early 1950s. It is, perhaps, the most complete specimen of this species known. It is just under 10 feet (3 meters) in length. The skull was crushed flat but is in very good condition. This specimen was initially reported by Sternberg and Walker (1957), and then was the subject of a Masters thesis by Orville Bonner (1964). Note that it was described by Bonner as "Trinacromerum osborni" which was the accepted genus name at the time."

Graphic: Mounted skeleton of the Holotype of *Dolichorhynchops osborni* (from Williston, 1903), in the University of Kansans Museum of Natural History. Wikipedia, Public domain. MAK111126

Dolichorhynchops bonneri**:** (Adams 1997),



Synonym: *Trinacromerum bonneri*

Range: Sharon Springs Member, Pierre Shale of Wyoming & South Dakota, Taylor Marl of Texas. Early Campanian (Late Cretaceous)

Phylogeny: Dolichorhynchops **:** *Dolichorhynchops osborni* + *

Characters: See O'Keefe 2008

Comments One of the last, largest, and fastest of the Polycotylids. The taxonomy is very confusing, we have followed O'Keefe 2008.

[1] History of discovery. From Wikipedia: "Two very large specimens of a polycotylid plesiosaur (KUVP 40001 and 40002)were collected from the Pierre Shale of Wyoming and later reported on by Adams in her 1977 Masters thesis. Later (1997), she officially described (1997) as a new species of Trinacromerum (T. bonneri). Unknown to her at the time, Carpenter (1996) had revised the Polycotylidae and separated Dolichorhynchops from Trinacromerum. Thus the species would revert back to Dolichorhynchops bonneri"

[2] Phyogeny : From the abstract of O'Keefe 2008: "The taxonomic identity of two well-preserved polycotylid plesiosaur skeletons from the Pierre Shale of far northern Wyoming and southern South Dakota has been controversial since their discovery. Originally referred to *Dolichorhynchops osborni*, the material was almost immediately christened *Trinacromerum bonneri* Adams 1997; more recently the material has been referred to *Polycotylus*. Recent preparation of the well-preserved skull of one specimen permits detailed examination of the cranial morphology of this animal for the first time, and allows for its inclusion in a cladistic analysis of the Polycotylidae. This analysis reveals a stable sister-taxon relationship with *Dolichorhynchops osborni*. However, the taxon possesses a bewildering mosaic of character states, superficially resembling *Polycotylus* in overall size and tooth morphology and *Trinacromerum* in details of the palate and lower jaw, while sharing several critical synapomorphies with *Dolichorhynchops osborni*. This wide-ranging homoplasy among characters previously diagnostic among polycotylid genera challenges the alpha taxonomy of forms from the western interior seaway."

[3] Ecology: Phyogeny : From the abstract of Adams 1997 "The Pierre Shale represents the final days of the Western Interior Seaway before its regression at the end of the Mesozoic, and records the last of the marine reptiles that dominated the seas much as their contemporary dinosaur counterparts dominated the land. *Trinacromerum bonneri* , n.sp., is the first pliosaur (short-necked plesiosaur) to be described from this formation in the northern Great Plains; as such it represents the final radiation of polytcotylid plesiosaurs in North America. Pliosaurs have long been regarded as particularly high-speed swimmers, but in T. bonneri this trend is carried to an extreme. Development of the longest wingfins known in pliosaurs maximised its velocity. Unique limb and vertebral structures resisted pressures of the surrounding water that were generated by its own swimming velocity. Such adaptations include tongue-and-groove articular surfaces between critical limb elements and highly interlocking vertebrae."

Graphic: David Peters - Reptile Evolution

Plesiopleurodon: *P. wellesi* Carpenter 1996.

Range: Early Late Cretaceous (Cenomanian) of North America.

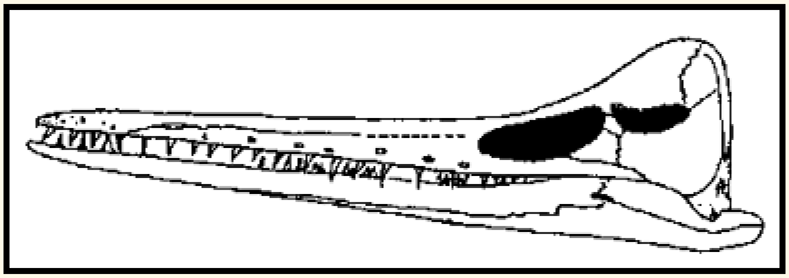
Phylogeny: Polycotylidae **:** *Plesiopleurodon* + (*Trinacromerum* + *Dolichorhynchops*)

Characters: relatively small (<3m); mandible with moderately long symphysis containing 8 pairs of large procumbent caniniform teeth; teeth circular in cross-section, with outer surface smooth except near base, which is striated; cervical vertebrae slightly wider than long; cervical ribs single-headed.

Comment: originally interpreted as a standard pliosaurid, appears as a basal Polycotylid in cladistic analysis by Hilary Ketchum and Roger Benson 2010, 2011

Links: Questions and Answers Late July 2001 - Zoom Dinosaurs; Plesiosauria Translation and Pronunciation Guide. ATW020705, revised MAK111126

Polycotylidae: *Ceraumasaurus, Dolichorhynchops, Georgiasaurus, Polycotylus, Trinacromerum*.



Range: K.

Phylogeny: Tricleidia : *Tricleidus* + (Cimoliasauridae + * : *Plesiopleurodon* + (*Trinacromerum* + *Dolichorhynchops*))

Characters: Short-necked, long-jawed elasmosaurs, up to 9m. Very long, slender premaxilla and maxilla; premaxilla forms dorsal & anterior margin of nares; dorsal process of premaxilla extends posteriorly to separate frontals and meet the parietals between the orbits (!!); replacement teeth grow in pits medially to extant teeth; pineal foramen closed dorsally; thin vomer separates premaxillae with anterior V-shaped slit possibly housing chemosensory vomeronasal (Jacobson's) organ; maxilla also extends posteriorly and forms much of lower rim of orbit; lachrymal absent; frontals form upper orbit and have wing-like process over top of orbit; temporal fenestrae very large, leaving parietal as a sort of tall, central, tent-like crest covering the braincase; large pterygoids, ectopterygoids and palatines cover most of ventral surface, leaving two small vacuities posterior to body of the parasphenoid process, and one small medial vacuity anterior to the parasphenoid; dentaries bear splenials and coronoids; quadrate short, wide & articulates with large squamosal and quadrate process of pterygoid; basioccipital forms ventro-posterior margin of braincase; stapes absent; cervical ribs are single-headed; scapular is separated by clavicular arch; pelvis large, with elongated ischia; distal bones of limbs very short.

Links: Kazmer's *Trinacromerum* bones; Royal Tyrrell Museum Tour: Bearpaw Sea; TMM - Exhibits - Scratching the Surface - Plesiosaur; The Plesiosaur Site - Species; Marine Reptiles (NOT Dinosaurs); Plesiosauria Translation and Pronunciation Guide; ???????? (Japanese). The Sternberg site at Oceans of Kansas has an exceptional number of good images. ATW020709. MAK990821.

Trinacromerum**:** *T. bentonianum* Cragin 1888, *T. kirki* Russell, 1935

Synonym: *Ceraunosaurus*

Range: Early Late Cretaceous (late Cenomanian/early Turonian) of North America.

Phylogeny: Polycotylidae **:** *Plesiopleurodon* + (*Dolichorhynchops* + *)

Comment: Similar to but earlier than *Dolichorhynchops*.

Links: Trinacromerum - Oceans of Kansas Paleobiology database; Trinacromerum (Julius T. Csotonyi); (paleo art) MAK111126

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

checked ATW040131. New page MAK111126

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

Sauropterygia: Dendrogram

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|LEPIDOSAUROMORPHA
|--SAUROPTERYGIA
|  |--Placodontia
|  |==Pachypleurosauridae
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
LEPIDOSAUROMORPHA ToL
|--SAUROPTERYGIA X (placodonts + plesiosaurs) MH
|  |--Placodontia •X MH HCW08
|  |   |--Paraplacodus •X
|  |   `--+--Placodus •X
|  |       `--Cyamodontoidea •X
|  |           |--+--Cyamodus •X
|  |           |  `--Henodus •X
|  |           `--Placochelyidae •X
|  |               |--Placochelys •X
|  |               `--Psephoderma •X
|  `--Nothosauria X (plesiosaurs > placodonts)
|     |--Wumengosaurus
|     |--Pachypleurosauridae X MH Rieppel (1998), HCW08
|     |  |--Hanosaurus •X
|     |  `--+--+--Dactylosaurus •X
|     |     |  `--Anarosaurus •X
|     |     `--+--Serpianosaurus •X  S89--Neusticosaurus •X (O'K&S99)
|     `--Eusauropterygia X (nothosaurs + plesiosaurs)
|        |--Nothosauridae X (nothosaurs > plesiosaurs) MH
|        |  |--Keichousaurus •X HCW08
|        |  `--+--Simosaurus •X HCW08
|        |     `--+--Nothosaurus •X HCW08
|        |        `--+--Ceresiosaurus •X
|        |           `--Lariosaurus •X HCW08
|        `--Pistosauroidea X   (plesiosaurs > nothosaurs)
|           |--Corosaurus •X HCW08
|           `--+--Cymatosaurus •X  R97
|              `--+--Pistosaurus •X HCW08
|                  `--+--Yunguisaurus
```

```
|                     `--+--Augustasaurus
|                        `--Plesiosauria X MH
|                           |--Pliosauroidea X MH
|                           |  |--Bishanopliosaurus •X
|                           |  |--Thalassiodracon •X
|                           |  `--+--Archaeonectrus •X
|                           |     |--Eurycleidus •X
|                           |     `--+--Rhomaleosauridae X MH
|                           |        |  |--Yuzhoupliosaurus •X
|                           |        |  `--+--Rhomaleosaurus •X
|                           |        |     `--+--Simolestes •X
|                           |        |        `--Leptocleidus •X
|                           |        `--Pliosauridae X MH
|                           |           |--Maresaurus •X
|                           |           |--Macroplata •X
|                           |           `--+--Kronosaurus •X
|                           |              `--+--Peloneustes •X
|                           |                 `--+--Liopleurodon •X
|                           |                    `--+--Pliosaurus •X
|                           |                       `--Brachauchenius •X
|                           `--Plesiosauroidea X
|                              |--Attenborosaurus •X
|                              `--+--Plesiosaurus •X
|                                 `--+--Eretmosaurus •X
|                                    |--Sthenarosaurus •X
|                                    `--+--Microcleidus •X
|                                       `--+--Elasmosauridae •X MH
|                                          `--Cryptocleidoidea X MH
|                                             |--Cryptocleididae X
|                                             |  |--Colymbosaurus •X
|                                             |  |--Cryptocleidus •X
|                                             |  `--Muraenosaurus •X
|                                             `--Tricleidia X
|                                                |--Tricleidus •X
|                                                `--+--Cimoliasauridae X
|                                                   |  |--Kimmerosaurus •X
|                                                   |  `--Cimoliasaurus •X
|                                                   `--Polycotylidae •X
|                                                        |--Plesiopleurodon •X
|                                                        `--+--Dolichorhynchops •X
|                                                           `--Trinacromerum •X
`--Lepidosauriformes MH
   |--Kuehneosauridae •X
   `--Lepidosauria
      |--SPHENODONTIA
      `--SQUAMATA
```

Alternate dendrogram, taking into account bone histology studies by Klein 2010, Hugi et al 2011, and Hugi 2011. Taxa for which there is information are in bold. The status of many taxa is uncertain due to lack of histological data:

```
SAUROPTERYGIA X
   |?--Hanosaurus •X
   |--+--Serpianosaurus •X --Neusticosaurus •X
   |  `--Nothosauridae X (nothosaurs > plesiosaurs)
   |      |--Keichousaurus •X
   |      `--+--Simosaurus •X
   |           `--+--Nothosaurus •X
   |              `--+--Ceresiosaurus •X
   |                 `--Lariosaurus •X
    `--+--+--+--Dactylosaurus •X
       |    |   `--Anarosaurus •X
       |    `--Placodontia •X
       |       |--Paraplacodus •X
       |       `--+--Placodus •X
       |           `--Cyamodontoidea •X
       |              |--+--Cyamodus •X
       |              |  `--Henodus •X
       |              `--Placochelyidae •X
       |                  |--Placochelys •X
       |                  `--Psephoderma •X
       `--Pistosauroidea X   (plesiosaurs > nothosaurs)
           |--Corosaurus •X
           `--+--Cymatosaurus •X
              `--+--Pistosaurus •X
                  `--+--Yunguisaurus
                     `--+--Augustasaurus
                        `--Plesiosauria X
```

Here the placodont-nothosauria, and pachypleurosaur-eusauropterygia clades are replaced by a nothosaur-pistosaur topology, with the pachypleurosaurs spread among both (and perhaps also basal to botrh?) and theplacodonts *included with the pistosaurs. As with molecular-based studies, this gives a very different result to the conventional morphology-based analysis. MAK111102*

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

---

last revised ATW080330, MAK111102

Sauropterygia: References

Abbreviated Dendrogram

```
DIAPSIDA
|--ARCHOSAUROMORPHA
|
Lepidosauromorpha
|--SAUROPTERYGIA
|  |--Placodontia
|  |--Pachypleurosauridae
|  `--+--Nothosauridae
|     `--Plesiosauria
|        |--Pliosauroidea
|        `--Plesiosauroidea
|           |--Elasmosauridae
|           `--Cryptocleidoidea
`--Lepidosauriformes
   |--SPHENODONTIA
   `--SQUAMATA
```

Contents

Adams, Dawn A.; 1997 *Trinacromerum bonneri*, new species. Last and fastest pliosaur of the Western Interior Seaway ; *Texas Journal of Science* ; 49 (3) ; 179-198
Dolichorhynchops bonneri

An osteological study of Nyctosaurus and Trinacromerum with a description of a new species of Nyctosaurus, Unpub. Masters Thesis, Fort Hays State University, 63 pages
Dolichorhynchops osborni

Borsuk-Bialynicka, M, & Evans, S.E. (2009). A long-necked archosauromorph from the Early Triassic of Poland. *Paleontologica Polonica* 65: 203-234. pdf
Pachypleurosauridae - Notes

Brown, DS (1981), *The Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria*. **Bull. Brit. Mus. Nat. Hist., Geol.** 35: 253-347.
Colymbosaurus, Cryptocleididae, Elasmosauridae, *Microcleidus*, *Muraenosaurus*, Plesiosauroidea, Pliosauroidea

Carpenter, K. 1996. A Review of short-necked plesiosaurs from the Cretaceous of the western interior, North America, *Neues Jahrbuch f�r Geologie und Pal�eontologie Abhandlungen*, (Stuttgart) 201(2):259-287.
Dolichorhynchops bonneri

Carpenter, K (1997), *Comparative cranial anatomy of two North American Cretaceous plesiosaurs*, in JM Callaway & EL Nicholls (eds.), **Ancient Marine Reptiles** Academic Press, pp. 191-216.
Liopleurodon, *Peloneustes*.

Carroll, RL (1981), *Plesiosaur ancestors from the Upper Permian of Madagascar.* **Phil Trans. R. Soc. Lond. B** 293: 315-383.
Sauropterygia

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp.
Sauropterygia.

Carroll, RL & Gaskill, P (1985), *The nothosaur **Pachypleurosaurus** and the origin of plesiosaurs*. **Phil. Trans. Roy. Soc. Lond. B** 309: 343-393.
Anarosaurus, *Neusticosaurus*, Nothosauria, Nothosauridae, *Nothosaurus*, Plesiosauria, Sauropterygia, *Simosaurus*.

Yen-nien Cheng, Xiao-chun Wu & Qiang Ji, Triassic marine reptiles gave birth to live young. *Nature* 432, 383-386 (18 November 2004) | doi:10.1038/nature03050; **pdf**
Keichousaurus

Cheng, Y.-N.; Sato, T.; Wu, X.-C.; and Li, C. (2006). "First complete pistosauroid from the Triassic of China". Journal of Vertebrate Paleontology 26 (2): 501-503.
Pistosauridae - Overview, *Augustasaurus*, *Yunguisaurus*

Colbert, E.H., 1969 *Evolution of the Vertebrates*, John Wiley & Sons, 2nd ed.
Sauropterygia

Cox, B, RJG Savage, B Gardiner & D Dixon (1988) **Collins Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals**. Collins Publishers Aus. 312 pp.
Pliosauridae.

Cruickshank, ARI (1994), *A juvenile plesiosaur (Reptilia: Plesiosauria) from the Lower Lias (Hettangian: Lower Jurassic) of Lyme Regis, England: a pliosaurid-plesiosaurid intermediate?* **Zool. J. Linn. Soc.** 112: 151-178.
Eurycleidus.

Cruickshank, ARI & JA Long (1997), *A new species of pliosaurid reptile from the Early Cretaceous Birdsong sandstone of Western Australia*. **Recs. W. Aus. Mus.** 18.
Eurycleidus.

Cruickshank, ARI, P Small & M Taylor (1991), *Dorsal nostrils and hydrodynamically driven underwater olfaction in plesiosaurs*. **Nature** 352: 62-64.
Rhomaleosaurus.

J. Cubo, F. Ponton, M. Laurin, E. De Margerie and J. Castanet, Phylogenetic Signal in Bone Microstructure of Sauropsids, *Syst Biol* (2005) 54(4): 562-574 doi:10.1080/10635150591003461 **online / pdf**
Pachypleurosauridae - Clade or Grade?

deRicql�s, A (1989), *Les m�canismes h�t�rochroniques dans le retour des t�trapodes au milieu aquatique*, in **Colloque International du CNRS : Ontog�n�se et Evolution, Dijon, septembre 1986**, pp. 171-178.
Pachypleurosauridae.

deRicqlès A, Padian K, Knoll F, Horner JR (2008) On the origin of high growth rates in archosaurs and their ancient relatives: complementary histological studies on Triassic archosauriforms and the problem of a "phylogenetic signal" in bone histology. *Annales de Palaeontologie* 94: 57-76.
Pachypleurosauridae - Physiological diversity

Cajus G. Diedrich, C.G. (2011), Fossil middle triassic "sea cows" - placodont reptiles as macroalgae feeders along the north-western tethys coastline with pangaea and in the germanic basin *Natural Science*, Vol.3, No.1, 9-27 doi:10.4236/ns.2011.31002 SciRes. Online
Triassic sea cows, Placodus

Enlow, D.H. (1963). Principles of Bone Remodeling. An account of post-natal growth and remodeling processes in long bones and the mandible. Springfield, IL: C.C. Thomas.

Pachypleurosauridae - Physiological diversity

New data regarding the skull of Dolichorhynchops osborni (Plesiosauroidea: Polycotylidae) from rediscovered photos of the Harvard Museum of Comparative Zoology specimen. *Paludicola* 4(3):74-80.
Dolichorhynchops osborni

Frey, E & Reiss, J (1982), *Considerations concerning plesiosaur locomotion*. **N. Jb. Geol. Palaont. Abh.** 164: 188-192.
Plesiosauria

Gaudant, J & FJ Meunier (1996), *Observation d'un cas de pachyostose chez un Clupeidae fossile du Mio�ne terminal de l'ouest Alg�rien, **Sardina ? crassa** (Sauvage, 1873)*. **Cybium** 20: 169-83.
Pachypleurosauridae

Gauthier, J. A. (1986), "Saurischian monophyly and the origin of birds", in Padian, K., The Origin of Birds and the Evolution of Flight. Memoirs of the California Academy of Sciences, 8, California Academy of Sciences, pp. 1-55, ISBN 780940228146
Pachypleurosauridae - Clade or Grade?

Godfrey, SJ (1984), *Plesiosaur sub-aqueous locomotion: a reappraisal*. **N. Jb. Geol. Palaont. Abh.** 11: 661-672.
Plesiosauria

Hampe, O (1992), *Ein grosswuechsiger pliosauride (Reptilia: Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien*. **Courier Forsch. Senckenberg**. 145: 1-32.
Kronosaurus.

Holmes R, Y-N Cheng & X-C Wu (2008), *New information on the skull of **Keichousaurus hui** (Reptilia: Sauropterygia) with comments on sauropterygian interrelationships*. **J. Vert. Paleont.** 28: 76-84.

Hugi, J (2011) The long bone histology of Ceresiosaurus (Sauropterygia, Reptilia) in comparison to other eosauropterygians from the Middle Triassic of Monte San Giorgio (Switzerland/Italy). *Swiss Journal of Palaeontology* [doi: 10.1007/s13358-011-0023-6].
Pachypleurosauridae - Physiological diversity

Hugi, J., Scheyer, T. M., Sander, P. M., Klein, N., and M. R. S�nchez-Villagra. 2011. Long bone microstructure gives new insights into the life of pachypleurosaurids from the Middle Triassic of Monte San Giorgio, Switzerland/Italy. *Compte Rendus Palevol* 10:413-426. doi:10.1016/j.crpv.2011.03.009
Pachypleurosauridae - Physiological diversity

Jiang D-Y, Rieppel O, Motani R, Hao W-C, Sun Y-I, Schmitz L and Sun Z-Y. 2008. A new middle Triassic eosauropterygian (Reptilia, Sauropterygia) from southwestern China. *Journal of Vertebrate Paleontology* 28:1055-1062.
Wumengosaurus

Ketchum, H. F., and Benson, R. B. J. (2010). "Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses".*Biological Reviews* 85: 361�392. doi:10.1111/j.1469-185X.2009.00107.x. PMID 20002391.
Plesiopleurodon

Hilary F. Ketchum and Roger B. J. Benson (2011). "A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids". *Special Papers in Palaeontology* 86: 109�129. doi:10.1111/j.1475-4983.2011.01083.x.
Plesiopleurodon

Klein N (2010) Long Bone Histology of Sauropterygia from the Lower Muschelkalk of the Germanic Basin Provides Unexpected Implications for Phylogeny. *PLoS ONE* 5(7): e11613. doi:10.1371/journal.pone.0011613 **online**
Pachypleurosauridae - Clade or Grade?, Pachypleurosauridae - Physiological diversity, Anarosaurus, Nothosauridae, Pistosauridae

Oskar Kuhn, 1969 *Handbuch der Palaeoherpetologie, Teil 9: Proganosauria, Bolosauria, Placodontia, Araeoscelidia, Trilophosauria, Weigeltisauria, Millerosauria, Rhynchocephalia, Protorosauria*, Gustav Fisher-Verlag, Stuttgart
Sauropterygia, Placodontia - Evolutionary relationships

Li, Chun; Olivier Rieppel, Xiao-Chun Wu, Li-Jun Zhao and Li-Ting Wang (2011). "A new Triassic marine reptile from southwestern China". Journal of Vertebrate Paleontology 31 (2): 303�312. doi:10.1080/02724634.2011.550368.

Hanosaurus

Lucas, Spencer G. 2001, *Chinese Fossil Vertebrates*, Columbia University Press, New York
Hanosaurus, *Keichousaurus*

Jun Liu, Olivier Rieppel, Da-Yong Jiang, Jonathan C. Aitchison, Ryosuke Motani, Qi-Yue Zhang, Chang-Yong Zhou, and Yuan-Yuan Sun, 2011, A New Pachypleurosaur (Reptilia: Sauropterygia) from the Lower Middle Triassic of Southwestern China and the Phylogenetic Relationships of Chinese Pachypleurosaurs *Journal of Vertebrate Paleontology* 31(2):292-302. 2011 doi: 10.1080/02724634.2011.550363
Pachypleurosauridae - Clade or Grade?

Mazin, J.-M. & Pinna, G. 1993. Palaeoecology of the armoured placodonts. *Paleontologia Lombarda*, N. S. 2: 83-91.
Placochelyidae

Molnar, RE (1991), *Fossil reptiles of Australia*, **in** P Vickers-Rich, JM Monaghan, RF Baird & TH Rich (eds.), **Vertebrate Paleontology of Australia**. Pioneer Design Studio (Melbourne), pp.605-689.
Cimoliasaurus

M�ller, J. 2004. The relationships among diapsid reptiles and the influence of taxon selection. In: G. Arratia, M.V.H. Wilson, and R. Cloutier (eds) *Recent Advances in the Origin and Early Evolution of Vertebrates*, 379-408. Verlag Dr Friedrich Pfeil, M�nchen.
Pachypleurosauridae - Notes

O'Keefe, F. R., 2001: A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica*: Vol. #213, pp. 1-63
Augustasaurus, *Thalassiodracon*

O'Keefe, F. R. 2004. On the cranial anatomy of the polycotylid plesiosaurs, including new material of Polycotylus latipinnis Cope, from Alabama. *Journal of Vertebrate Paleontology* 24(2):326-340. *Dolichorhynchops osborni*

O'Keefe, F. R., . 2008. Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotylid (Sauropteryga: Plesiosauria) from the Pierre Shale of Wyoming and South Dakota. *Journal of Vertebrate Paleontology* 28(3):664-676
Dolichorhynchops bonneri

O'Keefe, F. R. and P. M. Sander (1999) Paleontological paradigms and inferences of phylogenetic pattern: a case study. *Paleobiology* 25: 518-533 abstract
On discovering ancestors

O'Keefe, FR, O Rieppel & PM Sander (1999) *Shape disassociation and inferred heterochrony in a clade of pachypleurosaurs (Reptilia, Sauropterygia)*. **Paleobiology** 25: 504-517.
Neusticosaurus, Pachypleurosauridae.

Ray S, Mukherjee D and S Bandyopadhyay S 2009 Growth patterns of fossil vertebrates as deduced from bone microstructure: case studies from India; *J. Biosci*. 34 661-672] DOI 10.1007/s12038-009-0055-x **pdf**
Pachypleurosauridae - Physiological diversity

Reid, R.E.H. (1984). "Primary bone and dinosaurian physiology". *Geological Magazine* 121 (06): 589-598. doi:10.1017/S0016756800030739.
Pachypleurosauridae - Physiological diversity

Reid, R.E.H (1997). "How dinosaurs grew". In Farlow, J.O. and Brett-Surman, M.K.. *The Complete Dinosaur*. Bloomington: Indiana University Press. pp. 403-413. ISBN 0-253-33349-0.
Pachypleurosauridae - Physiological diversity

Rieppel, O.. 1989. A New Pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London, Series B*, Biological Sciences 323(1212):1-73 [J. Mueller/T. Liebrecht]

Pachypleurosauridae - Clade or Grade?

O. Rieppel. 1998. The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. *Journal of Vertebrate Paleontology* 18(3):545-557
Hanosaurus

Rieppel, O., (2000), *Sauropterygia I, placodontia, pachypleurosauria, nothosauroidea, pistosauroidea: In: Handbuch der Palaoherpetologie*, part 12A, 134pp. Verlag Dr. Friedrich Pfeil
Pachypleurosauridae - Clade or Grade?

Rieppel, Olivier & Lin, Kebang. 1995. Pachypleurosaurs (Reptilia: Sauropterygia) from the lower Muschelkalk, and a review of the Pachypleurosauroidea. *Fieldiana, Geology*, new series, no. 32 **online**

Rieppel, O (1989), *A new pachypleurosaur (Reptilia: Sauopterygia) from the Middle Triassic of Monte San Giorgio, Switzerland*. **Phil. Trans. Roy. Soc. Lond. B** 323: 1-73.
Anarosaurus, *Dactylosaurus*, *Keichousaurus*, *Neusticosaurus*, Nothosauria, Pachypleurosauridae,*Serpianosaurus*, *Simosaurus*.

Rieppel, O (1995), *The pachypleurosaur **Neusticosaurus** (Reptilia, Sauropterygia) from the Middle Triassic of Perledo, Northern Italy*. **N. Jahrb. Geol. Pal. Mon.** 1995: 205-216.
Neusticosaurus, Pachypleurosauridae, *Serpianosaurus*.

Rieppel, O (1997), *Sauropterygia: Introduction*, in JM Callaway & EL Nicholls (eds.), **Ancient Marine Reptiles** Academic Press, pp. 107-119.
Eusauropterygia

Rieppel, O. 1997b. Revision of the Sauropterygian reptile genus Cymatosaurus v. Fritsch, 1894, and the relationships of Germanosaurus Nopcsa, 1928, from the Middle Triassic of Europe. *Fieldiana. Geology*, new ser., no. 36 **Online / pdf**
Cymatosaurus

Rieppel, Olivier, (2001). The cranial anatomy of *Placochelys placodonta* Jaekel, 1902, and a review of the Cyamodontoidea (Reptilia, Placodonta). *Fieldiana, Geology*, new series, no. 45. **Online**

Cyamodontoidea, Placochelys

Rieppel, O & H Hagdorn (1997), *Paleobiogeography of Middle Triassic Sauropterygia in Central and Western Europe*, in Callaway, JM & EL Nicholls (eds), **Ancient Marine Reptiles**, Academic Press, pp. 121-44.
Pachypleurosauridae.

Rieppel, O & L Kebang (1995), *Pachypleurosaurs (Reptilia, Sauropterygia) from the Lower Muschelkalk, and a review of the Pachypleurosauroidea*. **Fieldiana Geol.** N.S. 32: 1-44.
Anarosaurus, *Dactylosaurus*, Pachypleurosauridae.

Rieppel O, Sander PM and Storrs GW 2002. The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern Nevada. *Journal of Vertebrate Paleontology* 22(3):577-592. **pdf**
Pistosauridae - Overview, *Augustasaurus*

Rieppel, O & R Wild (1996), *A revision of the genus **Nothosaurus** (Reptilia: Sauropterygia) from the Germanic Triassic, with comments on the status of **Conchiosaurus clavatus***. **Fieldiana Geol.** No.1479, 82 pp.�
Nothosauridae

Robinson, JA (1975), *The locomotion of plesiosaurs*. **N. Jb. Geol. Palaont. Abh.** 149: 286-332.
Plesiosauria

Robinson, JA (1977), *Intercorporal force transmission in plesiosaurs*. **N. Jb. Geol. Palaont. Abh.** 153: 88-128.
Plesiosauria.

Sachs, S (2005), ***Tuarangisaurus australis** sp. nov. (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of northeastern Queensland, with additional notes on the phylogeny of the Elasmosauridae*. **Mem. Queensl. Mus.**, 50: 425-440.
Elasmosauridae.

Sander, PM (1989), *The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of a new species*. **Phil. Trans. Roy. Soc. Lond. B** 325: 561-666.
Neusticosaurus, *Serpianosaurus*.

Sander PM, Rieppel OC and Bucher H 1997. A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. Journal of Vertebrate Paleontology 17:526-533.
Augustasaurus

Adam S. Smith and Gareth J. Dyke (2008). "The skull of the giant predatory pliosaur Rhomaleosaurus cramptoni: implications for plesiosaur phylogenetics". *Naturwissenschaften* 95: 975-980. doi:10.1007/s00114-008-0402-z. **pdf**
Rhomaleosaurus.

Adam S. Smith and Peggy Vincent (2010). "A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany". *Palaeontology* 53 (5): 1049-1063. doi:10.1111/j.1475-4983.2010.00975.x. **pdf**
Rhomaleosaurus.

Sternberg, G. F. and M. V. Walker. 1957. Report on a plesiosaur skeleton from western Kansas. *Kansas Academy of Science, Transactions*, 60(1):86-87 *Dolichorhynchops osborni*

Storrs, G. W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. American Journal of Science. 293-A. 63-90. **pdf**
Placodontia - Evolutionary relationships

Storrs, G. W. 1997, *Morphological and taxonomic clarification of the genus* ***Plesiosaurus***, in JM Callaway & EL Nicholls (eds.), **Ancient Marine Reptiles** Academic Press, pp. 145-190.
Plesiosaurus.

Storrs, GW & MA Taylor (1996), *Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England*. **J. Vert. Paleontol.** 16: 403-420.
Eurycleidus.

Tarsitano, S & Riess, J (1982), *Plesiosaur locomotion -- underwater flight versus rowing*. **N. Jb. Geol. Palaont. Abh.** 164: 193-194.
Plesiosauria.

Taylor, MA (1981), *Plesiosaur rigging and ballasting*. **Nature** 290: 628-9
Plesiosauria, Plesiosauroidea.

Taylor, MA (1986), *Lifestyle of plesiosaurs.* **Nature** 319: 179.
Plesiosauria.

Taylor, MA (1992), *Functional anatomy of the head of a large aquatic predator* ***Rhomaleosaurus zetlandicus*** *(Plesiosauria: Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England.* **Phil. Trans. Roy. Soc. Lond. B** 335: 247-280.
Rhomaleosaurus.

Taylor, MA & ARI Cruickshank (1993), *A plesiosaur from the Linksfield Erratic (Rhaetian, Upper Triassic) near Elgin, Morayshire*. **Scot. J. Geol.** 29: 191-196.
Eretmosaurus.

Welles, SP (1962), *A new species of elasmosaur from the Aptian of Columbia, and a review of the Cretaceous plesiosaurs.* **Univ. Calif. Publ. in Geol. Sci.** 46: 54.
Brachauchenius.

White, TE (1940), *Holotype of* ***Plesiosaurus longirostris*** *Blake and the classification of the plesiosaurs*. **J. Paleontol.** 14: 451-467.
Macroplata, *Microcleidus*, *Sthenarasaurus*.

Zhang, Y (1985), *A new plesiosaur from Middle Jurassic of Sichuan Basin*. **Vertebrata PalAsiatica** 23: 235-240.
Yuzhoupliosaurus

Williston, S. W. 1902. Restoration of Dolichorhynchops osborni, a new Cretaceous plesiosaur, *Kansas University Science Bulletin*, 1(9):241-244, 1 plate.
Dolichorhynchops osborni

Williston, S. W. 1903. North American plesiosaurs, *Field Columbian Museum*, *Pub. 73*, *Geological Series*, 2(1):1-79, 29 plates.
Dolichorhynchops osborni

Wu X-C, Cheng Y-N, Li C, Zhao L-J and Sato T 2011. New Information on Wumengosaurus delicatomandibularis Jiang et al., 2008, (Diapsida: Sauropterygia), with a Revision of the Osteology and Phylogeny of the Taxon. Journal of Vertebrate Paleontology 31(1):70�83.
Pachypleurosauridae - Clade or Grade, *Wumengosaurus*

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

Sphenodontia: Overview

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--Clevosaurinae
      `--Stem Group Sphenodontinae
         |--Pleurosauridae
         `--+--Sphenodontinae
            `--+--Sphenodontini
               `--Eilenodontini
```

Contents

Introduction

The Rhynchocephalia, or Sphenodontia, are the sister group of the hugely successful Squamata. The diversity of these poor relations to the snakes and lizards has always been somewhat limited. Now, they are represented only by the genus *Sphenodon* -- two closely related species of tuataras, small numbers of which still eke out a living among the bird hatcheries on a few islands off the coast of New Zealand.

Dethe confrounteth Everyman (and *Sphenodon*). From Everyman

Anatomically, *Sphenodon* is rather plain vanilla; and, paradoxically, therein lies its interest. It lies just downstream in phylospace from the split between archosauromorphs and lepidosauromorphs. It is rather unspecialized and, consequently, is about as close to the basic reptile morphotype as one might hope to find. When Romer (1956) wrote his incomparable **Osteology of the Reptiles**, his constant anatomical point of reference was *Sphenodon*. Carroll's (1988) **Vertebrate Paleontology and Evolution** continued this tradition; and, when the next landmark text on vertebrate paleontology is produced, it will doubtless carry on the tradition. There really is no alternative. No reptile more basal than *Sphenodon* survives. Its closest relatives are the iguanid lizards -- products of the Cretaceous squamate radiation. Iguanids are fairly basic, but have the loose, specialized squamate skull: the very feature which has permitted the squamates to radiate into thousands of separate specialized forms. *Sphenodon* has a classic, solid skull construction which doesn't permit a great deal of variation. Think, for example, of crocodylomorphs, temnospondyls or Mesozoic mammals. That we are here proves that a solid, akinetic skull doesn't necessarily doom a taxon to morphological stagnation. However, it is certainly a consideration.

So, while we wait patiently for some scholar to pen the successor to Williston, Romer and Carroll, we may as well take a brief look at the phylogenetic neighborhood of paleontology's Everyman. ATW020406.

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

checked ATW050616

Sphenodontia

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
|
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--o Sphenodontia
       |-- Diphydontosaurus
       `--+-- Planocephalosaurus
          `--Sphenodontidae
             |--Clevosaurinae
             `--Stem Group Sphenodontinae
                |--Pleurosauridae
                `--Sphenodontinae
```

Contents

Taxa on This Page

1. *Diphydontosaurus* X
2. *Gephyrosaurus* X
3. *Planocephalosaurus* X
4. Rhynchocephalia
5. Sphenodontia

Descriptions

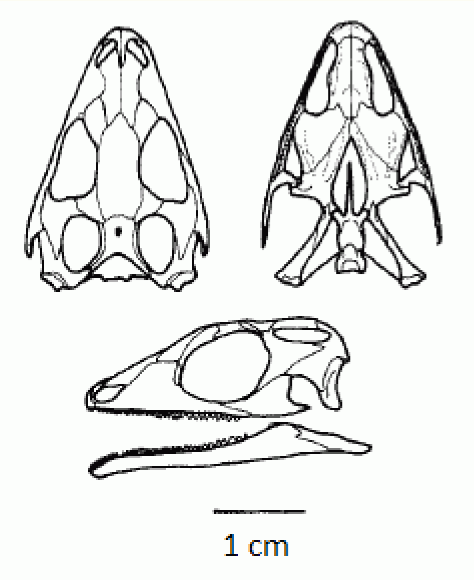
Rhynchocephalia

Range: from the Late Triassic.

Phylogeny: Lepidosauria **:** Squamata + * **:** Sphenodontia + Gephyrosaurus. ATW001116, MAK101016.

Comments: generally used as the most exclusicve clade for the sphenodontian reptiles, equivalent to Order Sphenodontia MAK120707

Gephyrosaurus:



Range: Known from the Early Jurassic fissure infills of Wales

Phylogeny: Rhynchocephalia **:** Sphenodontia + *.

Comments: This small animal (25-30 cm long) has numerous primitive characters, and shows a number of lepidosauromorph and many lepidosaur synapomorphies . Variously classified as a basal squamate or near- squamate, or more often as a basal sphenodontian.

Graphic: Benton 1985

Sphenodontia Williston 1925

Range: from the Late Triassic.

Phylogeny: Rhynchocephalia **:** Gephyrosaurus + * **:** *Diphydontosaurus* + (*Planocephalosaurus* + Sphenodontoidea /Sphenodontidae)).

Characters: Share a number of synapomorphies absent in *Gephyrosaurus* and other lepidosauromorphs. See Gauthier et al 1988 p.25 for a list of details taht i won't reproduce verbatum here. See also Sphenodontidae

Comments: Benton 1985 recommends the name Sphenodontia in preference to Rhynchocephalia because the latter was used to include rhynchosaurs (which are archosauromorphs) and other taxa. With adoption of *Gephyrosaurus* as sister taxon to the remaining Sphenodontia, Rhynchocephalia was ressurrected for by *Gephyrosaurus* + Sphenodontia, and presumably also for any species closer to *Sphenodon* than to *Lacertia* (to use a stem based definition). Alternative terms such as Sphenodontoidea Nopcsa 1928 and Sphenodontida Estes 1983 have also been proposed, but Williston’s name Sphenodontia has priority.

Diphydontosaurus:

Range: Rhaetian of England

Phylogeny: Sphenodontia **:** (*Planocephalosaurus* + Sphenodontidae) + *

Planocephalosaurus:

Range: late Triassic of England

Phylogeny: Sphenodontia **:** *Diphydontosaurus* + (Sphenodontidae + *)

Characters: several diagnostic sphenodontid characters. but differs from *Sphenodon* in having teeth on the palate, a broader parietal, an emarginated quadrate, a retroarticular process, an incomplete lower temporal bar (primitive/ancestral feature also in Gephyrosaurus), and precision shear bite Benton 1985 p.148. Planocephalosaurus presents Differs also from the clevosaurs which it otherwise resembles by the lack both the anterior process of the quadratojugal and squamosal-jugal contact Gauthier et al 1988 p.25 (i.e. incomplete lower temporal bar, in contrast to Sphenodon)

Comments: According to Reynoso 2000, Planocephalosaurus + Sphenodontidae share numerous synapomorphies to the exclusion of more basal taxa like *Diphydontosaurus* and *Gephyrosaurus*

Page Back | Unit Home | Page Top | Page Next

Sphenodontia: Pleurosauridae

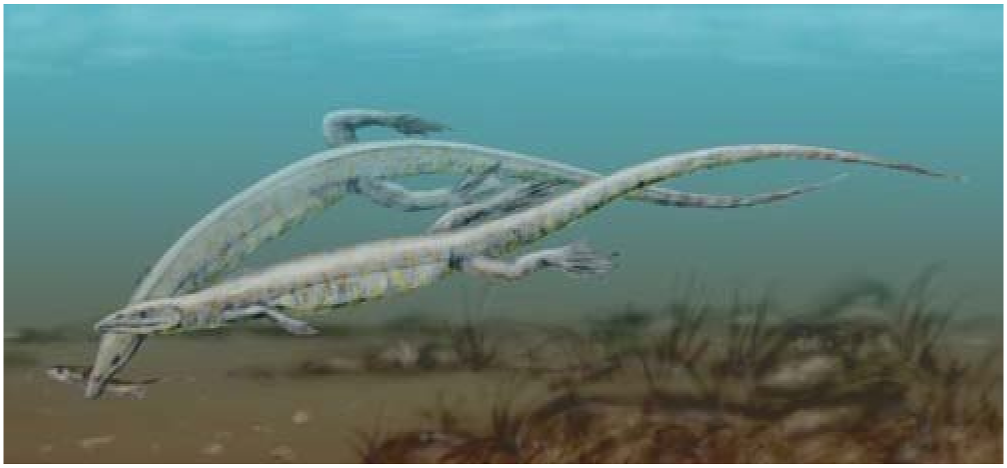
Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--Clevosaurinae
      `--Stem Group Sphenodontinae
         |--oPleurosauridae
         |   |--Palaeopleurosaurus
         |   `--Pleurosaurus
         |
         `--+--Sphenodontinae
            `--+--Sphenodontini
               `--Eilenodontini
```

Contents

Taxa on This Page

1. *Palaeopleurosaurus* X
2. Pleurosauridae X
3. *Pleurosaurus* X



Pleurosaurus goldfussi, a pleurosaur from the late Jurassic of Germany and France; artwork by Nobu Tamura, Wikipedia

The pleurosaurs were an extraordinary group of mostly European, Jurassic to Early Cretaceous, sphenodontids.

Evolving from terrstrial forms during the Early Jurassic, by the ned of teh period they had attained a very specialised, serpentine form, remarkably similar to other aquatic amphibians and especially reptiles. The body was elongated and the legs small, so most of the propulsion was provided by the very long tail. The pleurosaurs were not the only aquatic sphenodontia, there is also the mid Cretacous possible Eilenodontine *Ankylosphenodon* from Mexico

Pleurosaurs have traditionally been placed in their own family, the Pleurosauridae, and were thought to have diverged from the rest of the sphenodontians very early. Cladistic analysis incorporating the more recently discovered transitional form *Palaeopleurosaurus* shows in fact that they are highly specialised descendants of more typical sphenacodontids, although the representative genus *Pleurosaurus* bears very little resemblance to its terrestrial ancestors. Only three species are known to date, the early Jurassic *Palaeopleurosaurus posidoniae*, the late Jurassic *Pleurosaurus goldfussi*, and the early Cretaceous *P. ginsburgi* perhaps representing an anagenetic lineage. MAK120706

Descriptions

Pleurosauridae: *Palaeopleurosaurus; Pleurosaurus*.

The basal pleurosaur *Palaeopleurosaurus posidoniae*, Toarcian of Bavaria. Specimen in the Staatliches Museum für Naturkunde, Stuttgart. Photograph by Ghedoghedo, Wikipedia

Range: Early Jurassic to Early Cretaceous of Europe (Central Laurasia).

Phylogeny: traditionally Rhynchocephalia **:** Sphenodontidae + *. , but now: Stem Group Sphenodontinae **:** *Homoeosaurus* + (*Sapheosaurus* + Sphenodontinae) + *

Characters: Elongated (<58 vertebrae.) with long tail; acrodont teeth; incomplete lower temporal bar. Marine, progressive reduction of limbs (normal structure). ATW

Comments: These highly specialised animals (convergent with many Triassic marine reptiles) were previously considered a very early offshoot of the sphenodoontian lineage. More recent cladograms, e.g. Reynoso 2000, Apesteguía & Novas 2003, and Arantes et al 2009 place *Palaeopleurosaurus* (and hence Pleurosauridae) within the Sphenodontidae, making the latter a paraphyletic taxon as originally defined MAK101016

Were we to follow a strictly cladistic nomenclature we would have to subsume Pleurosauridae under Sphenodontidae, to avoid the latter becoming a paraphyletic taxon. Such an approach would obscure the unique and very distinctive nature (both ecologically and morphologically) of the pleurosaurs in relation to the more generalised sphenodontids. Acknowledging the need for an inclusive taxonomic as well as phylogenetic approach, the current author (MAK) disagrees with the anti-Linnaean paradigm advocated by many vertebrate paleontologists, and prefers to retain the family ranking for Pleurosauridae as a highly distinct offshoot of the main sphenodontid lineage. MAK120706

Palaeopleurosaurus:

Range: Early Jurassic (Toarcian) of Bavaria

Phylogeny: Pleurosauridae **:** Pleurosaurus + *.

Comments: Intermediate between terrestrial sphenodontids amd aquatic pleurosaurs. Both stratigraphically and morphologically, this is a fully transitional form. Reveals theat pleurosaurs are derived sphendodontids, rather than primnitive sphenodontians. This shows how difficult it is to place highly specialised taxa in cladograms, if their original synapomorphies have been lost or highly modified. The present author would argue that highly derived forms as mesosaurs and placodonts are certainly much more advanced than their apparent basal position on cladograms (as basal parareptiles and basal sauroptyerguia respectively) would seem to indicate MAK120706

***Pleurosaurus*:**

Range: Late Jurassic Kimmeridgian (Lithographic Stone) ; Bavaria, and Cerin, France., Early Cretaceous..

Phylogeny: Pleurosauridae **:** Palaeopleurosaurus + *.

Characters: From Zittel/Eastman/Woodward 1902 (copyright expired): "Body serpentiform, upwards of 1.5 meters long, the tail forming one-third the total length. Snout tapering in front. Presacral vertebrae with stout single-headed ribs ; abdominal ribs well developed.Fore-limbs shorter than the hinder pair.

Comments: Prior to the discovery of *Palaeopleurosaurus*, the exact relationship of these highly specilaise danimals was ubnknown. In size and gross morphology, and doubtless habits, these animals are very similar to other medium-sized serpentine, aquatic, Paleozoic and Mesozoic amphibians and reptiles, such as embolomeri, younginiformes, thalattosaurs, basal ichthyosaurs, pachypleurosaurs, and agilosaurs. MAK120706

Image: *Pleurosaurus* sp. Canjuers, France. Photo by Michel Royon, GNU Free Documentation License. Creative Commons Attribution Share Alike, Wikipedia

---

Page Back | Unit Home | Page Top | Page Next

page MAK120706

Sphenodontia: Sphenodontidae

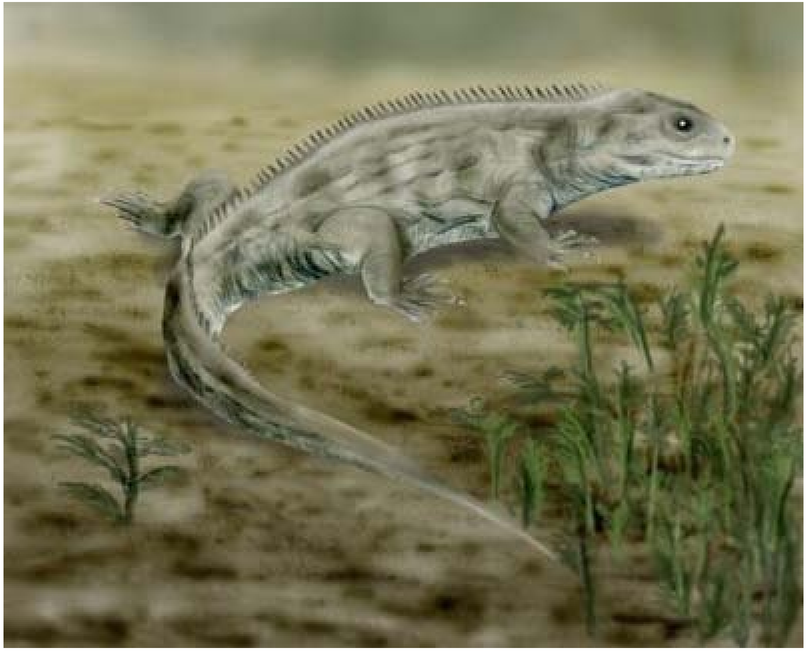
Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
|
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--o Clevosauridae
      |   |--Polysphenodon
      |   `--+-- Brachyrhinodon
      |      `-- Clevosaurus
      `--o Stem Group Sphenodontinae
         |-- Homoeosaurus
         |--Pleurosauridae
         `--+--Sphenodontinae
           `--+--Sphenodontini
              `--Eilenodontini
```

Contents

Taxa on This Page

1. *Brachyrhinodon* X
2. Clevosauridae X
3. *Clevosaurus* X
4. *Homoeosaurus* X
5. *Polysphenodon* X
6. Sphenodontidae
7. Stem Group Sphenodontinae



Brachyrhinodon taylori, a clevosaur from the Late Triassic of Scotland; artwork by Nobu Tamura, Wikipedia

---

Descriptions

Sphenodontidae: *Kallimodon, Homoeosaurus, Sapheosaurus, Pamizinsaurus*.

Range: from the Late Triassic.

Phylogeny: Sphenodontia **:** *Diphydontosaurus* + (*Planocephalosaurus* + * **:** Clevosauridae + Stem Group Sphenodontinae).

Characters: VS-M size. See Clevosaurs entry for basic skull structure. **$** Teeth fused to jaw margin (fully *acrodont*) and not replaced; less than 4 (7?) premaxillary teeth; **$** marginal teeth added posteriorly as jaw grows; dentary fits between maxillary teeth and parallel row of palatal teeth; Meckelian canal runs along midline of jaw & is at least partially open; broad mandibular symphysis; prominent coronoid process of dentary, posterior process of dentary ends posterior to coronoid; with posterior surangular facet; frontals not fused (??); **$** lacrimal absent; large upper temporal fenestra; complete lower temporal bar; quadratojugal retained; rigid quadrate; well-developed posterior tubercle on posterior margin of ischium; epiphyses present with determinate growth; may have osteoderms (*Pamizinsaurus*); food crushed thoroughly (insects & birds).

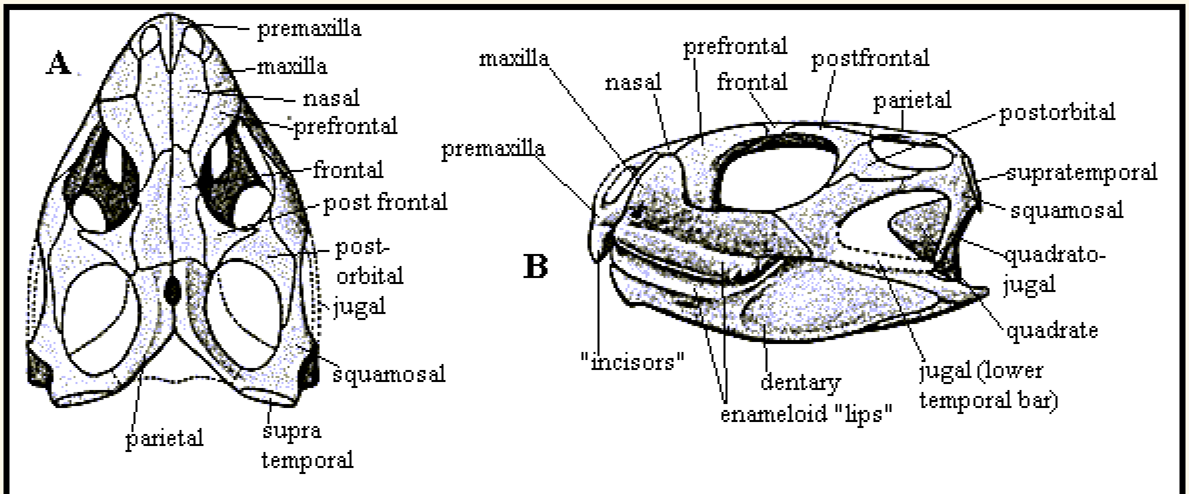
Comments: Cladistically, this taxon (equivalent to the standard Linnean taxonomic Sphenodontidae) should perhaps be called something like Sphenodontoidea, as it includes Clevosauridae, Pleurosauridae,. Crown Group Sphenodontidae, etc

Links: Introduction to the Sphenodontidae; Turtle, Tuatara, Crocodile Checklist--3; Jurassic Page´s gallery : the terrestrial wildlife (*Sapheosaurus*); Lebende Fossilien, Intro, Teil 2 (*Homoeosaurus*).

References: Evans & Sigogneau-Russell (1997); Reynoso (1996); Reynoso (1997); Reynoso & Clark (1998).

Image: *Kallimodon* (among a very good collection of fossil photos) from Herbert Krause. Reproduced by permission.

Note: The nomenclature of sphenodont taxa tends to be rather confused. The scheme used here is adopted from the sensible system of Mikko Haaramo, who credits Wu, X-C (1994), *Late Triassic - Early Jurassic sphenodontians from China and the phylogeny of the Sphenodontia*, in Fraser, NC & H-D Sues (eds.), **In the Shadow of the Dinosaurs**, Cambridge Univ. Press. ATW001117.



Clevosaurus bairdi **in (A) dorsal and (B) left lateral view. Modified from Sues et al. (1994)**

Clevosaurs / Clevosauridae : *Brachyrhinodon, Clevosaurus*. *Clevosaurus* > *Sphenodon*?

Range: Early Jurassic to Early Cretaceous(?).

Phylogeny: Sphenodontidae **:** Stem Group Sphenodontinae + *.

Characters: 1 or more robust "incisor" teeth forming chisel edge ankylosed to premaxilla; palatine dentition; marginal dentition acrodont or absent; shearing (not crushing or piercing) bite with simple orthal (up-and-down) jaw motion; **$** long thin posterior process of premaxilla excludes maxilla from margin of nares; **$** lacrimal absent; may have dentine "lips"; **$** antorbital skull very short (<25% of total skull); triradiate postfrontal broadly contacts frontal; complete lower temporal bar formed by jugal loosely contacting slim quadratojugal; **$** dorsal process of jugal elongate; **$** large (> 25% skull length) lower temporal fenestra; gap between jugal and quadratojugal small; proximal caudal vertebrae have large transverse processes; caudal autotomy septa may be present distally; humerus strongly bent and expanded at both ends; femur gently S-shaped.

Note: For reasons I have not been able to determine, no one seems to have gotten around to giving this group a Latinized family name. ATW. Update: this has now been rectified. On the basis of new material Arantes et al 2009 formalises the family Clevosauridae, composed of *Clevosaurus*, *Brachyrhinodon* and *Polysphenodon*. MAK101016

Links: Diapsida; Clevosaurus bairdi (but server is frequently reduced or absent!); Autapomorphies of diapsid clades; Untitled Document; Lecture 12 - Early Jurassic.

References: Reynoso (1996); Reynoso & Clark (1998); Sues et al. (1994). ATW

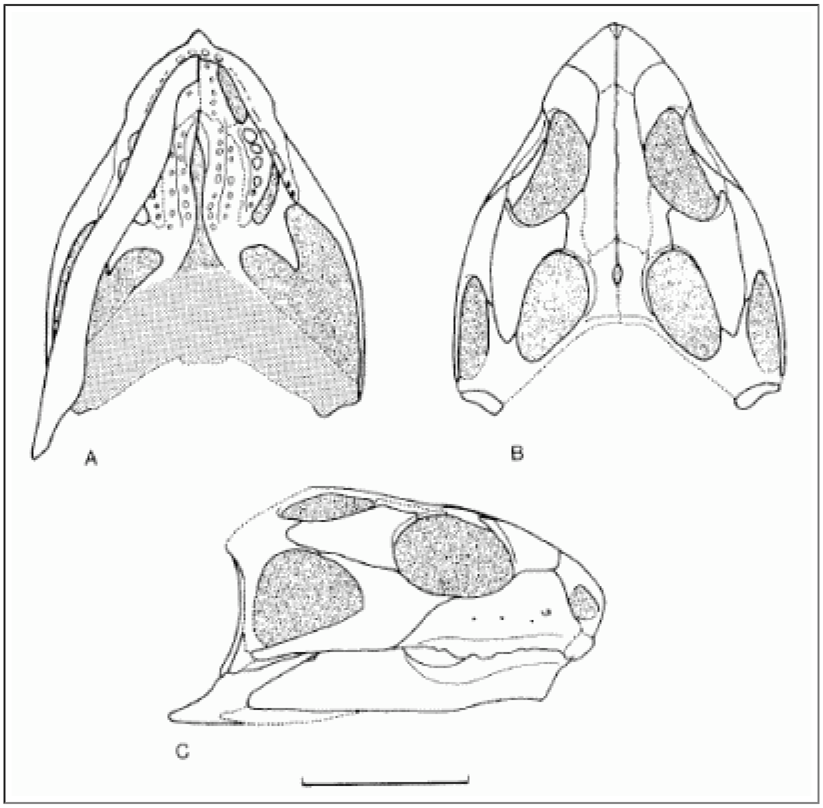
Polysphenodon:

Range: Middle Keuper (Early Norian) of Hannover, W Germany

Phylogeny: Clevosauridae **:** (*Brachyrhinodon* + *Clevosaurus*) + *.

Characters: short snout like *Brachyrhinodon*, multiple rows of teeth on the palate. It shows sphenodontian characters such as a groove between the maxilla and palatine for the dentary

Comments: Known from a partial skull and skeleton. The only known specimen went missing in the 1930s, but a number of casts and plaster moulds are available (Fraser & Benton 1989 p.416.)



Brachyrhinodon taylori, skull in ventral (A), dorsal (B) and lateral (C) view. From Fraser & Benton 1989 p.416. Scale bar 1 cm. Note palatal teeth in (A); teeth on the upper palate (roof of the mouth) are a primitive feature found in most basal amniotes

Brachyrhinodon: *Brachyrhinodon taylori*

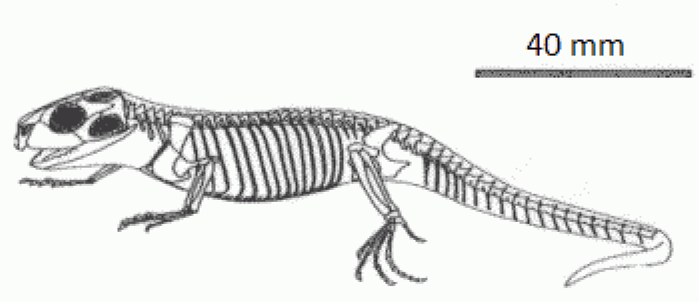
Range: Late Carnian of Elgin, Scotland;

Phylogeny: Clevosauridae : *Polysphenodon* + (*Clevosaurus* + *).

Characters: small (c. 15 cm long), short-snouted skull with premaxillary beak. Benton 1985

Comments: One of the earliest known sphenodontians

Clevosaurus:



Synonyms: *Asiacephalosaurus; Rarojugalosaurus; Dianosaurus*

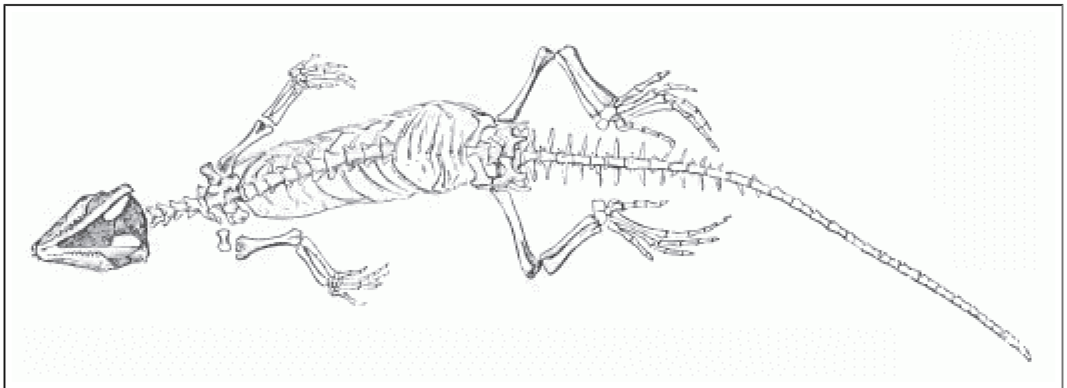
Range: Late Triassic to Early Jurassic. WEu. ENAm. EAs, S Am

Phylogeny: Clevosauridae : *Polysphenodon* + (*Brachyrhinodon* + *).

Comments: a very successful and widespread, species-rich genus

Links: Wikipedia

Graphic: From Fossil Reptiles of Great Britain



Stem Group Sphenodontinae: here used to mean *Sphenodon* > *Clevosaurus*

Range: from the Early Jurassic

Phylogeny: Sphenodontoidea : Clevosaurinae + * : *Homoeosaurus* + Pleurosauridae + (*Sapheosaurus* +

Sphenodontinae).

Kallimodon pulchellus (Zittel), 1887. Late Jurassic; Kelheim, Bavaria. Ventral aspect. From Zittel/Eastman/Woodward 1902 p.151. This represents a type similar to or intermediate between *Homoeosaurus* and *Sapheosaurus*

Characters: Vertebrae amphicoelous, sometimes with persistent notochord; intercentra present in cervical (neck) and caudal (tail) regions. External nares separated ; interclavicle T-shaped; dermal scales subrectangular. Greatiy enlarged postfrontal bone extending far posteriorly (to the rear) on parietal. Except for a few teeth on the vomer in juveniles and the palatine row, all other palatal teeth absent (i.e. teeth on the roof of the mouth, in contrast to primitive amniotes). Premaxillae each with a small pointed tooth. A single series of enlarged, depressed, triangular, acrodont teeth present on maxillae, mandibles, and outer edge of the palatines; vomer toothless. pattern of tooth wear facets, tooth ultrastructure, and anteroposterior length of the mandibular articulation, all of which indicate development of the propalinal masticatory movements (front to rear chewing) as with the Recent *Sphenodon* Zittel/Eastman/Woodward 1902, Gauthier et al 1988 p.25

Comments: replaced the Clevosaurs in the middle and late Jurassic

***Homaeosaurus*: **v. Meyer

Range: Kimmeridgian (Lithographic Stone) of Bavaria, and Cerin, France. Kimmeridgian of Hanover, and Purbeckian (Tithonian) of England.

Phylogeny: Stem Group Sphenodontinae **:** Pleurosauridae + (*Sapheosaurus* + Sphenodontinae) + *.

Characters: From Zittel/Eastman/Woodward 1902 (copyright expired): "Attaining a length of between 20 and 40 cm., and differing from the recent *Sphenodon* in that intercentra are absent between the dorsal vertebrae ribs without uncinate processes, and humerus not pierced by entepicondylar foramen. Mandibular rami united at the symphysis by ligaments ; second sacral rib bifid distally." applies also to *Sapheosaurus* and *Kallimodon* Gauthier et al 1988 p.26: Compared to sphenodontines and sapheosaurs, *Homoeosaurus* is distinguished by smaller size, gracile and elongate limbs, and a broad parietal table (skull roof above the orbits (eye holes)), all of which, with the possible exception of the limb proportions, are plesiomorphic (shared ancestral) features.

Comments: highly lizard-like forms.

Links: Wikipedia (not much text but some nice photos)

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

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

Sphenodontia: Sphenodontinae

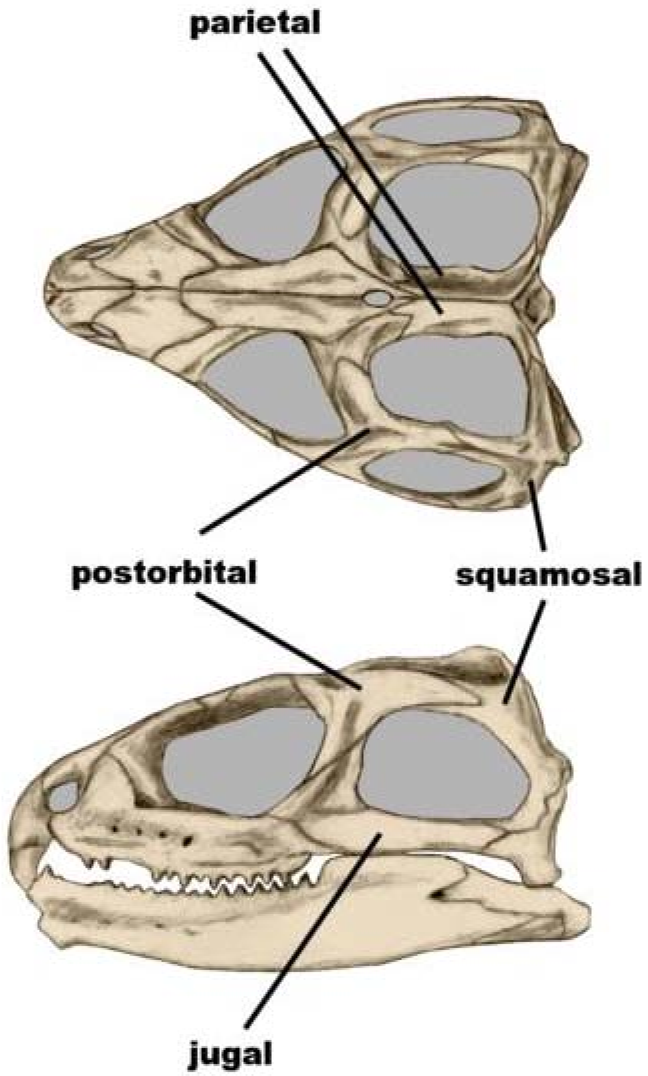
Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--Clevosaurinae
      `--Stem Group Sphenodontinae
         |--Pleurosauridae
         `--+--o Sapheosaurini
            |   |-- Kallimodon
            |   `-- Sapheosaurus
            `--o Sphenodontinae
               |--o Sphenodontini
               |  |--Cynosphenodon
               |  `--Sphenodon
               `--o Opisthodontia
                  |-- Opisthias
                  `-- Eilenodontini
```

Contents

Taxa on This Page

1. *Cynosphenodon* X
2. Eilenodontini X
3. *Kallimodon X*
4. *Opisthias X*
5. *Opisthodontia X*
6. *Sapheosaurini X*
7. *Sapheosaurus X*
8. *Sphenodon*
9. *Sphenodontinae*
10. *Sphenodontini*



Sphenodon skull, with selected bones marked, from The Lépidosauriens - Rhynchocephalia (in French)

The unspecialised, akinetic skull is little changed from ancestral forms, the main distinguishing feature being the narrower parietals (the bar along the top of the skull), enabling a lighter and more open structure

---

Descriptions

***Sapheosaurini**: Leptosaurus neptunius, Kallimodon cerinensis, Sapheosaurus thiollierei*

***Range:** Kimmeridgian of France and Germany.*

***Phylogeny:** Stem Group Sphenodontinae* **:** *Homoeosaurus* + *Pleurosauridae* + (*Sphenodontinae* + * **:** *Kallimodon* + *Sapheosaurus*)

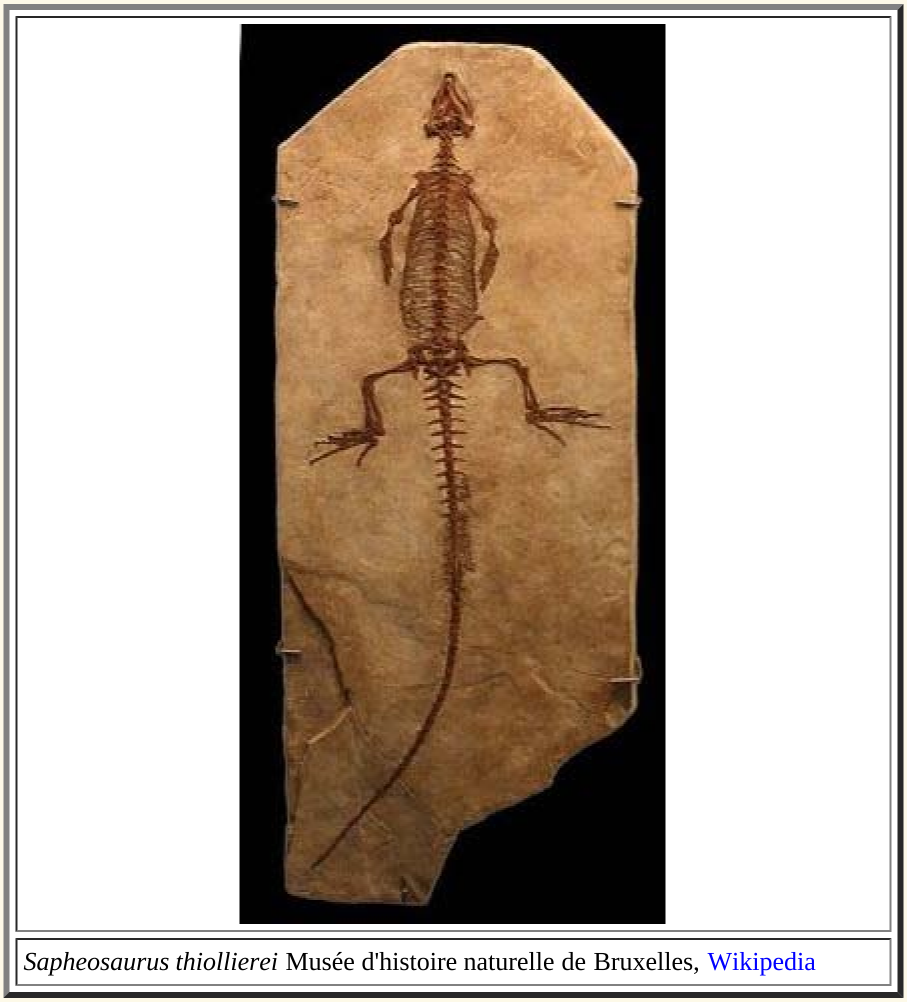
***Characters:** From Gauthier et al 1988 p.26: broad upper temporal arch, elongate upper temporal fenestra, postorbital (rear, behind the eyes) region of the skull longer than the preorbital (snout, in front of eyes) region, laterally compressed caudal (tail) vertebral centra*

Comments: *On the basis of studies of a new species of Clevosaurus, Wu, 1994's cladogram has a linear series Homaeosaurus, Kallimodon, Sapheosaurus but no Sapheosaurini. But on the basis of detailed analysis of another species of the ubiquitous Clevosaurus, Arantes et al 2009 confirmed the clade for Kallimodon + Sapheosaurus, as well as confirming Wu, 1994's monophyletic Clevosaurs.*

Kallimodon:

Range: *Kimmeridgian of France and Germany*

Phylogeny: *Sapheosaurini* **:** *Sapheosaurus* + *.



Sapheosaurus thiollierei Musée d'histoire naturelle de Bruxelles, Wikipedia

Sapheosaurus:

Synonyms: *Piocormus*

Range: *Kimmeridgian of France and Germany.*

Phylogeny: *Sapheosaurini* **:** *Kallimodon* + *.

Characters: *Similar to Homoeosaurus, but skull was longer and narrower*

Comments: *Variously included under the suborder Homoeosauria and the family Sapheosauridae From Wikipedia: Sapheosaurus laticeps differed from Sapheosaurus thiollierei by its smaller size and more vertebrae. S. thiollierei had 22 back and neck vertebrae, while S. laticeps had 26. Also, the two differ in relative limb length.*

Sphenodontinae: *Cynosphenodon, Eilenodon, Sphenodon, Zapatadon. Probably: Sphenodon > Eilenodon. However, it may be more useful (and is used here) as Sphenodon + Eilenodon + ??, or all Sphenodontians closer to Sphenodon than to Homoeosaurus, Sapheosaurus, and other similar forms.*

Range: *from the Early Jurassic. 2 (3?) living species of Sphenodon; fossorial, live in association with sea birds on islands off New Zealand.*

Phylogeny: *Stem Group Sphenodontinae* **:** *Homoeosaurus* + *Pleurosauridae* + + (*Sapheosaurus* **:** *Opisthodontia* + *Sphenodontini*.

Characters: *Sphenodon is the giant of this largely diminutive group. Generally triangular, teeth with round cross-section; teeth added from posterior of jaw;* ***$*** *caniniform teeth posterior to edentulous ridge at anterior end of dentary;* ***$*** *proplinal jaw movement, as judged from wear facets on teeth; prominent coronoid process of dentary; dentary markedly straight ventrally, with small, ventral "chin" projection under symphysial area; retroarticular process reduced; central region of pterygoid long; lower temporal fenestra small (<25% skull length); posterior process of ischium present.*

Links: *Sphenodontidae; Tuatara Printout- EnchantedLearning.com; Family: Sphenodontidae; Tuatara Skull Replica from Skulls Unlimited; Untitled Document; Untitled Document; Information about U.S. FDC: 32¢ Opisthias; Growth patterns and ontogenetic variation of the teeth and jaws of ... (Reynoso abstract on tooth development); Today, lepidosaurs are a diverse group of reptiles. With more than ... (sphenodontines remained dominant until the Cenozoic).*

References: *Reynoso (1996); Reynoso (1997); Reynoso & Clark (1998).*

Image: *Sphenodon punctatus. tuatara. ATW040220.*

Sphenodontini: *Cynosphenodon, Sphenodon*

Range: *Middle Jurassic to Recent.*

Range: *Middle Jurassic of Mexico; Recent, islands off New Zealand.*

Phylogeny: *Sphenodontinae* **:** *Opisthodontia* + * **:** *Cynosphenodon* + *Sphenodon*

Characters: *propalinal jaw action, anterior caniniform tooth on jaw and dentary (Reynoso 2000)*

Cynosphenodon:

Range: *Middle Jurassic of Mexico.*

Phylogeny: *Sphenodontini* **:** *Sphenodon* + *.

Sphenodon: *the Tuatara*

Range: *Recent, islands off New Zealand.*

Phylogeny: *Sphenodontini* **:** *Cynosphenodon* + *.

Characters: *From Zittel/Eastman/Woodward 1902 (copyright expired): "Inferior border of the large orbits formed by maxilla external nares divided ; a single tooth on either side of the premaxillary beak; intercentra present between all the vertebrae, humerus with both entepicondylar and ectepicondylar foramina or grooves."*

Links: *Wikipedia - Tuatara, and many other links*

Opisthodontia:

Range: *Late Jurassic to Cretaceous of North and South America*

Phylogeny: *Sphenodontinae* **:** *Sphenodontini* + * **:** *Eilenodontini* + *Opisthias.*

Comments: *This name has also been given to a genus of moth of the family in the family Lasiocampidae.*

Opisthias: Opisthias rarus Gilmore, 1909

Range: Late Jurassic (Late Kimmeridgian-Early Tithonian) the Morrison Formation of western North America,

Phylogeny: Opisthodontia **:** Eilenodontini + *.

Comments: known only from lower jaws, had Sphenodon-like teeth and a propalinal (front-to-back motion) jaw action (Benton 1985 p.149)

Links: The World of Dinosaurs - Stamps (see illustration at right)

Eilenodontini: Ankylosphenodon, Eilenodon, Priosphenodon, Toxolophosaurus

Range: Known from the Late Jurassic to Cretaceous of North and South America

Phylogeny: Opisthodontia **:** Opisthias + *.

Characters: propalinal jaw action, deep mandible, retroarticular process reduced, marginal teeth expanded mediolaterally (Reynoso 2000)

Comments: A diverse assemblage of Jurassic and Cretaceous forms. Eilenodon and Toxolophosaurus were deep-jawed forms with very wide grinding teeth, indicating a herbivorous diet. Priosphenodon reached a metre in length, the largest known sphenodontian. The aquatic Ankylosphenodon is included here but may have a more basal position, if so this group would be known from North America only

References: Benton 1985 p.149, Reynoso 2000, Apesteguía & Novas 2003

Page Back | Unit Home | Page Top | Page Next

checked ATW050616

Sphenodontia: Dendrogram

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--Clevosaurinae
      `--Stem Group Sphenodontinae
         |--Pleurosauridae
         `--+--Sphenodontinae
            `--+--Sphenodontini
               `--Eilenodontini
```

Contents

```
EUREPTILIA
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA VPP, DC, ToL
   |--Sauropterygia X (placodonts + plesiosaurs) DC, MH
   `--Lepidosauria
      |--Rhynchocephalia MH
      |  |-- Gephyrosaurus
      |  `--o Sphenodontia
      |     |-- Diphydontosaurus
      |     `--+-- Planocephalosaurus
      |        `--o Sphenodontidae
      |           |--o Clevosaurinae
      |           |  |--Polysphenodon
      |           |  `--+--Brachyrhinodon
      |           |     `-- Clevosaurus
      |           `--o Stem Group Sphenodontinae
      |              |--Homoeosaurus
      |              |--o Pleurosauridae
      |              |    |--Palaeopleurosaurus
      |              |    `--Pleurosaurus
      |              `--+--o Sapheosaurini
      |                 |    |--Kallimodon
      |                 |    `--Sapheosaurus
      |                 `--o Sphenodontinae
      |                    |--o Sphenodontini
      |                    |  |--Cynosphenodon
      |                    |  `--Sphenodon (tuatara)
      |                    `--o Opisthodontia
      |                       |-- Opisthias
      |                       `--o Eilenodontini
      |                          |--Ankylosphenodon
      |                          |--Toxolophosaurus
      |                          `--+--Priosphenodon
      |                             `--Eilenodon
      `--SQUAMATA
```

Rhynchocephalia: References

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SQUAMATA
`--o Rhynchocephalia
   |--Gephyrosaurus
   `--Sphenodontidae
      |--Clevosaurinae
      `--Stem Group Sphenodontinae
         |--Pleurosauridae
         `--+--Sphenodontinae
            `--+--Sphenodontini
               `--Eilenodontini
```

Contents

References

Apestegu�a, S. & Novas, F.E. 2003 Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. *Nature* 425, 609-612 (9 October 2003) abstract
Eilenodontini

Arantes, B. de A., Soares, M. B,. and Schultz, C. L., 2009, Clevosaurus brasiliensis (Lepidosauria, Sphenodontia) do Triassico superior do Rio Grande do Sul: anaaomia pos-craniana e relacoes filogeneticas: Rev. Bras. Paleontol, v. 12, n. 1, p. 43-54. pdf
Clevosauridae, Pleurosauridae

Benton M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97-164.
Eilenodontini, *Opisthias*

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp.
Overview

Evans, SE & D Sigogneau-Russell (1997), *New sphenodontians (Diapsida: Rhynchocephalis) from the Early Cretaceous of North Africa*. **J. Vert. Paleontol.** 17: 45-51.
Sphenodontidae.

Gauthier J., R. Estes, & K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. In: R. Estes and G. Pregill (ed.) *Phylogenetic relationships of the lizard families*: 15-98. Stanford: Stanford University Press. pdf
Sapheosaurini

Reynoso, V-H (1996), *A Middle Jurassic* ***Sphenodon****-like sphenodontian (Diapsida: Lepidosauria) from Huizachal*

Canyon, Tamaulipas, Mexico. **J. Vert. Paleontol.** 16: 210-221.
Clevosaurinae; Sphenodontidae; Sphenodontinae.

Reynoso, V-H (1997), *A "beaded" sphenodontian (Diapsida: Lepidosauria) from the Early Cretaceous of Central Mexico*. **J. Vert. Paleontol.** 17: 52-59.
Sphenodontidae; Sphenodontinae.

Reynoso, V.-H., 2000: An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayua Formation (Albian), Central Mexico. �Journal of Paleontology: Vol. 74, #1, pp. 133-148 abstract
Eilenodontini, Sphenodontini

Reynoso, V-H & JM Clark (1998), *A dwarf sphenodontian from the Jurassic La Boca formation of Tamaulipas, Mexico*. **J. Vert. Paleontol.** 18: 333-339.
Clevosaurinae; Sphenodontidae; Sphenodontinae.

Romer, AS (1956), **Osteology of the Reptiles.** Krieger Publ. Co. (1997 ed.): 772 pp.
Overview.

Sues, H-D, NH Shubin & PE Olsen (1994), *A new sphenodontian (Lepidosauria: Rhynchocephalia) from the McCoy Brook Formation (Lower Jurasic) of Nova Scotia, Canada*. **J. Vert. Paleontol.** 14: 327-340.
Clevosaurinae.

Wu, X-C. 1994: Late Triassic-Early Jurassic sphenodontians from China and the phylogeny of the Sphenodontia. in Fraser, N. C. & Sues, H-D. 1994: *In the Shadow of the Dinosaurs*. Cambridge University Press, New York. 1994
Sapheosaurini

Karl A. von Zittel. Translated and edited by Dr Charles R. Eastman. Vol. II. Second English edition revised, with additions, by Sir Arthur Smith Woodward. *Text-Book of Palaeontology.*. New York: MacMillian. Public domain - Internet Archive.
Stem Group Sphenodontinae, *Homaeosaurus*

vonZittel, KA (1932), **Text-book of Palaeontology** vol.II, (2nd Eng. rev. ed.), trans. & ed. by CR Eastman, rev'd with additions by AS Woodward. MacMillan and Co, Ltd, London

---

Page Back | Unit Home | Page Top | Page Next

checked ATW050616

Squamata: Overview

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
|
SQUAMATA
|--Iguania
|  |--Tropiduridae
|  |--Acrodonta
|  |  |--Priscagamidae
|  |  `--+--Agamidae
|  |     |  |--Amphibolurinae
|  |     |  `--Draconinae
|  |     `--Chamaeleonidae
|  `--Iguanidae
|
Scleroglossa
```

Contents

Introduction

The Squamata are the most successful order of Cenozoic reptiles, with some six thousands recent species (more species than there are mammals!). They are found on every continent except Antarctica, in such diverse modes of life as climbers, burrowers, crawlers, aquatic forms, and even gliding types.

Technically, the Squamata are lepidosaurs, distinguished from other related and similar forms by a flexible and powerful jaw structure. This came about through the loss of the lower temporal bar in the skull, which gave more room for the jaw muscles to develop, and the development of a special moveable hinge, the quadratojugal hinge, between the quadrate and squamosal bones in the skull. (This is termed *streptostyly*). This hinge gives greater flexibility and allows the pterygoideus (jaw) muscle to exert more force. It is clearly this dual adaptation that has been key to the success of the Squamates.

The Squamata were traditionally divided into two suborders - Lacertilia (lizards) and Ophidia (snakes). This division is rather simplistic, being based on superficial features. It is now believed that the Iguania represent a lineage separate from the others. In addition to iguanas, the Iguania include agamids, chameleons and a few lesser known groups.

The rest of the modern lizards, as well as the snakes, are classified as Scleroglossa.

Proto-lizards evolved perhaps during the Late Triassic (the earliest putative squamate is the poorly known *Tikiguana*, from the Late Carnian of India) or Early Jurassic from lepidosaur ancestors sphenodont-like ancestors. They underwent a great evolutionary radiation during the Middle and late Jurassic, and by the Early Cretaceous had replaced the sphenodonts as the dominant "lizard" ecomorph. These reptiles are often ornamented with a crest of scales along the back, as well as assorted spines, frills, and throat fans; all this gives them a remarkably prehistoric appearance. Primitive forms are small and insectivorous, but where there is less competition or predation they may develop into larger herbivores, as represented by the famous marine iguana of the Galapagos.

MAK000207, MAK990716, MAK101106.

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

checked ATW060219

Squamata

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
`--SQUAMATA
   |--Iguania
   |  |--Tropiduridae
   |  |--Acrodonta
   |  |  |--Priscagamidae
   |  |  `--+--Agamidae
   |  |     |  |--Amphibolurinae
   |  |     |  `--Draconinae
   |  |     `--Chamaeleonidae
   |  `--Iguanidae
   `--Scleroglossa
```

Contents

Taxa on This Page

1. *Huehuecuetzpalli* X
2. Squamata

Descriptions

Squamata: lizards, mosasaurs and snakes.

Range: from the Early Jurassic.

Phylogeny: Lepidosauria **:** Rhynchocephalia + * **:** *Huehuecuetzpalli* + (Scincogekkonomorpha + Iguanomorpha).

Characters: premaxillae fused [C&L]; sutured mandibular symphysis [LBC]; anterior & posterior lower jaw elements immobilized relative to each other [LBC]; **$** angular short, not reaching level of mandibular condyle [C&L]; **$** coronoid process large, formed only by coronoid bone (not surangular) [C&L]; **$** surangular bears transverse shelf [d&R]; maxilla, palatine & pterygoid sutured to other elements and are akinetic [LBC]; **$** palatines with choanal groove [C&L]; **$** transverse flanges of pterygoid point anterolaterally & are at or above level of marginal teeth [d&R]; **$** pterygoids do not meet at midline [C&L]; **$** pterygoids broadly enter suborbital fenestrae [C&L]; nasals reduced; **$** anteroventral border of orbit formed by jugal rather than maxilla (frequent reversals) [C&L]; **$** posterior process of jugal absent [C&L]; **$** frontal-parietal suture simple & transverse [d&R][C&L]; flexible frontal-parietal articulation (mesokinetic joint) allows some raising of snout [LBC]; frontals and/or parietals [**$** per C&L] may be fused at midline; **$** parietal table short, with posterior exposure of braincase [C&L]; metakinetic hinge between parietals and occiput [LBC]; **$** loss of lower temporal bar [d&R]; **$** loss of quadratojugal [d&R][C&L]; **$** flexible hinge at articulation of quadrate and squamosal (streptostyly: rotation of quadrate around squamosal allows pterogoideus muscle to exert maximum force near closure) [d&R] [LBC]; quadrate embayed to support stapes for hearing; squamosal reduced; **$** squamosal rod-like, without ventral process [C&L], & squamosal does not wrap around posterior of skull [d&R]; **$** stapes slender [C&L]; **$** proatlas absent [C&L]; vertebral centra amphicoelous in basal forms, derived forms are often procoelous (**$** of [C&L]); **$** >7 cervical vertebrae [C&L]; **$** intercentra absent [C&L]; **$** gastralia absent [C&L]; primitively, scapulocoracoid sometimes fenestrated, **$** thyroid fenestration of pelvis [C&L]; ends of humerus not twisted >20 deg. relative to each other; primitively, proximal tarsals not fused; strong tendency to reduction or loss of limbs; determinate growth (related to insectivory?).

Note: Remarkably little overlap between synapomorphies of C&L and d&R. Note how many of the C&L synapomorphies are either absences of a feature or quantitative differences (*e.g.* parietal short). These are not *necessarily* a bad thing, but do raise questions about homology. Recall that the issue is whether these are derived features inherited from a common ancestor. This is less likely to be true of absences and quantitative differences.

Image: *Lacerta vivipara* © Bioimages (UK), used by permission.

Links: Rattlesnake... from Skulls Unlimited; The Boa Constrictor Subspecies; Literature - Squamata; SQUAMATA; EMBL; Wild Herps; Order Squamata; Discover Canada's Aquatic Reptiles - Snakes and Lizards: Order Squamata; Squamata Verlag (English & German); Palaeoscincosaurus middletoni; Encyclopedia.com - Results for snake; temp; Squamata (ToL); Squamata (Mikko's Phylogeny); SQUAMATA; Squamata (Snakes & Lizards).

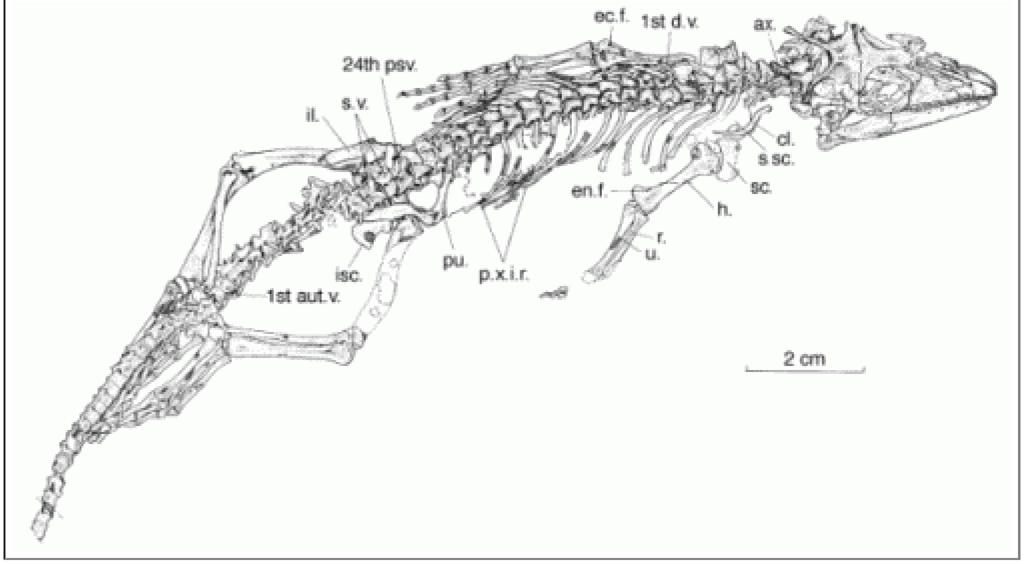
References: Caldwell & Lee (1997) [C&L]; deBraga & Rieppel (1997) [d&R]; Lee *et al*. (1999) [LBC]. ATW040220.

***Huehuecuetzpalli*:** *Huehuecuetzpalli mixtecus* Reynoso, 1998

Range: Middle Cretaceous (Albian) of Mexico

Phylogeny: Squamata :(Scincogekkonomorpha + Iguanomorpha) + *

Characters: elongation of the snout and the apparent retraction



Skeleton of holotype of *Huehuecuetzpalli mixtecus*. Image © 1998 The Royal Society. Most of the long tail is missing from this specimen

of the external nares

Comments: Includes some Iguanian characters, but also a large number of basal qualities which imply it belongs outside the crown squamatan group (Reynoso 1998, Evans 2003). Considered basal-stem Iguanian in the cladogram in Evans & Wang 2010. In view of Iguanians being strongly characterised by primitive features, and the tentative nature of the phylogeny in Evans & Wang 2010, I've followed Reynoso 1998 and Wiens et al 2010 in interpreting *Huehuecuetzpalli* as a stem squamate. The existrence of such a basal taxa so late in the Mesozoic made this long-snouted and long-tailed lizard a "living fossil" of its time. MAK101106

Page Back Unit Home Page Top Page Next

checked ATW050806

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

Squamata: Iguania

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
`--SQUAMATA
   |--Iguanomorpha
   |   |--Hoyalacerta
   |   `--Iguania
   |      |--Tropiduridae
   |      |--Acrodonta
   |      |  |--Priscagamidae
   |      |  `--+--Agamidae
   |      |     |  |--Amphibolurinae
   |      |     |  `--Draconinae
   |      |     `--Chamaeleonidae
   |      `--Iguanidae
   `--Scleroglossa
```

Contents

Taxa on This Page

1. *Hoyalacerta* X
2. Iguania
3. Iguanidae
4. Iguanomorpha
5. Tropiduridae

Descriptions

Iguanomorpha

Definition: All taxa sharing a more recent common ancestor with *Iguana iguana* than with *Gekko gecko*, *Scincus*

scincus, or *Varanus varius*. Conrad, 2008 p.73

Range:from the Early Cretaceous.

Phylogeny: Squamata :*Huehuecuetzpalli* + (Scincogekkonomorpha + * **:** *Hoyalacerta* + Iguania).

Note: Sukhanov (1961) coined the terms Iguanomorpha and Scincogekkonomorpha to refer to the two fundamental groups of iguana-like lizards and all other squamates. These terms were then adopted in a cladistic context by Conrad, 2008, who lists two unambiguous synapomorphies and whose definition is followed here. The interpretation of some other previously defined basal Iguanians is less clear. *Euposaurus*, previously considered a basal iguanian, is now known to be a chimera of an undetermined squamate and a sphenodontian. The Gondwnan taxa *Tikiguania* (late Triassic) and *Bharatagama* (Early Jurassic) are poorly known forms that may be basal Iguanomorphs, basal Squamata, or even for that matter basal Lepidosaurs. However *Arretosaurus*, another basal form, seems to be chamaeleontiform (Conrad, 2008 p.91) and hence is nested in the Acrodonta. MAK101106

Hoyalacerta: *Hoyalacerta sanzi* Evans & Barbadillo, 1999

Range: Early Cretaceous (Barremian) of Las Hoyas assemblage, Spain

Phylogeny: Iguanomorpha :Iguania + *

Comments: A very basal form, despite its relatively late occurance, placed on the squamate stem by Evans 2003 but relocated to the Iguanian stem by Conrad, 2008 and Evans & Wang 2010 MAK101106

Iguania: Iguanas, chameleons, and their relatives

Range: from the Late Cretaceous.

Phylogeny: Iguanomorpha :*Hoyalacerta* + * **:** Tropiduridae + Acrodonta + Iguanidae.

Characters: Skull tall; temporal arch is present; fleshy tongue; teeth pleurodont or acrodont; **$** frontals fused; **$**parietal foramen on frontal - parietal suture; eyelids well developed; pupils round; most have dorsal crest and extensible dewlap; often ornamented with crests, spines, frills, and throat fans; six cervical vertebrae; usually robust bodies, short necks, distinct heads; breaking-point septa present in caudals and some forms have rather fragile tails; overlapping non-iridescent scales; four or more transverse belly scales per body segment; frequently brightly colored. Smaller, insectivorous forms primitive, but larger herbivores where less competition, including marine forms. Largely ambush predators; diurnal; either arboreal, terrestrial or semi-marine.

Links: Higher Reptile Taxa (EMBL database); Iguania; herplab9.pdf; herplab3.pdf; Eric Pianka's Ctenotus Research; home2; Iguanidae; Foraging and Trophic Ecology; Iguania (**Best on the Web**).

The ToL page still has only a vague polyotomy for a cladogram, and a list of references a decade old. As for the cladogram, perhaps that's all there is. Mikko's Phylogeny has the same, but Mikko includes some more recent references. ADW has some really excellent material on the individual families, but nothing worth visiting at this level. The EMBL site is its usual authoritative and encyclopedic self, but is really designed for use at the genus level and below. Even the Swiss-Prot folks have shown only limited interest in the gene sequences of this taxon. Fortunately, true afficionados of lizard phylogeny on the web may consult Frost *et al*. (2001). This is one of the combined morphological - molecular studies the AMNH has pioneered in recent years. Other articles of interest include Delheusy & Bels (1999) on iguanid feeding kinematics. The only pages we located with a list of shared characters are brief lists on a VMNH page, a lab manual from the University of Texas and Anthony Herrel's site at the University of Antwerp. However, we have saved the best for last: Vitt & Pianka (2005) combine squamate ecological and phylogenetic data to create a really convincing *explanation* of the phylogeny based on diversification of feeding strategies. ATW

Tropiduridae: *Leiocephalus*, *Liolemus*, *Microlophus*, *Stenocercus*, *Tropidurus* (= *Plica?*)

Phylogeny: Iguania :Acrodonta + Iguanidae + *.

Range: South America, Indonesia.

Characters: small- to moderate-sized; distinct head and neck; $angular reduced; splenial extended posteriorly; teeth *pleurodont*; tails typically at least as long as body; body scales usually coarse ("spiny"); sternum with posterior extension with enlarged, median *fontanelle*; limbs & digits well developed; some have tail spines, dorsal crests or similar ornamentation; color typically cryptic; most insectivores or omnivores; diurnal; males may exhibit territorial and sexual displays involving stereotypic head and body movements.

Links: Amphibians and Reptiles checklist - Project Amazonas field sites in the Peruvian Amazon; Tropiduridae (**Best on the Web**); A SEMI-ANNOTATED BIBLIOGRAPHY AND TAXONOMY OF THE; ADW: Tropiduridae: Information.

Image:*Tropidurus itambere*. Photo by Prof. Guarino R Colli. ATW040220.

Iguanidae:

Phylogeny: Iguania: Tropiuridae + Acrodonta + *.

Range: Maastrichtian to Recent of North and South America, Madagascar, and some Pacific islands.

Characters: tongues short & barely protrusible; pleurodont dentition; tail usually longer than body; well-developed limbs; fourth toe nearly twice as long as fifth; most have long tails, crest, and dewlaps; head covered with larger scales or plates; belly scales small, in several rows, or not obviously in longitudinal series; belly scales pointed or rounded, but not quadrangular; males are bright and varied in coloring; desert & forest dwellers mainly herbivores, while smaller iguanidae insectivores or omnivores.

Comments: small to large lizards, terrestrial or semi-aquatic herbivores, long-legged, swift running, some have scaly crest along the back. Teeth on the inner side of the jaws.

Links: Family Iguanidae; Iguanidae; Iguanidae; Die Iguanidae-Webseite; Iguanas; Iguanidae.html.

Note: Probably polyphyletic group with numerous families. ATW060219

Page Back Unit Home Page Top Page Next

checked ATW050806

Squamata: Acrodonta

Priscagamids, Amphibolurines, Draconines, & Chameleons

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
`--SQUAMATA
   |--Iguania
   |  |--Tropiduridae
   |  |--Acrodonta
   |  |  |--Priscagamidae
   |  |  `--+--Agamidae
   |  |     |  |--Amphibolurinae
   |  |     |  `--Draconinae
   |  |     `--Chamaeleonidae
   |  `--Iguanidae
   `--Scleroglossa
```

Contents

Taxa on This Page

1. Acrodonta
2. Agamidae
3. Amphibolurinae
4. Chamaeleonidae
5. Draconinae
6. Priscagamidae X

In another context, we looked at the molecular phylogenetics work of J. Robert Macey and his coworkers. Cuculiformes. Dr. Macey recently (1999) completed his Ph.D. at Washington University in St. Louis, Missouri where he studied with Profs. Allan Larson and Jonathan Losos. Since we are presently on the subject of lizard phylogenies, this seemed an auspicious time to look in a bit more detail at what Macey has been doing.

In the prior discussion, we discussed Macey's work tracing phylogeny through changes in gene order in mitochondrial DNA. Macey *et al* (2000). Here, we examine the companion paper, in which Macey and a large group of coworkers developed trees based more conventional DNA sequencing work. Macey *et al* (2000a). This paper turns out the way molecular phylogenetics ought to turn out, but seldom does. The results give us a very clear picture -- not only of the phylogeny, but of the biogeography of these lizards. In truth, one suspects Macey's methods stack the deck a little, but only a little, because geography is explicitly considered in the development of the tree structure. However the correspondence of geography to genetics seems to have been statistically tested with some rigor. Surely this is no worse than the usual cladistic methods which combine genetic and morphometric information; and, in fact, the use of geographical information is just another sort of grist for the cladistic mill.

The resulting cladogram (simplified to the generic level) is as follows.

```
ACRODONTA
|--Chamaeleonidae (Chamaeleo)
`--+--Uromastycinae (Uromastyx)
   `--+--Leiolepidinae (Leiolepis)
      `--+--Amphibolurinae
         |  |--Physignathus cocinius
         |  `--+--Lophognathus
         |     `--+--+--Physignathus lesuerii
         |        |  `--+--+--Arua
         |        |     |  `--Chelosania
         |        |     `--+--Hypsilurus
         |        |        `--Moloch
         |        `--+--+--Amphibolurus
         |           |  `--Chlamydosaurus
         |           `--+--+--Ctenophorus
         |              |  `--Rankinia
         |              `--+--+--Caimanops
         |                 |  `--Diporiphora
         |                 `--+--Pogona
         |                    `--Tympanocryptis
         `--+--Hydrosaurinae (Hydrosaurus)
            `--+--Draconinae
               |  |--+--+--Draco
               |  |  |  `--Japalura tricarinata
               |  |  `--*--Otocryptis
               |  |     `--Sitana
               |  `--+--Calotes
               |     `--+--+--Salea
               |        |  `--+--+--Ceratophora
               |        |     |  `--+--Cophotis
               |        |     |     `--Lyriocephalus
               |        |     `--+--+--Aphaniotis
               |        |        |  `--Gonocephalus
               |        |        `--Bronchocela
               |        `--+--Acanthosaura
               |           `--+--Japalura flaviceps & splendida
               |              `--Pseudocalotes
               `--Agaminae
                  |--Agama
                  `--+--+--Pseudotrapelus
                     |  `--Trapelus
                     `--Laudakia (including Phrynocephalus)
```

What Macey's work suggests is that each of the various taxa of agamid lizards crossed the Tethys on different continental plates, like so many groups of immigrants arriving on crowded steamers. Each of the seven major acrodont groups can be identified with a particular fragment, or, at worst, series of fragments of the Gondwanan plate which drifted across the Tethys Sea to contact Laurasia (now Eurasia) over the last 120 My or so.

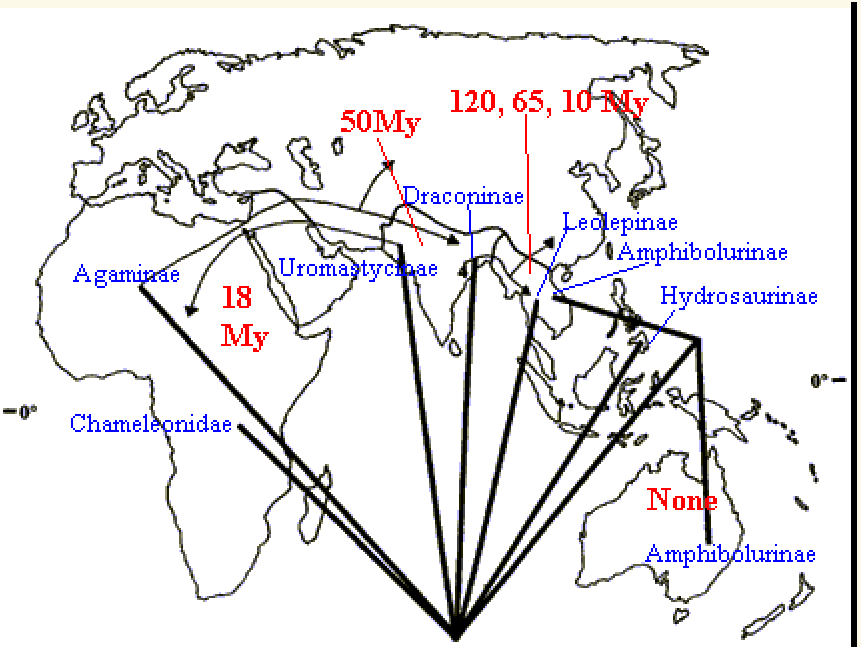


Fig. 1. Taxonomic distribution of Agamidae, indicating dates of accretion of various Gondwanan blocks onto Laurasia. Modified from Macey et al. (2000a).

Unfortunately, when we compare the cladogram to Figure 1, it is immediately clear that there are problems. For example, the Chamaeleonidae and Agaminae are, respectively, the first and last branches from the acrodont stem. Yet they appear together on the same continental block. One very basal species of the amphibolurine (*Physignathus cocinius)*, which presumably developed in Australia, is found in Southeast Asia. These are not insurmountable concerns, but they do suggest that the picture may not be quite as straightforward as it first appears. It would be very interesting, for example, to look at the evolution of the chameleons in a bit more detail.

Despite minor rough spots like this, the paper is a rich and elegant piece of work, and only the broad conclusions are summarized here. However, it does leave us with a real difficulty. Here is, undoubtedly, a piece of mtDNA phylogeny that worked. Why *didn't* it work for birds? See Mindell et al. (1997)**.** Macey and coworkers seem to have taken a much more cautious approach to aligning the mitochondrial tRNA gene sequences which make up a large portion of the mtDNA segment used for the study. Ultimately, Macey discarded much of the tDNA sequence as "phylogenetically uninformative," primarily because it was too variable to be useful. This may, according to the views of the reader, be considered either a good use of judgment or hopelessly biased data selection.

For what it may be worth, I am inclined to the former opinion for reasons I have explained in the other essay. Proteins and tRNAs do not function as linear information. They function because of their tertiary and quaternary structure. This means that the DNA sequences coding for these structures are inter-related in ways we absolutely cannot predict from primary sequence data alone. The best we can do is to use judgment to find portions of these genes that seem to behave *as if* they were independent variables over the time spans of interest. The process is, even at its best, no more objective than cladistic analysis from morphological characters. That does not mean that it is worthless. It simply means that, like a lot of science, absolute and mechanical objectivity is an asymptote we must always approach without quite reaching. The greatest danger is not failing to reach it, but in believing that we already have.

Descriptions

Acrodonta:

Range: Africa, SE Asia, India, Indonesia, Australia

Phylogeny: Iguania **:** Tropiduridae + Iguanidae + * **:** Priscagamidae + (Agamidae + Chamaeleonidae).

Characters: $ acrodont dentition (teeth fused to top of jaw margin).

Links: Acrodonta; Herpetology: Lizards; Abstracts 49(2); Replication Slippage May Cause Parallel Evolution in the ...; Testing the Hypothesis That a Clade Has Adaptively Radiated ..; ADW- Agamidae- Information; Evaluating

Trans-Tethys Migration- An Example Using Acrodont ... (Macey paper discussed above); Evolution and Phylogenetic Information Content of Mitochondrial ... (another great paper by Macey). ATW040220.

Priscagamidae: *Mimeosaurus, Pleurodontagama, Priscagama*.

Range: Late Cretaceous.

Phylogeny: Acrodonta ::(Agamidae + Chamaeleonidae) + *.

Agamidae: Small to large "Old World Iguanas."

Range: Late Cretaceous (Campanian) to recent.

Phylogeny: Acrodonta ::Chamaeleonidae + * **:** Amphibolurinae + Draconinae.

Characters: Acrodont, heterodont marginal teeth; Many with dentary fangs; dentary canal for Meckelian cartilage open; adductor fossa small to moderate; palatine & pterygoid teeth absent; nasals paired; nasals contact prefrontals; frontals fused; borders of frontals constricted between orbits; broad frontal shelf below nasals; postfrontal & postorbital present as separate elements; eyelids well developed; pineal foramen present; maxilla extends back between orbits; jugal large & post-orbital bar complete; jugal-squamosal contact on supratemporal arch; supratemporal fenestra widely open; supratemporal bone present; parietals fused; opisthotic fused with exoccipital; >6 cervical vertebrae; <26 presacral vertebrae; zygosphenes & zygantra absent; moderately long tail; well-developed limbs; 5th toe absent or reduced; often conspicuously scaly; visually oriented lizards with frill, horns, bright colors common (most frequently in males); largely insectivores, but some herbivorous; generally oviparous; autotomy rare, but convergently developed in some groups as *inter*vertebral break; autotomy septa never present; diurnal; terrestrial or arboreal.

Comments: A large and diverse family of 2 subfamilies, 52 extant genera with more than 400 species; these are small to medium-sized, terrestrial lizards, mostly insectivores, differ from the Iguanids in that their teeth are on the rims of the jaws.

Image: *Chlamydosaurus kingii* from the Virtual Museum of Natural History, reproduced by permission.

Links: The signal to noise ratio for websites on this taxon is particularly low. Agamidae (EMBL); Jon Loman - herp photos; Dragons of Townsville; Family: Agamidae; Agamidae; Reptilia, Squamata, Agamidae - Agamen; BEARDED DRAGON - POGONA - FROM AN AUSTRALIAN PERSPECTIVE.; LIZARDS of JAPAN; Agamidae; Agamidae.html; Agamidae Familyasi; Gli Agamidi, Agamidae (Italian); familia Agamidae; Agamidae (Dragon Lizards).

References: Caldwell (1999); Macey *et al*. (2000a). ATW021207.

Amphibolurinae: *Physignathus, Moloch,* Australian agamids.

Phylogeny: Agamidae :Draconinae + *.

References: Macey et al. (2000a).

Links: The Reptiles of Australia, Agamid page; Moloch; Chinese Water Dragons (Physignathus Cocincinus); Digimorph - Physignathus cocincinus (Chinese water dragon); Physignathus Leseurii. ATW031026.

Draconinae: *Calotes*, *Draco*, *Japalura*, *Sitana*, South Asian & Sri Lankan agamids.

Range: from the Late Jurassic?

Phylogeny: Agamidae :Amphibolurinae + *.

Characters: "horns" (not always present, but only in draconines)

Image: *Calotes versicolor* from the Virtual Museum of Natural History reproduced by permission.

Notes: There is enormous variation in the members of this group, which seem more closely related by geography than by any easily determined physical characteristics. Most are long-bodied insectivores with varied spines and color display characters. The links above are only a very small sample of the resources available on the species in the taxon. ATW020720.

Links: What's It Like Where You Live?; Species: Japalura; Lizards of Japan; Species: Sitana; Bloodsucker Lizard; Agamidae; Laboratory of Animal Systematics (Japanese); CMV, Brainatlas of Calotes versicolor; changeable lizard (calotes versicolor): info fact sheet, photos; Rostral Horn Evolution among Agamid Lizards of the Genus ... (phylogeny of horns).

References: Macey et al. (2000a). ATW040707.

Chamaeleonidae: chameleons! *Brookesia*, *Chamaeleo*, *Furcifer*

Range: from the Paleocene (Thanetian). Presently in Africa and Madagascar, with a few species in the Middle East, Asia, and Southern Europe.

Phylogeny: Acrodonta :Agamidae + *.

Characters: 2.5 - 50+ cm; Protrusible tongue; acrodont teeth, independently moveable, raised eyes; body laterally compressed; prehensile tail; digits modified for grasping (2-3 digits modified to form grasping pads); color change; often elaborately ornamented with horns, etc.; insectivorous.

Comments: about 130 extant species, about half of which are from Madagascar. Most are small insectivores, 15–25 cm long; but the smallest, the tiny *Brookesia minima*, is only about 3 cm long and one of the world's smallest reptiles, whereas the largest, *Furcifer oustaleti* (image, right), can reach over 60 cm and is known to eat small birds and other lizards. & Arboreal, tails and feet adapted for climbing, eyes able to move independently, skull may have horns or crests. Tongue half as long as animal (used to catch insects)

Links: Familia Chamaeleonidae; Marikan herppisivut (Finnish); CiN - Chameleon information NETWORK; Family: Chamaeleonidae; chameleon; The Chameleon Journals; Chameleons; JEB -- Summaries: Meyers and Nishikawa 203 (18): 2833; Chamaeleonidae.html; I Camaleonidi, Chamaleonidae (Italian); The Reptipage: Chameleons; chameleon. The Columbia Encyclopedia, Sixth Edition. 2001 Wikipedia.

Image: *Furcifer oustaleti* from Herp Pictures - Lizards (former site). ATW011112, modified MAK101106.

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

checked ATW060219

Squamata: Scincogekkonomorpha

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
`--Scincogekkonomorpha
    |-- Bavarisaurus
    |-- Ardeosaurus
    `--+-- Eichstaettisaurus
       `--+-- Scandensia
           |-- Liushusaurus
           `--Scleroglossa
               |--Gekkota
               `==Scincomorpha
                      `--+--Anguimorpha
                         `--Pythonomorpha
```

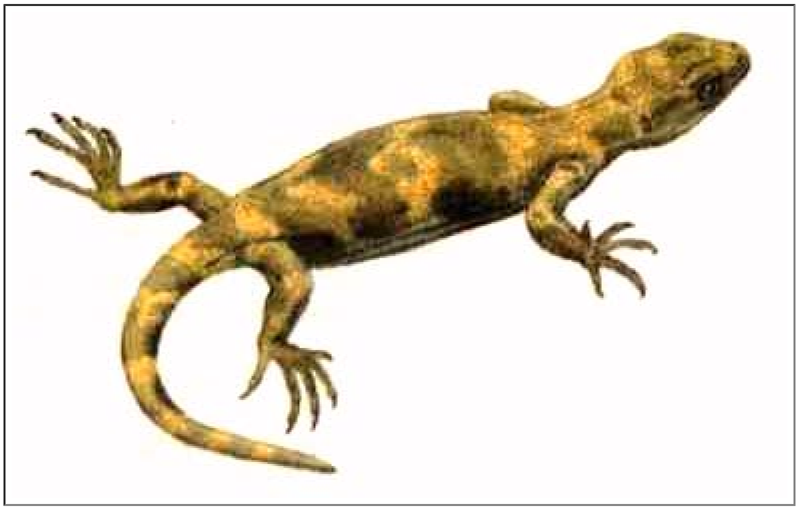
Contents

Introduction

Taxa on This Page

1. *Ardeosaurus* X
2. *Bavarisaurus* X
3. *Eichstaettisaurus* X
4. *Liushusaurus* X
5. *Scandensia* X
6. Scincogekkonomorpha

Scincogekkonomorpha



The basal Scincogekkonomorph *Ardeosaurus*, Kimmeridgian of Europe. Although superficially gekko-like in appearance, this small lizard actually occupies a much more basal position in the squamatan evolutionary tree. Artwork from *The Marshall Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*

During the period from the Late Jurassic to the Middle Createcous, a number of persistently primitive lizards continued to flourish alongside more advanced squamatan clades such as scincomorphs and anguimorpha. Many of these small lepidosaurs were previously classified among the gekkos, which are the most primitive and unspecilaised of the Scleroglossa, but are now known to belong on the stem of the Scincogekkonomorpha, the larger clade that includes not only extant Scleroglossans but also Mesozoic stem forms. Judging from their diversity and frequence of occurance, these basal Scincogekkonomorpha clearly played an important role in the microvertebrate ecology as terrestrial insectovores, there small size meaning that they often ended up in the stomachs of larger micro- and mesovertebrates, such as sphenodontians, small coelurosaurs, and doubtless pterosaurs and early mammals as well. MAK101106

Descriptions

Scincogekkonomorpha Scleroglossa > Iguania

Range: fr midJ.

Definition: All taxa sharing a more recent common ancestor with *Gekko gecko* and *Scincus scincus* than with *Iguana iguana* Conrad, 2008 p.92

Phylogeny: Squamata :*Huehuecuetzpalli* + Iguanomorpha + * **:** *Bavarisaurus* + (*Eichstaettisaurus* + *Ardeosaurus* + (*Scandensia* + *Liushusaurus* + Scleroglossa)).

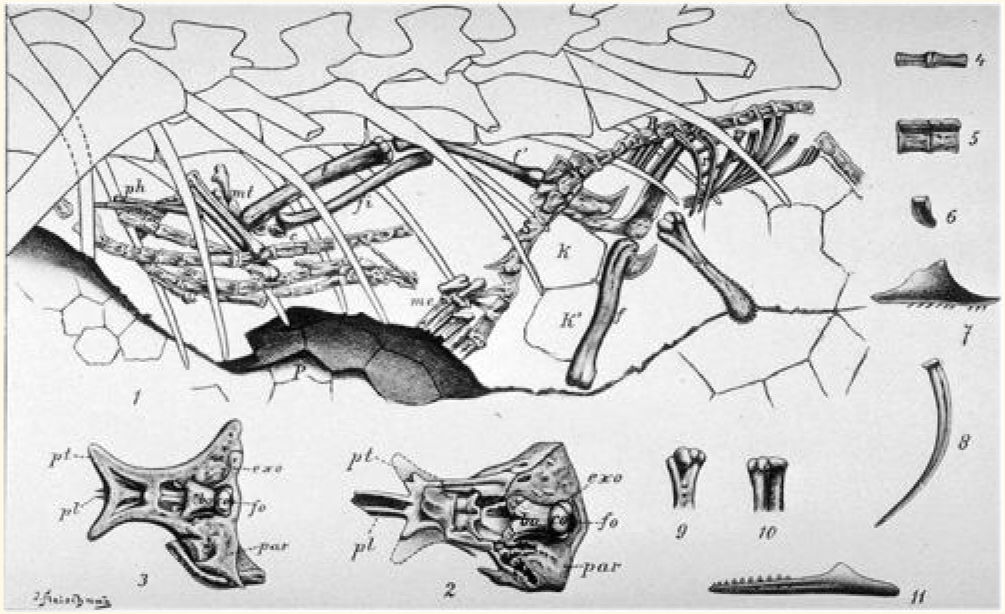
Comments: Clade defined by Conrad, 2008 on the basis of a number of characters, and utilised by Evans & Wang 2010 for stem Scleroglossa forms. the Basal taxa include species previously considered stem-geckos (e.g. *Bavarisaurus, Eichstaettisaurus*) or scincomorphs or geckos (*Ardeosaurus*) Conrad, 2008 p.93 MAK101106

***Bavarisaurus*:** *macrodactylus* *Homoesaurus*	*Bavarisaurus* (originally *macrodactylus*

Wagner, 1852),

Range: Late Jur of Europe (Solnhofen limestone of Bavaria, early Tithonian)

Phylogeny: Scincogekkonomorpha :(*Eichstaettisaurus* + *Ardeosaurus* + (*Scandensia* + *Liushusaurus* + Scleroglossa)) + *.



Comments: The only known specimen (right) reveals that these animals were among the prey of small coelurosaurs. Like Ardeosaurus and Eichstaettisaurus, Bavarisaurus was at first classified as a gekkotan, in this case on the basis of its amphicoelous vertebrae, but subsequent analyses have shown it to be a more basal form (Evans et al 2004). This reptile was about 20 cm in length

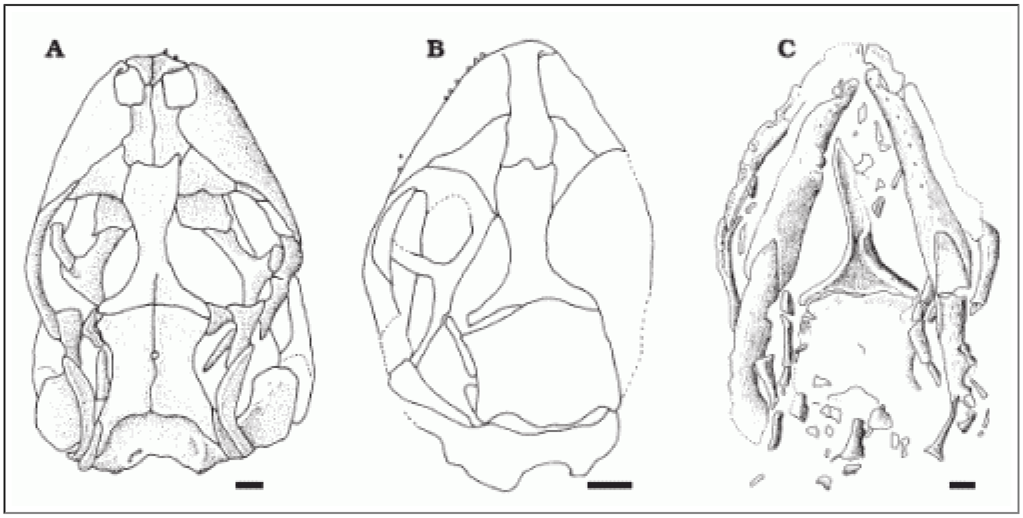
Link: *Archaeopteryx* and *Bavarisaurus* - Dinosaur art, Michael Skrepnick

Graphic: 1903 illustration by Franz Nopcsa showing *Bavarisaurus* in the stomach region of *Compsognathus*, public domain, from Wikipedia. MAK101106

***Eichstaettisaurus*:** *Eichstaettisaurus schroederi* (Broili, 1938) (type species); *Eichstaettisaurus gouldi*

Range: Late Jur (Tithonian) to Mid Cret (Albian) of Europe

Phylogeny: Scincogekkonomorpha :*Bavarisaurus* + (*Ardeosaurus* + (*Scandensia* + *Liushusaurus* + Scleroglossa) + *).



Comparison of the skulls of three species of the scincogekkonomorph *Eichstaettisaurus*, showing the persistance of this type over an extended period of Mesozoic Europe. A. *Eichstaettisaurus schroederi*, Solnhofen, Germany (Early Tithonian, late Jurassic). B. *Eichstaettisaurus* sp. (specimen too fragmentary to describe further), Montsec, Catalonia, Spain (Berriasian, earliest Cretaceous). C. *Eichstaettisaurus gouldi* Evans, Raia, and Barbera 2004, Pietraroia, Italy (Albian). A, B, dorsal (top down) views, C, ventral view. Scale bars 1 mm. Graphic © from Evans et al 2004 p.403

Comments: This long lived genus is known not only from the Tithonian of Germany and Berriasian of Spain but also the Albian of Pietraroia in Southern Italy, the three occurances represnted by distinct species. The skeleton is gracile, with limbs relatively short in relation to the presacral axial skeleton; implying this was predominantly a ground-dwelling reptile. Its presence at Pietraroia, in association with late surviving Laurasian rhynchocephalians indiccates that this was an archaic island refugium of relict Jurassic forms. The presence of a skull of Eichstaettisaurus within the stomach cavity of a Rhynchocephalian shows that these small animals sometimes fell prey to their larger lepidosaurian cousins. (Evans et al 2004). MAK101106

Link: *Scipionyx* and *Eichstaettisaurus* - artwork, Davide Bonadonna

***Ardeosaurus*:**

Range: Late Jur of Europe

Phylogeny: Scincogekkonomorpha :*Bavarisaurus* + (*Eichstaettisaurus* + (*Scandensia* + *Liushusaurus* + Scleroglossa)) + *).

Comments: Although this small, gecko-like lizard seems to be safely included among the Scincogekkonomorpha, a more precise placement is not clear. Like the related *Eichstaettisaurus*, it represents an example of basal scincogekkonomorphs possessing some of the characteristics attributed to the Gekkota, an example of mosaic evolution (where primitive and advanced character states occur together. *Ardeosaurus* may be more basal Conrad, 2008 or more derived (Evans & Wang 2010) than *Eichstaettisaurus*. MAK101106

Link: Getty images

***Scandensia*:** *Scandensia ciervensis* Evans & Barbadillo 1998

Range: Early Cretaceous (Barremian) of Las Hoyas, Spain

Phylogeny: Scincogekkonomorpha :*Bavarisaurus* + (*Eichstaettisaurus* + (*Liushusaurus* + Scleroglossa + *)).

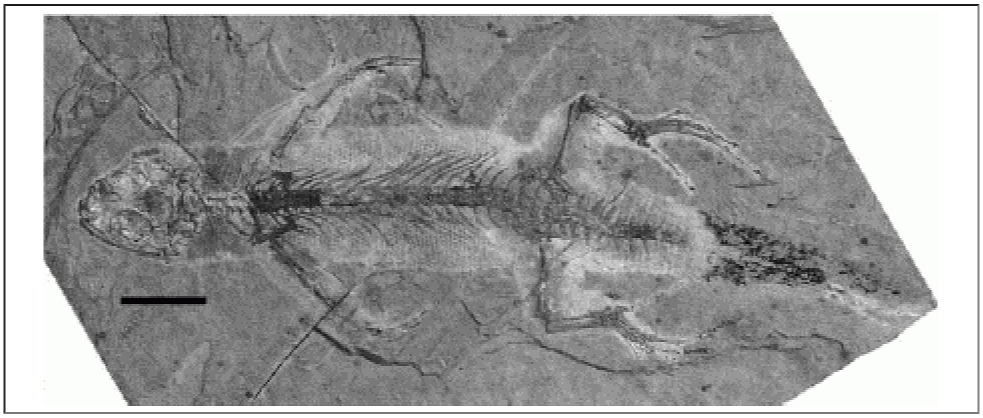
Comments: Not to be confused with Scandentia (Tree Shrews), this is another basal squamate species superficially similar to gekkos, but actually much more primitive. This specialised climbing form, one of a number of primitive squamatans recovere dfrom the Las Hoyas assemblage in Spain, has been variously interpreted as being a sister taxon to living squamates Evans & Barbadillo 1998, a stem Scincogekkonomorphan (Evans & Wang 2010), or a basal Scleroglossan Conrad, 2008. It may represent a basal Scincogekkonomorpha evolving towards, or just at the very base of, the Scleroglossan crown group. According to Conrad, 2008 p.93, *Eichstaettisaurus schroederi* + *Scandensia ciervensis* + Scleroglossa form a clade that is united by a number of synapomorphies not found in the more basal genera *Ardeosaurus* and *Bavarisaurus*. MAK101107

***Liushusaurus*:** *Liushusaurus acanthocaudata* Evans & Wang 2010

Range: Early/Middle Cretaceous of China

Phylogeny: Scincogekkonomorpha : *Bavarisaurus* + (*Eichstaettisaurus* + (*Scandensia* + Scleroglossa + *)).

Comments: Known from a number of specimens of different growth stages, some with preservation of soft tissue impressions including scales, pigmentation, and claw sheaths. The combination of characters shows that *Liushusaurus* cannot be placed in any crawn groyup taxa, and instead represents a stem Scincogekkonomorphan close to the Scleroglossa. MAK101107



Beautifully preserved specimen of *Liushusaurus acanthocaudata*, from the Jehol biota of theYixian Formation, Liaoning, Early/Middle Cretaceous, showing outline of the body, skin, and scales. Scale bar 1 cm. Photo © 2010 The Natural History Museum, from Evans & Wang 2010 p.89

Page Back Unit Home Page Top Page Next

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

Squamata: Scleroglossa

Abbreviated Dendrogram

```
SQUAMATA
|
Scleroglossa
|--+--Dibamidae
|  |--Gekkota
|  `--Evansauria
|     |--Bainguidae
|     `--Autarchoglossa
|        |--+--Scincomorpha
|        |   `--Amphisbaena
|        `--+--Anguimorpha
|           |   |--Anguoidea
|           |   `--Varanoidea
|           |      |--Monstersauria
|           |      `--+--Necrosauridae
|           |         `--+--Varanidae
|           |            `--Lanthanotidae
|           `--Pythonomorpha
`--Iguania
```

Contents

Introduction

"Scleroglossa" means "hard tongue," which surely has some significance, although its a bit hard to see. Many of the members of this group have split tongues. However, the reference is probably to the notched, inelastic distal part of the tongue in **anguimorphs**. Since **skinks**, **gekkos** and **amphisbaenids** don't share this characteristic, the name is somewhat inappropriate. Since few of us think in Classical Greek, little harm is done.

The Sceroglossa includes three kinds of relatively common lizards (skinks, gekkos and **varanoids**), as well as the legless lizards (amphisbaenids), the mosasaurs and all of the snakes. The latter two groups will be treated in a later section. The relationships of all of these groups are not very well understood, but it is relatively clear that all are related to each other more closely than any of them are to the iguanas and their kin. For example, Michael (MSY) Lee, a well-known paleontologist, has written several papers placing the pythonomorphs (snakes and mosasaurs) among the varanoids. In this he is strongly opposed by Olivier Rieppel and co-workers. Rieppel and Lee have been head-to-head on a number of other issues, including the phylogeny of pareiasaurs, the ancestry of turtles, and the marine (Lee) or terrestrial (Rieppel) origin of snakes. Their various, often heated, disputes are chronicled in a number of places on this site. We have cautiously chosen a sort of middle ground in this particular dispute, based on the work of Michael Caldwell.

Taxa on This Page

1. Autarchoglossa
2. Bainguidae X
3. Evansauria
4. Dibamidae
5. Gekkota
6. Scleroglossa

Descriptions

Scleroglossa

Range: fr midJ.

Phylogeny: Squamata :Iguania + Scincogekkonomorpha :::* **:** Gekkota + Dibamidae + Evansauria.

Comments: A well defined clade with at least 27 synapomorphies; the most important adaptations being prey capture through jaw prehension (holding in the mouth), the tongue then becomes a well-developed chemosensory system. The name *(scleros*, tough, hard; *glossa*, tongue) refers to the flattening and keratinization of at the rear of the tongue. Estes et al 1988's division of Squamata into Iguania and their new clade Scleroglossa revolutionised squamatian phylogenetics and systematics and established the morphological paradigm still used today. However molecular phylogeny consistently fails to recover these two clades (Hedges & Vidal 2009). For now we have retained the morphological arrangement.

Dibamidae: blind lizards

Range: Recent of East Asia (eastern Indochina), East Indies and Mexico

Phylogeny: Scleroglossa :Autarchoglossa + Gekkota + *.

Comments: Small to moderate-sized, burrowers, reduced limbs. Highly specialised, so beyond a scleroglossan placement morphology does not provide much information as regards relationships, in molecular phylogeny they tend to come out at the base of the squamate tree, and so are tentatively placed here. 2 genera with 11 species are known. No fossil record. MAK101106

Gekkota:

Range: from the Late Jurassic.

Phylogeny: Scleroglossa :Evansauria + Dibamidae + *

Characters: Usually small (<15 cm); upper temporal arch, postorbital arch, lachrymal, squamosal, and postorbital all absent; jugal bone

small or absent; frontals fused and surround the forebrain; pleurodont in marginal teeth; palatal teeth absent; eyelids present; tongue uncleft or slightly cleft; usually four or more transverse rows of belly scales per body segment; amphicoelous vertebrae; facial artery ant. to stapes; unique karyotype; eyes adapted to low light. Typically moving hunters.

Links: Global Gecko Association (lots of good stuff); Herpbreeder.dk (references); Gekkota (also a good, basic site); Gekkota (Mikko's Phylogeny); ADW- Gekkota- Classification (ADW -- not much here yet except photos); Gekkonidae; Herpetology- Lizards. ATW040205.

Evansauria

Definition: All taxa sharing a more recent common ancestor with *Lacerta viridis* and *Varanus varius* than with *Gekko gecko* or *Iguana iguana*.

Range: fr midJ.

Phylogeny: Scleroglossa :Gekkota + Dibamidae + * **:** Autarchoglossa + Bainguidae.

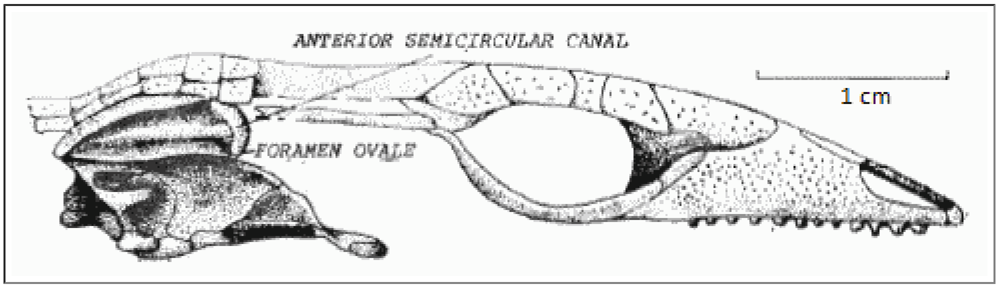
Comments: Named in honor of Professor Susan E. Evans, who has made many important contributions to our understanding of lepidosauromorph and squamatan evolution, this clade was recovered by Conrad, 2008 and is defined by a number of synapomorphies. It constitutes the stem-based taxon for the node-based Autarchoglossa. MAK101107

Bainguidae**:** *Bainguis*, *Eoxanta*, *Myrmecodaptria*

Range: Late Kr of Mongolia

Phylogeny: Evansauria :Autarchoglossa + *.

Comments: Originally erected as a monospecific family for *Bainguis parvus*, considered to have both scincomorph and anguimorph (Borsuk-Bialynicka 1984), and later synonymized with Anguidae. The cladistic analysis by Conrad, 2008 groups with *B. parvus* with the non-anguimorph fossil taxa *Myrmecodaptria* and *Eoxanta*, and placed the Bainguidae basal to the Autarchoglossa. It is possible that this is a grade of primitive stem-Autarchoglossans rather than a clade . Results grouping bainguids with lacertoids may be the result of convergences between this clade and primitive Scincomorpha or Lacertiformes. MAK101107



Skulls of the small anguimorph-like basal autarchoglossan *Bainguis parvus*, from the Late Cretaceous (Late Santonian/Early Campanian) Djadochta Formation of Mongolia. Some of the armoured scales are visible preserved at the back of skull. Graphic © from Borsuk-Bialynicka 1984 p.20

Autarchoglossa (= Unidentata)

Range: fr midJ.

Phylogeny: Evansauria :Bainguidae + * **:** Scincomorpha + Xantusiidae + (Lacertiformes + (Anguimorpha + Pythonomorpha)).

Characters: Loss of jugal-squamosal contact on supratemporal arch, M. rectas abdominis lateralis present (Estes et al 1988), single egg tooth (for hatching) (Vidal & Hedges 2005)

Comments: This taxon was originally defined by Camp 1923 and is retained in cladistic systems although diagnosed by only a few characters Estes et al 1988 pp.206-7). As defined here it is used to refer to all "higher" squamates, including Scincomorpha, Anguimorpha, Amphisbaenia, and Serpentes (snakes). Inasmuch as most molecular studies give the Gekkota and Dibamidae a basal position, they have an equivalent clade (although in the molecular phylogeny this also includes the Iguania), called Unidentata because of the presence of a single egg tooth (Vidal & Hedges 2005). Because some most molecular phylogenies recover a paraphyletic Scincomorpha (in which are nested further groups like Amphisbaenia, Iguania, Anguimorpha, and Serpentes (Hedges & Vidal 2009)) this makes Autarchoglossa synonymous the latter, cladistically speaking (assuming the phylogeny is correct). In contrast to Gekkota, who as mostly ambush foragers rely morey on olfactory and visual prey discrimination, and retain a relatively low metabolic rate, the Unidentata/Autarchoglossa are more active foragers, with a higher metabolic rate, and rely primarily on vomeronasal and visual prey discrimination (Vidal & Hedges 2005). MAK101105

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

Squamata: Scleroglossa: Scincomorpha

Abbreviated Dendrogram

```
SQUAMATA
|
Scleroglossa
|--+--Gekkota
|  |--Dibamidae
|  `--Autarchoglossa/Scincomorpha (paraphyletic
according to molecular phylogeny)
|     |--+--Paramacellodidae
|     |  `--+--Scincidae
|     |     `--Cordyloidea
|     |--Xantusiidae
|     `--+--Lacertiformes
|         |  |--+--Teiioidea
|         |  |  |--Teiidae
|         |  |  `--Gymnophthalmidae
|         |  `--Boreoteiioidea
|         |     |--Polyglyphanodontinae
|         |     `--Gilmoreteiidae
|         `--+--+--Lacertidae
|            |   `--Amphisbaena  (according to
molecular phylogeny)
|            `--+--Anguimorpha
|                |   |--Anguoidea
|                |   `--Varanoidea
|                |--Iguania (according to molecular
phylogeny)
|                `--Pythonomorpha
`--Iguania (according to gross morphology)
```

Contents

Taxa on This Page

1. *Adamisaurus* X
2. Amphisbaena
3. Boreoteiioidea X
4. Cordyloidea
5. Gilmoreteiidae (= Macrocephalosaurinae) X
6. Gymnophthalmidae
7. Lacertidae
8. Lacertiformes
9. Paramacellodidae X
10. Polyglyphanodontinae X
11. Scincidae
12. Scincoidea

Scincomorpha

Bronze Mabuya or Bronze Grass Skink - *Eutropis macularia* (family Scincidae)Andhra Pradesh, India. photo J.M.Garg, Wikipedia

The Scincomorphs are similar to and in morphological studies considered the sister group to the Anguimorphs (Estes et al 1988), but in molecular phylogeny they become a paraphyletic grade, or alternatively a number of smaller clades (Hedges & Vidal 2009). This latter arrangement is followed here, and Scincomorpha *sensu lato* are divided into Scincoidea/Scincomorpha and Lacertiformes, while a third group, Xantusiidae , could go with either. In both Scincomorphs (traditional morphological definition) and Anguimorphs there is a tendency for the body to become elongated and the limbd to be reduced (it is easy also to see how this can lead to the evolution of snakes). Many also have devoped armoured scales (osteoscutes) that cover the head and trunk (Carroll 1988 p.617). Both groups appear during the middle to late Jurassic, and become particularily diverse and successful during the late Cretaceous. During the early or mid Cretaceous the Lacertiformes gave rise the to a very successive and diverse clade of highly specialised forms: the herbivorous terrestrial Boreoteiioids, and from a basal Anguimorph origin there developed the Pythonomorpha. This latter group includes both the giant marine carnivorous mosasaurs and the highly successful snakes. If some molecular phylogenies are to believed, than the Iguanians share a common origin with anguimorphs and snakes, making up the Toxicofera clade (all sharing unique venom glands). As appealing as this hypothesis is, it is hard to believe that specialised ancestors could undergo so many morphological reversals to become such generalised and primitive descendents (see discussion on Iguania and Scleroglossa), and it is perhaps more likely that venom glands evolved twice. Even so, like all hypotheses, this one should not be rejected out of hand.

Scincomorphs, Lacertiformes, and Anguimorphs each have a rich is somewhat patchy fossil record. Scincomorphs *sensu lato* dominate most Laurasian lizard assemblages in the Mesozoic, but there is insufficient data to determine their pattern in Gondwana. Most early taxa are based on fragmentary remains, usually jaws, and cannot be further classified with certainty. Many Jurassic records belong to the early and very successful group Paramacellodidae, and extant scincomorph (Scincoidea and Lacertiformes) groups are not known with certainty until the late Cretaceous.

(Evans 2003 pp.525-6). MAK101106

Descriptions

Scincomorpha: skinks and their relatives.

Definition: All taxa sharing a more recent common ancestor with *Scincus scincus* than with *Gekko gecko, Anguis fragilis*, or *Varanus varius*. Conrad, 2008 p.98

Range: from the Middle Jurassic.

Phylogeny: Autarchoglossa :Lacertiformes (morphology)/Episquamata (molocules) + Xantusiidae + * **:** Paramacellodidae + Scincoidea

Characters: Pleurodont; dorsal temporal arch is usually present; parietals fused; tongue simple; heads not clearly demarcated from body; six cervical vertebrae; slim bodies; fewer than four rows of transverse belly scales per body segment. Common: limb reduction and elongation, osteoscutes on head & trunk, upper fenestra filled in, simple, kinetic frontal-parietal articulation, pineal opening on suture.

Comments: Estes et al 1988 definition (morphologically, and also as sister group of Anguimorpha) is paraphyletic according to molecular phylogeny (Vidal & Hedges 2005, Hedges & Vidal 2009), and hence equivalent to basal Autarchoglossa. In this case the above characters also apply to basal Episquamata. To avoid paraphyly, Hedges & Vidal 2009 use a more restricted definition of Cordylidae + Scincidae. Conrad, 2008's phylocode style definition and use of anchor taxa gives a broader stem based definition. If a morphological definition is preferred over a molecular one, than the Lacertoidea/Lacertiformes and Cordyloidea, and possibly also the Amphisbaena, are included under a monophyletic Scincomorpha. Conrad, 2008 pp.98-9

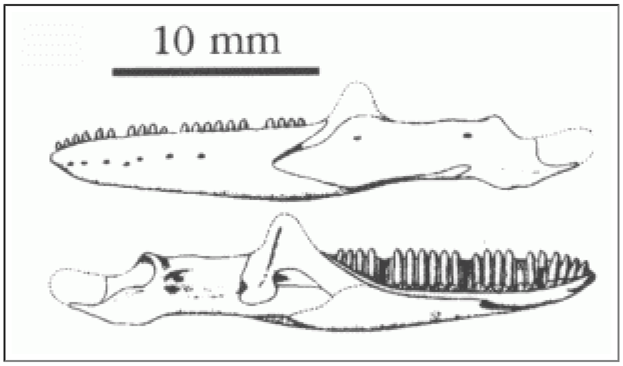
Links: Scincomorpha; BuchstabeS (German); The EMBL Reptile Database. ATW021203, amended MAK101106.

Paramacellodidae: .

Range: Middle Jurassic (Late Bathonian) to Early Cretaceous of Europe, North America, Tanzania, China and Japan

Phylogeny: Scincomorpha :Paramacellodidae + Scincoidea

Comments: A predominately Laurasian group of small to medium-sized scincomorphs with a covering of rectangular bony plates (osteoderms), similar to those of some living cordyliforms, with which they have been associated. (Evans 2003 pp.525-6) and which they doubtless resembled in life. The peg-like teeth of the tiny *Paramacellodus* (right) suggest an insectoivorous diet (Benton 2000 p.239) MAK101103



Paramacellodus oweni Hoffstetter, 1967, left lower jaw in lateral and medial views. From Fossil Reptiles of Great Britain from Estes 1983

Scincoidea

Range: Middle Jurassic to Recent, Cosmopolitan

Phylogeny: Scincomorpha :Paramacellodidae + * **:** Cordyloidea + Scincidae

Comments: Estes et al 1988 defined this as node-based taxon as "the most recent common ancestor of Scincidae and

Cordylidae and all of its descendants" and list 16 synapomorphies, making this a well-defined clade. The Mesozoic stem-group Paramacellodidae has often been associated with the Cordylidae, and may also belong in this clade, but for now is considered separately.

Cordyloidea: Cordylidae and Gerrhosauridae .

Range: Eocene of Europe, Miocene to Recent of Africa

Phylogeny: Scincoidea :Scincidae + *

Comments: medium sized lizards that inhabit arid and semi-arid regions in Madagascar and eastern Africa. They have flattened heads and bodies, and are distinguished by a heavy armour of osteoderms and large, rectangular, scales, arranged in regular rows or spines around the body and tail. Among some general there is a tendency to reduced or loss of limbs. Two families are distinguished: Cordylidae, (Spinytail lizards or Girdle-tailed lizards) and Gerrhosauridae (plated lizards, photo), although Carroll 1988 p.617 synonymises the two. Hedges & Vidal 2009 suggest the superfamily Cordyloidea.

Links (and image): Wikipedia Wikipedia

Scincidae: Skinks.

Range: Late Cretaceous to Recent, Cosmopolitan

Phylogeny: Scincoidea :Cordyloidea + *

Comments: The second largest of the lizard families (after the geckos) with about 1200 species. The legs tend to be small, reduced, or in a few cases even absent (e.g., *Typhlosaurus*. The form of movement may also be snake-like.

Links: Wikipedia

Eastern Blue-tongued Lizard (*Tiliqua scincoides scincoides*), Eastern Australia, photo by Benjamint444, Creative Commons, Wikipedia Wikipedia

---

Xantusiidae: Night lizards.

Range: Middle Paleocene to Recent of North and Central America

Phylogeny: Autarchoglossa :Lacertiformes (morphology)/Episquamata (molocules) + Scincomorpha + *

Comments: An small enigmatic group of very small (about 4 cm to 12 cm), viviparous (live-bearing), omnivorous lizards. There are only three genera and about 23 extant species.. Depsite their common name, they are not nocturnal. Their phylogenetic position is uncertain. Conventionally they are included in the Scincomorpha (morphological definition) (e. g. Camp, 1923; Romer, 1956; Estes, 1983, Carroll 1988 p.617)), but other studies suggest gekkotan affinities, and Lee 1998 united them with gekkos, dibamids, and amphisbaenians in a new clade, Nyctisauria, as the sister group of other scleroglossans. Estes, 1983 placed them as the sister group to the scincids and cordylids, but in a revised study Estes et al 1988 found they share a greater number of derived characters with the Lacertiformes. Using molecular phylogeny Hedges & Vidal 2009 return the Xantusiids to the scincid-cordylid clade, which they call Scinciformata. In view of all this confusion, i've placed the Xantusiidae between the Scincoidea and Lacertiformes, recognising they could belong to either group, although if the findings of molecular phylogeny are correct and the Scincomorpha in the traditional definition are paraphyletic it probably doesn't matter that much . MAK101104

Links: Wikipedia

Episquamata

Range: Middle Jurassic to Recent, Cosmopolitan

Phylogeny: Autarchoglossa :Scincomorpha + Xantusiidae + * **:** Lacertiformes + Toxicofera

Comments: A clade that appears in molecular phylogeny, further develops Unidentatan vomeronasal prey discrimination, have deeply bifurcated tongues, the most developed Jacobson's organs and the highest metabolic rates among the squamata (Vidal & Hedges 2005). Implies a paraphyletic Scincomorpha, in that the Lacertiformes are included in the traditional Scincomorpha, whereas the Toxicofera is a new clade that groups Anguimorpha, snakes, and, most controversially and perhaps dubiously the Iguania, in a single higher taxon. However not all molecular phylogenies support this classification (Albertetal2009).

Lacertiformes (Laterata).

Definition: The most recent common ancestor of lacertids, teiids, and gymnophthalmids and all of its descendants. (Estes et al 1988)

Range: Late Cretaceous to Recent, Europe, Africa, Asia, North & South America

Phylogeny: Scincomorpha **:** Scincoidea + (Xantusiidae + * **:** Teiioiformes + Lacertidae) (following morphological arrangement of Estes et al 1988) *or*
Episquamata :Toxicofera + * **:** Teiioiformes + (Lacertidae + Amphisbaena) (following molocular phylogeny of Hedges & Vidal 2009)

Characters: Step or offset in tooth margin of maxilla and 14 other synapomorphies (Estes et al 1988) , lateral tile-like ventral (belly) scales (Vidal & Hedges 2005). See also Scincomorpha

Comments: Recognition of the relationship between lacertids and teiids (including gymnophthalmids) was accepted by Camp 1923 and many succesive authors. The clade appears to be one of the most stable within squamates (Estes et al 1988). An equivalent clade, Laterata, is identified by molecular phylogeny of Hedges & Vidal 2005 & Hedges & Vidal 2009, who however include the amphisbaenians. If the latter are included then they have lost typical Lacertiform characteristics, which is not unlikely given their specialised lifestyle. I have followed this convention here but retained the older name. As defined here, and as an attempot at synthesis of the morphological and molecular approaches and their contradictory phylogenies, the Lacertiformes are the sister group of the Anguimorpha + Pythonomorpha MAK101105

The western whiptail, *Aspidoscelis tigris* of the southwestern United States, a representative of the family Teiidae. Photo by Tigerhawkvok, Wikipedia. Although contemporary Teiioids are only about a quarter or so as diverse in terms of species as skinks, and less geographically wide-ranging, this was not the case in the past, when during the late Cretaceous the Boreoteiioids constituted an important and diverse clade of herbivours and omnivorous lizards with an efficient feeding apparatus.

"Teiioiformes" (new name): Teiioidea of Estes et al 1988 plus associated Cretaceous forms.

Definition: The most recent common ancestor of teiids, gymnophthalmids, and boreoteiioids, and all of its descendants.

Range: Late Cretaceous to Recent, Europe, Africa, Asia, North & South America

Characters: Retain (or reversal of loss of) the dorsal process of the squamosal, a primotive feature found otherwise only in the Iguanians and more basal lepidosaurs (Carroll 1988 p.231).. In other respects however they are more specialised (Estes et al 1988)

Phylogeny: Lacertiformes :(Lacertidae + Amphisbaena) + * **:** Boreoteiioidea + Teiioidea

Comments: Common and diverse in the Late Cretaceous of Central Asia and North America. Today known only from Central and South America (Carroll 1988). Supported by a number of synapomorphies, previously referred to simply under a single family, Teiidae (Estes et al 1988 pp.213-5). So far there does not seem to be a name for the clade uniting Boreoteiioidea and Teiioidea, hence the new (informal) name "Teiioiformes" is offered here. In many ways, these are the most primitive of the scincomorphs in that the skull closely resembles that of the iguanids (Carroll 1988 p.231), MAK101104

Teiioidea

Range: Late Cretaceous to Recent, Europe, Africa, Asia, North & South America

Phylogeny: Teiioiformes :Boreoteiioidea + * **:** Gymnophthalmidae + Teiidae

Comments: The close relationship of teiids and gymnophthalmids is long recognised and they have often been included in a single family. Teiidae (Estes et al 1988)..

Teiidae: Whiptails.

Range: Late Cretaceous to Recent, Asia (Cretaceous only), North, Central, & South America

Phylogeny: Teiioidea :Gymnophthalmidae + *

Characters: large rectangular scales that form distinct transverse rows ventrally and generally small dorsal granular scales, head scales that are separate from the skull bones, teeth are solidly set in the jaw, forked, snake-like tongue, well-developed limbs.

Comments: 230 extant species in ten genera; 75% of the species are included under *Aspidoscelis* and *Cnemidophorus*. This family includes both parthenogenic (periods of female-only "virgin birth" reproduction, hatching from unfertilised eggs) (e.g. *Cnemidophorus* and *Aspidoscelis*), and non-parthenogenic (e.g. *Tupinambis*, right) genera.

Image, references and Links: Wikipedia

Gymnophthalmidae: Spectacled lizards.

Range: No fossil record, known from the recent of Central and South America

Phylogeny: Teiioidea :Teiidae + *

Comments: generally small; tendency to reduce limbs. Unusually it is generally the hind limbs that are reduced or absent, rather than the front

Links and image: Wikipedia

Image: photo by Esteban Alzate, creative commons, Wikipedia

Polyglyphanodon sternbergi, a Polyglyphanodontine lizard from the Maastrichtian of North America (), Carnegie Museum of Natural History. Photo by Daderot, Wikipedia

Boreoteiioidea: Laurasian herbivorous scincomorphs.

Definition: The most recent common ancestor of the clade containing *Chamops* Marsh, 1892 and *Prototeius* Denton and O'Neil, 1995 and the clade containing *Polyglyphanodon*, *Dicothodon*, and *Penetieus*, and all of its descendents. (Nydam et al 2007)

Range: Late Cretaceous of Asia, Europe and North America

Phylogeny: Teiioiformes :Teiioidea + * **:** *Adamisaurus* + (Gilmoreteiidae + Polyglyphanodontinae+ Tuberocephalosaurs)

The tuberocephalosaur *Aprisaurus bidentatus*, an advanced Boreoteiioid from the late Cretaceous of Mongolia, from Lizards in the era of dinosaurs, photo © VR Alifanov 2007

Characters: United by several synapomorphies, see Nydam et al 2007 for details. Polyglyphanodontidae of Conrad, 2008 p.103 is equiavlent, and supported by a number of synapomorphies.

Comments: The largest known radiation of herbivorous lizards, but also the only Late Cretaceous terrestrial lizard clade that did not survive the K-T extinction (Mo et al. 2009). The Teiioidea and Borioteiioidea seem to have diverged from a common ancestor by the Early Cretaceous, the Teiioidea entered South America (Gondwana) where they are currently represented by the Teiidae and Gymnophthalmidae, whereas Borioteiioidea may have had an East Asian origin and radiated throughout North America with subsequent dispersal to Asia and Europe; hence the etymology: *boreas*, north; in reference to the distribution of the included taxa (Nydam et al 2007). This asseblage includes up to four separate families; Adamisauridae, Gilmoreteiidae (=

Macrocephalosauridae), Mongolochamopidae, and Polyglyphanodontidae, although some of these taxa may not stand up to cladistic analysis, amnd a number of other, mostly unnamed, clades can be constructed (Conrad, 2008 pp.102-104).

***Adamisaurus*:** *Adamisaurus magnidentatus* Sulimski, 1972

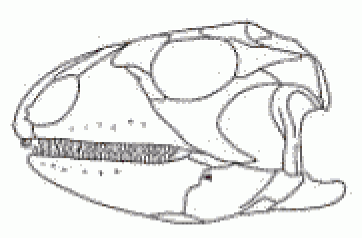
Range: Late Cretaceous of Mongolia (Djadokhta and Lower Nemegt)

Phylogeny: Boreoteiioidea :(Gilmoreteiidae + Polyglyphanodontinae + Tuberocephalosaurs) + *

Comments: a basal Boreoteiioid, with a short skull about 25 cm long, and teeth greatly increasing in size towards the rear of the jaws (Sulimski, 1972). The shape of the teeth are similar to those of some skinks and gekkos, but the structure of the lower jaw is more agamid (see link given below). Originally trentatively considered an Agamid, now known to be a Boreoteiioid (Mo et al. 2009)

Link: Nice photo here, Lizards in the era of dinosaurs, by VR Alifanov, 2007; an informative page about squamates of the Cretaceous of Mongolia (in Russian but translates reasonably well using Google translate)

Graphic: From Mo et al. 2009 from Estes 1983



Polyglyphanodontinae: *Polyglyphanodon*, *Peneteius*, *Dicothodon*.

Range: Latest Cretaceous of Europe and North America

Phylogeny: Boreoteiioidea :*Adamisaurus* + (Gilmoreteiidae + Tuberocephalosaurs + *)

Characters: teeth with transversely-oriented crests

Comments: large-bodied scincomorphan lizards with herbivorous dentition. These may have been stout-bodied forms not unlike a heavyset skink, at least according to the reconstruction in Dixon 2008, see photo of skeleton). In animals such as *Polyglyphanodon*, as with other Boreoteiioids, the skull is strong and deep-sided, with broad cheek teeth that show that this animal fed on tough vegetation (Benton 2000 pp.239-40). The teeth are efficient chewing mechanisms, transversely-oriented (i.e. at right angles to the front and rear of the animal) , becoming larger in the back of the mouth, and interlock neatly with each other, and crowned with tiny, asymmetrical serrations. In contrast to the also herbivous *Iguana*, simply crops vegetation with scissors-like teeth at the front of the mouth, *Polyglyphanodon* could have sliced food with its entire tooth row, cutting food into smaller pieces and hence improving digestion, in contrast to most reptiles which simply swallow bites of food whole, although strangely the teeth do not show signs of wear, so it seems that food processing was minimal (Nydam and Cifelli, 2005). A related (Nydam et al 2007) but smaller form, *Peneteius aquilonius* had mammal-like multicuspid teeth, which indicated an insectivorous lifestyle (Nydam et al., 2000). (Thanks to Emile of The World we don't live in blog for the research, see link below for more)

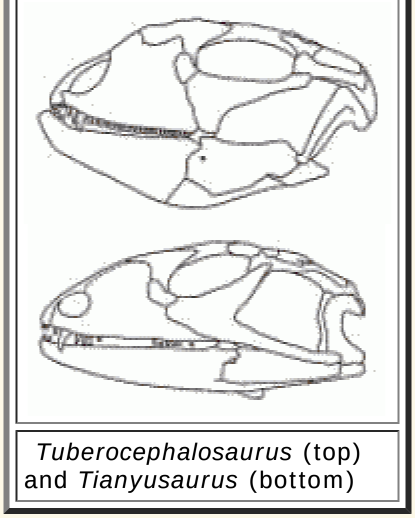
Link: Of polyglyphanodonts and their teeth

Graphic: From Mo et al. 2009 from Estes 1983

MAK101104

Tuberocephalosaurs: *Aprisaurus*, *Tianyusaurus*, *Tuberocephalosaurus*

Range: Late Cretaceous of Central and East Asia

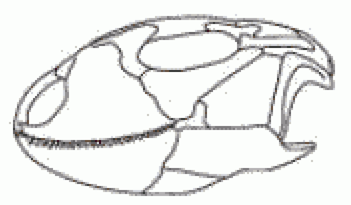


Tuberocephalosaurus (top) and *Tianyusaurus* (bottom)

Phylogeny: Boreoteiioidea :*Adamisaurus* + (Gilmoreteiidae + Polyglyphanodontinae + *)

Comments: This unnamed clade includes both more typical forms such as the Mongolian *Tuberocephalosaurus* and abbarent types like the extraordinary *Tianyusaurus* of China. The latter, while sharings many traits with other large Asian boreoteiioids, has a shallower skull and lower jaw, with, unique among squamates, a complete lower temporal bar, resulting from an extensive quadrate–pterygoid overlap. This results in a situation like that of crocodiles and *Sphenodon*, with a more robust bite and akinetic skull. Extant herbivorous lizards (and no doubt boreoteiioids) stabilize their quadrates during powerful static biting by means of a combination of temporal ligaments and muscle action. Although a complete lower temporal bar provides a better mechanical solution, this does not explain why the skull of *Tianyusaurus* is so distinct from that of its relatives (Mo et al. 2009 p.5).

Graphics: From Mo et al. 2009, *Tuberocephalosaurus* redrawn from Alifanov, V. R. 2000



Gilmoreteiidae: (= Macrocephalosauridae).

Range: Late Cretaceous of East Asia

Phylogeny: Boreoteiioidea :*Adamisaurus* + (Polyglyphanodontinae + Tuberocephalosaurs + *)

Comments: Unfortunately the exotic name *Macrocephalosaurus* (and hence "Macrocephalosauridae") is preoccupied (it was previously applied to a species of rhynchosaur) the group of Gobi lizards, and has to be replaced with the rather blander Gilmoreteiidae and *Gilmoreteius* (Langer, 1998)

Links: Gilmoreteius - basic text and good photos

Lacertidae: wall lizards.

Range: Eocene to Recent of Europe, Africa, and Asia

Phylogeny: Lacertiformes :Teiioiformes + (Amphisbaena + *) (Hedges & Vidal 2009)

Comments: small to medium-sized lizards, usually insectivorous, slender bodies and long tails, highly varied colours. Scales on the head large, often becoming osteoderms, small and granular on the back, and rectangular on the underside. Most species are sexually dimorphic, but a few are parthenogenic. Sometimes called "true lizards" (presumably as opposed to skinks, gekkos, monitors, etc) MAK101104

Links (and image): Wikipedia

Amphisbaena:

Range: fr upK of Africa, Eur, NAm & SAm.

Phylogeny: Scleroglossa :::Gekkota + *. (morphology Lee 1998) *or* Lacertiformes/Laterata :Teiioiformes + (Lacertidae + *) (molecular phylogeny Hedges & Vidal 2009)

Characters: 10-70 cm; rigid, consolidated skull; single median tooth on premaxilla; eyes reduced; postorbital skull elongate for large muscle attachment; brain completely surrounded by frontals; tail short; pelvic & pectoral girdles reduced or absent; most legless; annuli around body frees integument from trunk & allows concertina motion; right lung reduced; insectivorous; specialized to level of subsoil (skull for digging v. hunting). ATW010721

Comments: A specialised group with no clear morphological relationships, beyond basically Scleroglossan affinities. Variously included with gekkos and dibamids (Lee 1998), Scincomorpha (Conrad, 2008), or Lacertiformes/Laterata (Hedges & Vidal 2009). MAK101106

Links: Amphisbaenidae; xrefer - amphisbaena; Herpetology 1999 - October. ATW010721.

---

checked ATW050706

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

Squamata: Scleroglossa

Abbreviated Dendrogram

```
SQUAMATA
|
Scleroglossa
|--+--Gekkota
|  |--Dibamidae
|  `--+--+--Scincomorpha
|     |   `--+--Amphisbaena
|     `--Anguimorpha
|        |--Anguoidea
|        `--Varanoidea
|           |--Monstersauria
|           `--+--Necrosauridae
|              `--+--Varanidae
|                 `--Lanthanotidae
|
Pythonomorpha
```

Contents

Taxa on This Page

1. Anguimorpha
2. Anguoidea
3. Lanthanotidae
4. Monstersauria
5. Necrosauridae X
6. Varanidae
7. Varanoidea

Varanoidea

In retrospect, it might have been better to structure this area of phylospace on crown taxa: Anguimorpha = *Anguis* + *Xenosaurus* + *Varanus* and Varanoidea = *Heloderma* + *Varanus*. Then we could discuss Platynota = *Varanus* >

Anguis, even if it isn't clear that anything lived in that region that wasn't already accounted for as a Varanoid, except perhaps *Parviraptor*. As matters currently stand, I have used Varanoidea = *Varanus* > *Anguis* which may leave the Xenosaurs outside Anguimorpha. That was not the intention. However, Nydam (2000) reminds us that the current best guess is that the xenosaurs and anguids are two separate branches from the tree. Nydam's phylogeny, based on Gao, GK & MA Norell (1998) can be abbreviated somewhat as follows:

```
ROOT
|--Iguania
`--+--Scincomorpha
   `--+--Gekkota
      `--Anguimorpha
         |--Xenosauridae
         `--+--Anguidae
            `--+--Parviraptor
               `--+--Monstersauria
                  `--+--Necrosauridae (only Necrosaurus and Parviderma)
                     |--Proplatynotia
                     |--Saniwides
                     `--+--Paravaranus
                        `--+--Telmasaurus
                           `--+--Lanthanotidae
                              `--Varanidae (Varanus)
```

If this is correct, which it likely is, the neat division of Anguimorpha into Varanoidea and Anguoidea falls apart – Anguoidea is paraphyletic and includes Varanoidea. In addition, there is an ugly mess of unaffiliated species between the slimmed-down Necrosauridae and the varanids. For the moment, things will be left as they are; although a major overhaul seems inevitable.

It is interesting to reflect for a minute on what else was going on invertebrate phylospace. Granted, the Cretaceous was a long, long Period -- about 80My. Still, there was clearly something significant going on in the last half of that Period which is a bit mysterious. Mammals were diversifying, if not really amounting to much, in the last part of the Cretaceous. But, they were comparative late-comers. The lizards and mosasaurs diversified *and prospered*, as did the dinosaur offshoot, the birds. In the non-tetrapod area, the modern sharks established their dominance, and the teleosts completed the transition from small tanks to swift, unarmored forms. Two different lineages of turtles learned to keep their heads in. The rest of the turtles disappeared. Modern macrostomate snakes probably appeared, although, like the mammals, they were not a big numerical success immediately. Even crocs did rather well in the Late Cretaceous, spawning a number of new aquatic and terrestrial forms.

It is not at all clear what caused this polyphyletic radiation, and it is still possible that we are simply being misled by the sheer length of the Cretaceous. Still, it is curious that, except for mammals, every type of vertebrate which would have a meaningful role in the Tertiary diversified and evolved essentially modern forms in the last half of the Cretaceous. Even mammals and birds may have begun their radiations before the KT event, although here the evidence is more equivocal.

Were the dinosaurs losing their grip? There is no real sign of it. Earlier reports of a sharp decline in dinosaur diversity in the Late Cretaceous seem to have been largely refuted. The very latest part of the Cretaceous record (Maastrichian) is not well reflected in the geological record, so a decline could have occurred at this point. However, the events we are discussing mostly occurred over a longer period during which there is no doubt about the health of the dinosaur lineages.

What is more remarkable yet is that nothing like this has occurred since. After the end of the Cretaceous, the birds and mammals radiated strongly for about another 10-20 million years. But, by early or mid-Eocene times, almost all of the major types of both taxa had established themselves. Thus we have a major vertebrate turnover which seems to have taken about 50 My and affected essentially all vertebrate types. Before and after these periods, we see steady change but nothing quite as radical for quite some distance in either direction.

It would be easy to make too much of this and to get mired down in looking for a "cause." In fact, there is no reason to suppose that some major change in climate, vegetation, atmospheric composition or anything else caused the turnover. It is generally conceded that some cataclysmic event helped the process along at the KT boundary. However, faunal change was already well under way. The bolide or similar event probably prolonged and intensified the change, and may have weighed heavily in favor of mammals or birds and against non- avian dinosaurs. However, the most likely root cause for the entire process is random chance. Evolution is a non- equilibrium process. Life is sometimes metastable, or at some steady state. It is never at equilibrium. It should then require no more than the right local instability, produced by chance, to start a chain reaction which may take 50 My to damp out..

So, there is no need to find a cause for instability. The more interesting question is to explain the *rest* of vertebrate paleontology. Any reasonably complex non-equilibrium process is subject to these sorts of readjustments. The really strange thing is stability. *That* requires an explanation. ATW 010521

References: Caldwell (1999); Lee (1997a); Nydam (2000); Rieppel & Zahar (2000); Schultze (1994).

Descriptions

Toxicofera:

Range: Jurassic to Recent

Comment: Clade based on molecular phylogeny. Represents nearly 60% of extant squamates, including all venomous species and many related non-venomous species. Includes the following groups: Serpentes (snakes), Iguania and Anguimorpha, including Varanidae, Anguidae, and Helodermatidae (Gila monster and Mexican beaded lizard)-

Links: Wikipedia

Anguimorpha: *Paravaranus?* Used here to mean the node Anguoidea + Varanoidea. However, the more conventional definition is the stem (*Varanus* + *Anguis*) > *Scincus*. Hopefully, these are almost exactly the same group, except perhaps for *Paravaranus* (in stem but not node). *Paravaranus* really ought to be Scleroglossa *incertae sedis* because it is so incompletely known.

Range: from the Late Jurassic. Currently ~130 species of mostly predacious lizards worldwide, some very large.

Phylogeny: Scleroglossa :::Scincomorpha + * **:** Anguoidea + Varanoidea.

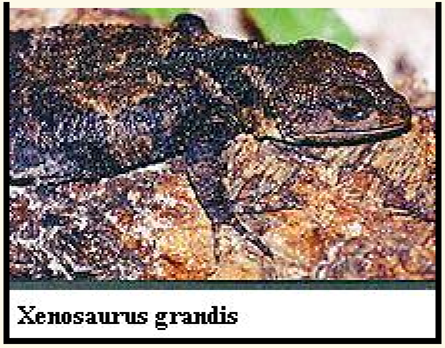
Characters: Tongue in 2 parts, with notched, inelastic forepart separated by transverse fold from the elastic hind part, which serves as a sheath when the tongue is withdrawn; tongue thin & protrusible for at least 1 head length; teeth nearly solid, not hollowed at base, replaced alternately (that is, new tooth comes up behind, not beneath, the older tooth); if body osteoderms present, scales are large, imbricate; body has lateral fold between axilla and groin.

Image: *Diploglossus.*

Links: Reptilian Systematics; Secondary structure .pdf.; Anguimorpha (Mikko's Phylogeny); Anguimorpha; Volume 21 No. 1 (abstract of Gauthier article on phylogeny); Digimorph - Shinisaurus crocodilurus (Chinese crocodile lizard) (detailed scans of skull); Herpetology- Lizards (brief discussion of included groups); 蛇蜥亚目 (Chinese: looks like a great site!); Volume 21 No. 1 (abstract of key phylogenetic paper); Molecular systematics of primary reptilian lineages and the ... ; Molecular Phylogenetics, tRNA Evolution, and Historical ... (Macey *et al.*, 1999: as discussed extensively elsewhere, Macey is one of the few who uses mitochondrial genome data in what we consider an appropriate manner), *see also*, Macey's vita, with additional publications; Kinematics of prey transport in lizards; The Excavations of Guimarota, Portugal (anguimorphs at Guimarota!!?).

References: Macey *et al*. (1997) (not really relevant, but very interesting); Nydam (2000). ATW040709

Anguoidea: *Xenosaurus*, anguids, shinisaurs, etc. Quite likely not monophyletic as generally used. The working definition used here is *Anguis* > *Varanus*.


Xenosaurus grandis

Range: from the Late Jurassic

Characters: tooth replacement posterolingual, with small resorbtion pits; opening of Jacobson's organ separated from choana (*neochoanate*); less than 14 scleral ossicles; frontals fused; frontals constricted between orbits; jugal contacts squamosal on supratemporal arch; clavicle curves anteriorly; pubes long; pubic tubercle anteroventral; osteoderms present.

Phylogeny: Anguimorpha :Varanoidea + *.

Links: Anguimorpha

References: Caldwell (1999); Lee (1997a). ATW030720.

Varanoidea (= Platynota)

Definition: Defined here as *Varanus* > *Xenosaurus* which is probably the same as the Platynota of most authors.

Range: from the Late Cretaceous, probably of Laurasian origin. Currently numerous species in Australia and Southern Asia, with 4 species in Africa and 2 in North America.

Phylogeny: Anguimorpha :Anguoidea + * **:** Monstersauria + (Necrosauria + (Varanidae + Lanthanotidae)).

Characters: Very conservative morphology, but size ranges over 5 orders of magnitude; recurved teeth with posterior serrations; premaxillary teeth smaller than maxillary teeth; marginal teeth widely spaced; teeth plicidentinate; **$** replacement teeth erupt posterolingual to functional teeth; mandible hinged in middle;**$** maxilla does not reach posterior orbit; **$** loose splenial - dentary contact; **$** reduced contact between dentary and all post-dentary bones; extensive medial exposure of angular; foramina for Jacobson's organ separate from choana & enclosed by vomers & maxillae (*neochoanate*); **$** ectopterygoids contact palatines; ectopterygoids expanded; frontals with descending processes located in middle & anterior region; hypoglossal (XII) and vagal (X) exits located very close to jugular foramen; carotid duct absent; cranial osteoderms fragmentary or absent; autotomy septa absent; clavicles rod-like or absent; epicoracoid cartilage does not contact meso- or suprascapular (huh?); short-term color changes absent; most are active hunters, some aquatic and arboreal; male combat dance.

Notes: The issue is whether the Varanoidea are big enough to contain the mosasaurs and snakes as Lee (1997a) argues. I have expressed my doubts elsewhere. As Caldwell (1999) argues, the recognition of Pythonomorpha does not require acceptance of Varanoidea as the root. The result depends strongly on the assumed homologies. See Rieppel & Zahar (2000), Schultze (1994). 010520.

Image: Skull of a monitor lizard. Bones in color are the dentary (yellow), squamosal (red) and quadrate (green). Photo by Dr. R. G. Sprackland. Courtesy The Virtual Museum of Natural History.

Links: Eric Pianka's Varanid Research (phylogeny); Varanus Reference List (refs); Higher Reptile Taxa (taxonomy); Fossil Monitor Lizards (origin); Warane (Einführung) (German); Untitled Document; Bibliography for Heloderma (Gila Monster, Beaded Lizard); Platynota sensu Pepin, 199?, and Caldwell, 1999; Envenomation; Digimorph - Varanus gouldii (sand monitor); Volume 21 No. 1 (abstract of a Gauthier revision of the Anguoids); Digimorph - Heloderma texana (fossil Gila monster).

References: Caldwell (1999); Lee (1997a); Nydam (2000); Rieppel & Zahar (2000); Schultze (1994). ATW030115.

Monstersauria: venemous lizards, including *Estesia* (upK of Asia), *Gobiderma* (upK of Mongolia), *Heloderma* (the Gila Monster, R of NAm), *Lowesaurus* (Oc of NAm), *Paraderma* (up? K of NAm), *Primaderma* (mK of NAm), *Telmasaurus*?

Range: fr mK.

Phylogeny: Varanoidea :(Necrosauridae + (Varanidae + Lanthanotidae)) + *.

Characters: venomous (probably not *Primaderma*); teeth strongly *plicidentinate*; 9-13 maxillary teeth; body of vomer rod-like; foramina for Jacobson's organ separate from choana & enclosed by vomers, maxillae & septomaxillae (not *Heloderma*?); palatines short; palatines toothed; large anterior processes of ectopterygoid covering palatine or pterygoid; ectopterygoid expanded and suborbital fenestra restricted; posterior end of maxilla does not reach mid-orbit (not *Heloderma*); coronoid with long anterior extension overlapping dentary; prefrontal contacts postfrontal (not *Gobiderma*); pineal foramen absent; supratemporal large; osteoderms present; fused, fragmented osteoderms on skull.

Links: Untitled Document; Monstersauria; Heloderma suspectum (Gila Monster): Narrative; Gila Monster (DesertUSA); Dr. Seward's Gila Monster Web; Gila Monster Printout- EnchantedLearning.com; Eric Pianka's Varanid Research.

References: Caldwell (1999); Lee (1997a); Nydam (2000).

Note: Many of these characters seem to be plesiomorphic for Varanoidea, if not more basal.. 011119.

Necrosauridae: *Colpodontosaurus*, *Eosaniwa*, *Necrosaurus* (= *Melanosauroides*?), *Parasaniwa*. One of those floating lineages which may or may not be monophyletic depending on what's included.

Range: upK- mEc or upOc of Eur, NAm & Asia.

Phylogeny: Varanoidea ::(Varanidae + Lanthanotidae) + *.

Links: Platynota after Pepin, 199?, Caldwell, 1999 and Balsai, 2001. 020102.

Varanidae: *Varanus*

Range: presently Old World tropics: Afr, Asia, Aus.

Phylogeny: Varanoidea ::Lanthanotidae + *.

Characters: medium to very large (6m); long, forked palatal process of premaxilla; palatal shelf on posterior maxilla; median ridge on ventral surface of vomers; no teeth on palatine or pterygoid; dorsal process of epipterygoid articulates with prootic; nasals do not contact prefrontals; descending processes of frontals meet medially; postfrontals absent; palpebrals absent; jugal very slender; postorbital bar incomplete; ribs absent of first 5 cervical vertebrae; 3 sternal ribs; long lateral arms of interclavicle; posterior emargination of coracoid; carpal intermedium absent; short pubis with short, ventrally-directed symphysial process; oviparous; carnivorous or insectivores; almost all terrestrial; use tails aggressively (in fact, they're just plain obnoxious and use *everything* aggressively); stylized male combat behaviors in upright position, balanced on tail.

Links: Varanidae; Family: Varanidae; -= V. rudicollis -- Family Varanidae =-; Varanidae; Eric Pianka's Varanid Research; Where V. rudicollis comes to bask!; Fossil Monitor Lizards; Jennifer C. Ast's half-completed Science Page; Varanidae.

References: Caldwell (1999); Lee (1997a).

Image: *Varanus exanthematicus*, the Savannah monitor, from the Honolulu Zoo. ATW010921.

Lanthanotidae: *Lanthanotus*, the "earless monitor"; *Cherminotus*.

Range: 1 extant species in Borneo, *Lanthonotus borneensis.*

Characters: 30-45 cm, semiaquatic; broad palatal shelf of maxilla; ectopterygoid with distinct notch on lateral margin; ectopterygoid expanded and suborbital fenestra restricted; angular & splenial articulate with vertical articular face with lateral lappet from angular behind splenial; anterior of coronoid does not overlap dentary; nostrils are moved back and upwards (aquatic adaptation); internal nares very thin, slit-like; descending process of frontals posterior; tiny eyes with moveable lids (lower lid transparent); less than 14 scleral ossicles; orbital rims form prominent lateral bulges projecting well beyond cheek; prefrontal contacts postorbital bones above orbit; pineal foramen absent; posterior opening of vidian canal at suture of basisphenoid and prootic; no ear opening; supratemporal fenestra open & supratemporal arch absent; slender, elongated body; sternum with with only 2 pairs of ribs; sternum short & triangular; clavicle curves anteriorly; interclavicle cruciform with large anterior process; pubes long, with symphysis ventrally directed and pubic tubercle anteroventral; short limbs; reduced phalangeal count; heterogenous scalation with underlying osteoderms.

Phylogeny: Varanoidea ::Varanidae + *.

Links: Lanthanotidae; Øreløs varan - Dyrebrevkassen (Danish); Eric Pianka's Varanid Research

References: Caldwell (1999); Lee (1997a).

Image: *Lanthanotus* from Prof. Eric Pianka's Varanid Research.. 010520.

Page Back | Unit Home | Page Top | Page Next

checked ATW050706

Squamata: Pythonomorpha

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
Scleroglossa
|
Pythonomorpha
|--+--Aigialosauridae
|  `--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   `--Alethinophidia
      |--Aniloidea
      `--Macrostomata
         |--Boidae
         `--Caenophidia
            |--Acrochordoidea
            `--Colubroidea
               |--Colubridae
               `--Viperidae
```

Contents

Taxa on This Page

1. Aigialosauridae X
2. Mosasauroidea X
3. Pythonomorpha
4. Serpentes

Pythonomorpha

Lee (1997a) is one of those rare papers that almost immediately convinced most paleontologists of its central proposition: that snakes are more closely related to mosasaurs than to varanid lizards. Varanids are represented today by monitor lizards, gila monsters, and a few close relatives. The extant varanids are all big, active hunters (at least by lizard standards). By contrast, mosasaurs were almost all gigantic aquatic predators who flourished in the Late Cretaceous and apparently died out with the dinosaurs. For many years, the orthodoxy was that snakes were highly derived varanids of some sort. However, as early as 1869, Edward Cope had argued that snakes were more closely related to mosasaurs, and he coined the term "Pythonomorpha" to describe the group that united them. This idea was occasionally also floated by others, but remained essentially dormant for almost five generations.

Michael Lee learned cladistic analysis in a rugged school. His doctoral work in England in the early 1990's concerned the origin of turtles. He advanced the idea that turtles are living pareiasurs. This hypothesis was, and remains, highly controversial; and Lee was forced to fight epic battles with unbelievers, culminating in two extensive, back-to-back articles by Lee (1997) and by deBraga & Rieppel (1997) in a single issue of the Zoological Journal of the Linnean Society.

By the time this work was published, Lee was already back in Australia preparing his next major project: the revival of Cope's pythonomorph concept. He attacked this project with characteristic energy and with his trademark attention to obscure fossil specimens. The work was published in the same year as the ZJLS article, but received a very different reception. As one paleontologist noted only a year later, "most of the workers I've spoken to that are aware of this work support it virtually 100%." It is truly a beautiful piece of work. Unlike most cladistic works, Lee provides figures for most of the characters he describes, which is enormously helpful for the 99% of his readers who are not lizard specialists. He carefully analyzes fabulously obscure specimens like *Saniwides* and *Paravaranus*. He explicitly states his higher-level phylogenetic assumptions. Almost the only element short of perfection is that, hidden in a mass of detail, are a substantial number of uncertain judgment calls about the scoring and polarity of certain characters. However, the end result is a convincing case that Pythonomorpha is a very strongly supported clade.

In fact, oddly enough, Pythonomorpha and its component clades were some of only a handful of clades which *were* strongly supported. Most of the relationships among the Varanoidea disappeared into vague polyotomies when bootstrapping tests were run. That is, their existence and position was very sensitive to minor variations in the data. Thus, Lee's use of poorly known taxa and the large number of assumptions made about higher level phylogeny and polarity make the rest of his cladogram fairly suspect. However, Pythonomorpha was extremely robust, and Lee identified 38 synapomorphies of the group, many of which dealt with the peculiar mobile lower jaw figured in the main entry in these Notes.

This conclusion was verified by Caldwell (1999), who used a rather different approach. To say "verified" is somewhat unfair, since Caldwell was working independently on the question and submitted his original manuscript three months *before* Lee did. However, the paper was held up in review for a year and in press for two more. Caldwell's primary work has always been in this phylogenetic area, particularly with aigialosaurs. Aigialosaurs are generally thought to be the sister group of mosasaurs, or may even include mosasaurs. Caldwell was once of the view that aigialosaurs were basal, largely terrestrial varanoids, probably close to snakes, and that mosasaurs were, at least morphometrically, something quite different. Caldwell et al. (1995). However, he seems to have come around to Lee's take on Pythonomorpha about the same time as Lee did.

As with Lee's work, Caldwell's 1999 study strongly supports Pythonomorpha. This is particularly informative because Caldwell's study is considerably different. He makes few assumptions about higher-level lizard taxonomy and includes gekkos, skinks and agamids among his ingroup taxa. He uses fewer of the poorly known fossil species and concentrates on well-characterized living groups, which minimizes the amount of missing or ambiguous data (at the risk, of course, of missing key transitional forms). His outgroup is *Sphenodon*, so there are no questionable assumptions about polarity. Caldwell also holds some rather different views about homology. He is far less likely than Lee to take osteological data at face value, and he attempts to exclude characters a priori when he perceives them as supporting fundamentally different structures.

Interestingly, Caldwell also used the ACCTRAN option in PAUP. ACCTRAN and DELTRAN are two different optimizing strategies. ACCTRAN assumes, whenever the results are ambiguous, that character transitions happen at the earliest possible point. Thus ACCTRAN tends to generate synapomorphies of higher level taxa and favors reversals over convergences. DELTRAN takes the opposite approach. DELTRAN therefore tends to generate apomorphies of terminal taxa and favors convergences over reversals. **[1]** He also seems not to have had access to a particularly good computer, as he was apparently forced to use the "heuristic" or step-wise option of PAUP. With this option, taxa are added one at a time, in random order, and tacked on to the tree as they are added. This can result in slightly different trees depending on the order of addition. The heuristic option therefore does not ensure a global most parsimonious result and requires many repetitions to avoid missing the optimum path. Possibly as a result of these constraints, Caldwell's strict consensus tree is one enormous polyotomy -- considerably less dramatic than Lee's result. However, application of the "majority rule" easily produced the same result as Lee's paper as far as the Pythonomorpha were concerned.

Not surprisingly, Caldwell's results outside Pythonomorpha are markedly different from Lee's. Lee constrains the Pythonomorpha to fall among the varanoids. Caldwell concludes that varanoids and pythonomorphs could not possibly be further apart without living on different planets. However, *both* of these results are scientifically insignificant. If anything, Caldwell's results demonstrate that the basal lizard polyotomy is even less resolvable than previously thought. However -- and this is the important thing -- Caldwell and Lee both find strong support for Pythonomorpha: the close relationship between mosasaurs and snakes.

Thus, Pythonomorpha is supported by two, quite divergent studies, which is as close to proof as one is likely to find in this area. Caldwell's higher-level taxonomy has been incorporated in these Notes, but the choice is relatively arbitrary. It is very uncertain where the ancestral pythonomorph derived from. However, somewhere in the early Cretaceous, a medium-large, low-slung, long-bodied, probably terrestrial predacious lizard developed a unique hinge in the middle of its lower jaw, loss of the symphysis joining the two halves of the lower jaw, and a unique way of stabilizing the spinal column (the zygosphene-zygantra articulation). These features (all of which were among those noted by Cope in 1869!) seem to have been a major evolutionary success in a number of quite different environments and may have driven the successive radiations of aigialosaurs, mosasaurs, and snakes, the last of which continues today. --ATW 000723

[1] I understand, thanks to a careful reader, that ACCTRAN is by far the more usual option. This would appear to be the more conservative approach. However, the fact remains that it promotes the formation of terminal polyotomies because the higher level nodes "soak up" the available synapomorphies, particularly if there is significant missing data. Suppose, for example, that taxa a, b & c are scored for "purple hair". Taxon 'c' has purple hair but 'a' and 'b' are fossils with no known hair. Under ACCTRAN, the node ABC will be scored as being supported by the synapomorphy "purple hair." Under DELTRAN, this character will be an apomorphy of taxon 'c'. If 'a' and 'b' are otherwise fairly similar, we may see a polyotomy at ABC under ACCTRAN, as well as a list of synapomorphies for ABC which is inflated by the addition of a characteristic which is in fact unknown. Normally, this is harmless. Sometimes, it is not. Back --ATW 011226.

"One if by Land and Two if by Sea"

According, to the Biblical literalists, the Serpent was responsible for getting Adam and Eve to try Apples. As punishment, the snake lost his legs, and the human race was burdened with the Windows OS. For all its obvious failings, this tale provides almost as much scientific satisfaction as the current state of research in the area.

This essay is, chronologically, the fourth attempt in these Notes to make some sense of early snake evolution. See the essays related to the Scolecophidia, Pythonomorpha, and Aniliidae. Many of the positions taken in these essays, all written within the last two years, are already pretty clearly wrong. TheAniloidea, for example, appear to be monophyletic; and the scolecophidians probably *are* a sideshow to the main line of snake evolution, after all. Having been steered wrong so often before, you may well ask why you should be getting on this particular bus again. The answer is that today we will not be attempting to actually *go* anywhere. Instead, this will be a simple sightseeing trip -- albeit one into the middle of a war zone.

The contending forces are familiar names. Arrayed on one side are Michael (MSY) Lee and Michael Caldwell, with a cast of numerous others. They contend for a marine, perhaps mosasauroid origin for snakes. Against them stand the Rieppel People, mostly Olivier Rieppel from the Field Museum and Hussam Zaher from the University of São Paulo (via the AMNH). They contend that Lee's marine snakes were already derived Macrostomates and that snake origins lie buried in the earth, among fossorial lizard-kind.

For a moderately obscure issue, this controversy has generated a remarkable amount of heat. Perhaps the story goes back to the disagreement between Rieppel and Lee concerning the relationship of turtles and pareiasaurs. The first sign of trouble on the snake front actually began before the pareiasaur matter wound down. In 1996, both Lee and Caldwell submitted papers supporting mosasaurs as (at least) the sister group of snakes. Lee (1997a); Caldwell (1999). While these papers were in review, the two collaborated on redescribing a possible intermediate form, an enigmatic "varanoid lizard" which had been gathering dust at the Hebrew University in Jerusalem since the mid-1970's. This specimen (actually two specimens) was *Pachyrachis*, which turned out to be a very early marine snake. Caldwell &

Lee (1997). Given the mosasauroid connection and the marine nature of *Pachyrachis*, Caldwell & Lee proposed that the snakes evolved from marine forms, rather than fossorial lizards. The two presented a very thorough cladistic analysis which appeared to support this hypothesis.

Just two months later, Hussam Zaher wrote and submitted a short rebuttal piece, which was published as a "Rapid Communication" in JVP the following year. Zaher (1998). Zaher argued that *Pachyrachis* was a derived, macrostomate snake so that its marine character proved nothing about the origin of snakes. Zaher, Rieppel and others then discovered *another* forgotten Israeli marine specimen from Hebrew University, *Haasiophis*, which they incorporated in a cladistic analysis which supported *their* view of the matter. Tchernov *et al.* (2000).

Caldwell replied to Zaher's piece in JVP in 2000. Caldwell (2000). Meanwhile, Lee literally went to the opposite ends of the earth. In Australia, he redescribed *Wonambi,* perhaps the only decently preserved madtsoiid snake in existence, and incorporated it into the Caldwell-Lee cladogram. Scanlon & Lee (2000). To the surprise of absolutely no one, the results confirmed their earlier conclusion that snakes came of marine ancestry. To complete the circle, I made a rough pass at coding *Wonambi* into the Zaher-Rieppel character matrix and ran it on PHYLLIP (the poor man's PAUP). It will shock no reader to hear that the results supported the Zaher-Rieppel terrestrial origin hypothesis.

So what is one to make of all this? Truthfully, its hard to say. These Notes reflect the Zaher-Rieppel model for now, but that choice was fairly arbitrary. The Caldwell-Lee character matrix is vastly more complete, and the analysis of post-cranial characters is incomparably better. But it is structured in a way that raises a number of questions to which there are no immediate answers.

For one, the number of dependent characters is striking. In the *Wonambi* paper, by way of example, character 97 is "Ectopterygoid. 0: large. 1: small. 2: absent." Characters 98, 99, and 100 then relate to various contacts and conformations of the ectopterygoid. Obviously if character 97 is coded as state '2' (ectopterygoid absent), characters 98-100 are rather meaningless. The note for character 99 states that it cannot be coded for animals without an ectopterygoid. Does this mean it is treated as missing data, as an additional character state of "unknown," or in some other way? What about characters 98 and 100? To make matters worse, character 100 is also expressly dependent on an *uncoded* state of the jugal, and the jugal itself is absent in advanced snakes (see character 44). Confused? It gets worse.

Most likely, the "not applicable" codings are treated as missing data, as this is the preferred method. What happens to missing data? Under PAUP, missing data can take any value and is treated so as to assume whatever value gives the smallest number of character changes. So the question is like asking, "what color is a chameleon?" It takes on the "color," or in this case the ectopterygoid, of its background. For anything but really small data sets, PAUP adds data stepwise, one taxon at a time. It draws the best tree it can from those data, then adds the next taxon. The order of addition is typically randomized and the process is repeated a few hundred times to find the shortest trees. (This is an oversimplification, but not too far off.) Now, consider what happens if we have a small number of taxa with lots of missing data: *Pachyrachis, Wonambi,* and *Dinilysia* for example. Most of the other taxa are living snakes with complete data sets. The first fossil taxon to be added will take on the ectopterygoid of the living example closest to it in other respects. Well and good. That's the way its supposed to work. But the *second* fossil taxon -- providing it is not too radically different from the first -- will be "attracted" twice as strongly to first because, in this way, it can minimize its distance from *two* other taxa. Thus, generally similar fossil taxa will tend to clump if they are mixed in with lots of living taxa. Also, taxa, living or fossil, with absent bones (*e.g.*, without an ectopterygoid) will tend to clump in a data set having lots of snakes *with* an ectopterygoid if there are many dependent characters.

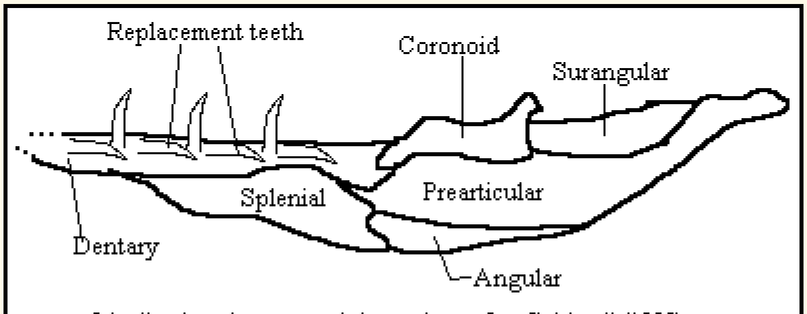
To make matters worse, Scanlon & Lee (2000) use soft tissue data -- lots of it. Characters 192 to 234 are all soft tissue, and thus *all* missing data for the three fossils. The soft tissue data set that they use is mostly that of Cundall et al (1993). This is discussed in connection with the anilliids. You may recall that Cundall's group was quite cautious about this data because, by itself, it resulted in phylogenetic gibberish. Osteological data alone showed a monophyletic Aniloidea. When combined with the soft tissue data, the total data yielded a paraphyletic Aniloidea, a result we now believe to be wrong. This suggests that convergent evolution is at work in the soft tissue characters. The legless lifestyle, after all, poses similar problems for all snakes, and there are only so many solutions. Since muscles seem to change much faster than bones, Cundall's results could be explained by invoking convergence and perhaps long branch attraction. This would tend to break up the monophyly of the aniloids by dragging some members closer to the macrostomate species which they most closely resemble by convergence and chance. The addition of fossil taxa compounds the problem of phenetic convergence because the misleading convergent soft tissues could create a completely erroneous phylogenetic center of gravity at which the fossil taxa would clump due to the large amount of missing data.

There's lots more, but the reader's patience for cladobabble is probably limited. None of these comments are intended as necessarily precluding the marine origin of snakes. Far from it! However, the Caldwell-Lee data set raises a number of issues that need to be addressed. Fortunately, these are the kinds of questions which can be answered by anyone with a reasonably good computer and a few days to spare. Perhaps we will do so ourselves the next time we return to this pit of contending vipers. ATW 010902

References: Caldwell (1999); Caldwell (2000); Caldwell & Lee (1997) [C&L]; Cundall *et al.* (1993); Hecht (1959); Lee (1997a); Lee *et al*. (1999) [LCS]; Lee *et al*. (1999a) [LBC]; Scanlon & Lee (2000); Tchernov *et al.* (2000); Zaher (1998). 010826.

Descriptions

Pythonomorpha: mosasaurs + snakes



Idealized pythonomorph lower jaw, after Caldwell (1999)

Range: from the Late Cretaceous.

Phylogeny: Scleroglossa: ((Amphisbaena + Gekkota) + (Scincomorpha + Anguimorpha)) + *: (Mosasauroidea + Aigialosauridae) + Serpentes.

Characters: **$** Recumbent replacement teeth; thecodonty; **$** four or fewer teeth on premaxilla; **$** mandibular symphysis absent (i.e. sides of the lower jaw are not firmly joined anteriorly); **$** vertical, mobile articulation of splenial and angular, allowing bulging of lower jaw (reversed in most scolecophidians) [LBC]; dentary overlap with post-dentary bones reduced or absent; splenial may be reduced or with reduced sutural contact with dentary; splenial does not overlap? contact? coronoid; coronoid articulates with dentary; supratemporal contacts prootic; posterior ramus of coronoid absent; septomaxilla with long posterior process (may reinforce central axis of elongated upper jaw); pterygoid teeth present; palatine with long anterior process; reduced *basipterygoid process*; reduced interpterygoid vacuities; parietal with large descending flange sutured to prootic; supratemporal contacts prootic; ribs begin with third cervical; **$** zygosphene-zygantra articulations in vertebral column; pelvic elements not sutured; femur stout (if present); osteoderms absent.

Links: Mosasaurs; Mosasauridae Translation and Pronunciation Guide (see entry for "Pythonomorpha"); Squamata. **Note:** For further information on this taxon, the Oceans of Kansas web site has a great deal of specialized information on mosasaurs, perhaps the most typical of pythonomorphs; Pythonomorpha (Mikko's Phylogeny); Molecular evidence for a terrestrial origin of snakes (reprint of Vidal & Hedges (2004) with a molecular study, also finding snakes outside of Varanoidea); The braincases of mosasaurs and Varanus, and the relationships of ... (same finding).

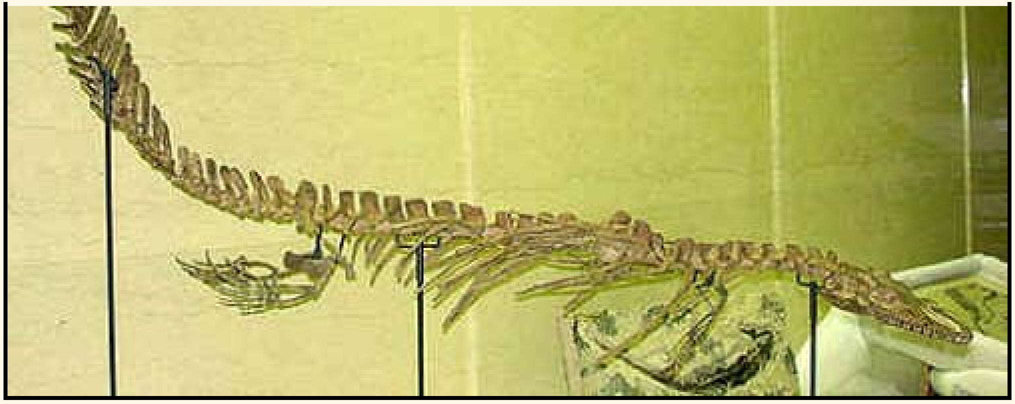
Note: Lee lists 38 synapomorphies of this group. Only a few are detailed here.

References: Caldwell (1999); Caldwell *et al*. (1995), deBraga & Rieppel (1997), Lee (1997), Lee (1997a); Lee *et al.* (1999a) [LBC] ATW040704.

Aigialosauridae: *Aigialosaurus*, *Carsosaurus*, *Coniasaurus*, *Opetiosaurus*.

Range: Late Jurassic (Tithonian) to Late Cretaceous (Turonian) of Europe.

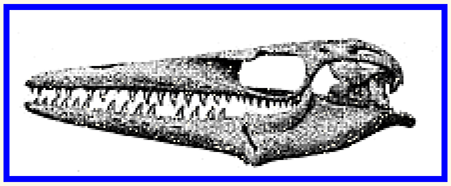
Phylogeny: Pythonomorpha:: Mosasauroidea + *.



Notes:paraphyletic?

Links: The Journal of Vertebrate Paleontology; Untitled Document; The Journal of Vertebrate Paleontology; 2002 The 15th Tokyo ATW030330

Mosasauroidea:



Range: upK.

Phylogeny: Pythonomorpha:: Aigialosauridae + *.

Characters: mesokinetic fronto-parietal hinge & metakinetic parietal-occipital hinge partially eliminated by tight overlaps but not closed sutures [LBC]; anguiliform motion w. limbs for steering; 10m; shallow marine; differ from Varanoidea in fusion of frontals, extension of premaxilla to frontals; joint in lower jaw; teeth specialized for various marine prey; post-cranial skeleton modified for aquatic motion & large size.

Links: Oceans of Kansas Paleontology (Obviously **Best on the Web**); The DOL Dinosaur Omnipedia; Mosasauroidea after Bell, 1994.

References: Lee *et al*. (1999a) [LBC].

Image: *Clidastes velox*, originally from Williston, SW (1898), *Mosasaurs*, *in* **The University Geological Survey of Kansas, Volume IV, Paleontology**. State Printer of Kansas, V(? or I?): 81-347, and reprinted at Mike Everhart's incomparable Oceans of Kansas site. **Note:** I have made no serious attempt to characterize this taxon, and gladly defer to the Oceans of Kansas. I would add only that mosasaurs are large, easily studied organisms known from many, beautifully preserved and relatively complete specimens almost worldwide. Anyone interested in vertebrate structure and function should pay particular attention to mosasaurs for that reason, as well as their marine adaptations and key phylogenetic position. Mosasaurs are relatively basal squamates but, at the same time, close relatives of snakes, the most derived squamates.

Serpentes: (~Ophidia): snakes. Since these Notes currently have nothing snaky which is more basal than the crown group of snakes, Ophidia and Serpentes are treated as synonymous. Actually, Ophidia = mambas > mosasaurs; and Serpentes = boas + blindsnakes. In these notes, Serpentes is used as a crown group, with Scolecophidia and Alethinophidia treated as complementary stem groups.

Range: fr upK.

Phylogeny: Pythonomorpha: (Mosasuroidea + Aigialosauridae) + *: Scolecophidia + Alethinophidia

Characters: skull highly kinetic, with up to 8 links permitting rotation or expansion, including lower jaw joint; advanced forms have essentially no rigid skull except braincase; **$** marginal teeth ankylosed to to rims of discrete sockets [C&L]; teeth frequently angulated rather than smoothly recurved [LCS]; **$** dentary with <3 mental foramina [C&L]; compound bone present [C&L]; at least some mobility of maxilla and palatal arch [LBC]; **$** palatines with distinct medial rectangular process [C&L]; chemosensory vomeronasal "Jacobson's" organ in roof of mouth -- tongue used to sample air, transport to organ; **$** premaxilla-maxilla articulation nonsutural and mobile [C&L]; lacrimal absent [C&L]; eyes permanently covered by transparent lower lid in most modern snakes; eyes: lens is moved, not bent, to focus; no fovea; no oil droplets; no sclerotic support; unique double cone (suggests ancestor was possibly blind cave, marine or burrowing form); mesokinetic fronto-parietal hinge eliminated [LBC]; frontal and parietals completely enclose brain; metakinetic parietal-occipital hinge eliminated [LBC]; supratemporal superficial to parietal [C&L]; jaw adductors "insert" (originate?) on dorsal surface of parietal [C&L]; parietal table reduced to sagittal crest [C&L]; **$** descending process of parietal contacts parabasisphenoid [C&L]; no tympanum or middle ear; **$** tympanic recess absent [C&L]; some detection of vibration through lower jaw and skin at low frequency (<1K cps); **$** >140 precaudal vertebrae [C&L]; vertebrae proceolous, with well-developed zygosphenes, zygantra, diapophyses; hypapophyses usually present in some region of spine; **$** pectoral girdle & limbs absent [C&L]; pelvic girdles, limbs rudimentary or absent; numerous specializations related to elongation & locomotion, e.g., loss of 1 lung (but elaborations of trachea may functionally serve as additional lung), 1 of paired gonads & kidneys displaced longitudinally.

Links: ANATOMY OF A SNAKE; The EMBL Reptile Database; Reptilia, Squamata, Ophidia - Schlangen (German); Ophidia -Faszination Schlangen- (German); The Ophidia Files; A revision of the Australasian Pythons - Hoser - 2000..

References: Caldwell (1999); Caldwell (2000); Caldwell & Lee (1997) [C&L]; Cundall *et al.* (1993); Hecht (1959); Lee (1997a); Lee *et al*. (1999) [LCS]; Lee *et al*. (1999a) [LBC]; Scanlon & Lee (2000); Tchernov *et al.* (2000); Zaher (1998). 010826.

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

checked ATW060222

Squamata: Mosasauridae

Abbreviated Dendrogram

```
(to be added...)
```

Contents

Image credit Jaime Chirinos / Science photo library

Unfortunately, this page is not ready yet. In fact, it's not even written. If you would like to write it, please contact us

---

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

Squamata: Pythonomorpha: Scolecophidia

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
Scleroglossa
|
Pythonomorpha
|--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   |  |--Anomalepididae
   |  `--+--Leptotyphlopidae
   |     `--Typhlopidae
   `--Alethinophidia
      |--Aniloidea
      `--Macrostomata
         |--Boidae
         `--Caenophidia
            |--Acrochordoidea
            `--Colubroidea
               |--Colubridae
               `--Viperidae
```

Contents

Taxa on This Page

1. Anomalepididae
2. Leptotyphlopidae
3. Scolecophidia
4. Typhlopidae

Descriptions

Scolecophidia (= Typhlopoidea): blind snakes.

Range: fr lwPc.

Leptotyphlops dulcis, the Texas blindsnake. Image © 1999 by Nathan Kley and reproduced by permission.

Phylogeny: Serpentes: Alethinophidia + *: Anomalepididae + (Leptotyphlopidae + Typhlopidae).

Characters: Small (10-100 cm long & down to 2 *mm* in width), fossorial; small, blunt heads tipped with rostral shield; integrated skull; **$** rostral shield formed by enlarged nasals reinforced at margins by prefrontals and premaxilla; small jaw gape; **$** dentaries are joined; reduced dentition with no teeth on pterygoid or palatine; dentaries or maxillae (but not both) highly mobile; eyes reduced and permanently covered with a scale, or absent; head contains numerous glands of unknown function; up to 600 vertebrae; short, blunt tails (1-18% of length); spine at end of tail, probably used to push off in locomotion; traces of pelvic girdle; spurs attached to pelvic girdle in some; 2 common carotid arteries; multi-lobed liver; round, polished uniform scales; feed on soft invertebrates or insect larvae; fossorial down to 2 m, but commonly hunt nocturnally above ground or even in trees; commonly follow insect pheromone trails; one species (*Ramphotyphlops braminus*) appears to be entirely female.

Links: Higher Reptile Taxa; Nate Kley (best on the web); Les serpents - ReptiWeb (French); Scolecophidia (wormsnakes).

Discussion:

Digging them out. Blind snakes look a great deal like earthworms and have about as many distinguishing features. This, and their secretive, nocturnal and underground life style have made them notoriously difficult to differentiate and to study. However, they are at the base of the snake clade -- if it is a clade. The monophyly of the snakes is very likely, but not certain. See discussion in Cundall *et al*. (1993). Thus blind snakes ought to be of serious evolutionary interest. However, they have historically been dismissed as "degenerate" forms, perhaps unworthy of serious study*. It is only in the last thirty years or so that enough information about the evolution of snakes has accumulated to ask the appropriate questions. As recently as 1997, Greene wrote that no serious study of blind snake feeding behavior had been conducted at all. This was perhaps an exaggeration, and is certainly untrue now. See, e.g. Kley & Brainerd (1999). But the study of snake evolution is certainly still in its infancy and there are still a remarkable number of matters that have not been addressed.

Leptotyphlops dulci feeding on ant larvae. © 1999 by Nathan Kley and reproduced by permission.

Pick and Shovel. One of the curious features of early snake evolution is that *all* living members of the most basal groups are digging ("fossorial") snakes, but are designed to dig in quite different ways. The Uropeltidae, for example, are a sister group to the aniliids which have not been taken up in these Notes as of this writing. Like the blind snakes, uropeltids are fossorial. The midline of the uropeltid skull is strongly reinforced to allow the snake to hack at the earth like a pick and to displace it to the sides. Cundall & Rossman (1993).

The blind snakes use a shovel instead of a pick. The scolecophidian nasal is broadly expanded to support a rostral blade. Instead of central reenforcement, the nasal is supported at the margins, and the force of digging is ultimately carried by the premaxilla, prefrontals and frontals. While no detailed study has been done, this arrangement probably sacrificies strength for speed. It may be related to the scolecophidian habit of attacking (even nesting in!) the colonies of social insects, largely ants and termites. This is earth that has already been turned. It requires no special strength to dig through. The premium is on speed to attack and ingest eggs and larvae before the small snake is overwhelmed by the insects themselves. This hypothesis is consistent with recent studies of feeding behavior in blind snakes whch also conclude that their highly specialized feeding mechanisms are designed for high-speed, hit-and-run tactics. Kley (1998); Kley & Brainerd (1999).

Dig In! The feeding studies mentioned above are available in great detail, with film clips, at Nathan Kley's web site. According to Kley & Brainerd (1999) and other work noted there, the Scolecophidia have a variety of distinct feeding styles which seem to involve substantial active kinesis of one jaw or the other and an assortment of unusual jaw joints. The common denominator may be the use of one highly mobile jaw element (either dentary or maxilla, but not both) to scrape or push food into the throat. However, the fossorial scolecophidian life constrains the skull to be relatively solid in order to assist in digging. By contrast, the Alethinophidia have a more kinetic skull overall, but use the kinesis passively: to allow large objects to be swallowed, rather than to rake small objects into the throat as in scolecophidians. The alethinophidian feeding style may be related to, and may have evolved from, locomotion.

Trench Warfare. All of this may have interesting implication for the origin of the snakes. The classical explanation for snakes is that they descended from lizards via some fossorial intermediate. This explains the fossorial habits of basal snakes and such peculiar adaptations as the ophidian eye, which has a number of unique features including the absence of a fovea centralis, the presence of double cones, and the absence of colored oil droplets. Further, unlike lizards (but somewhat like fish), snakes focus the eye by moving the lens rather than distorting the shape of the lens. These and other changes convinced early evolutionary biologists that snakes had evolved from some dark-adapted underground group which had re-evolved the eye after a period during which vision was of limited utility.

More recently, a number of workers have championed a marine varanid origin for snakes, even suggesting that snakes are survivors of the mosasaurs. One of the strong points in favor of this hypothesis is that the fossil record of snakes contains no fossorial forms, but does contain apparently marine species such as *Pachyrachis*. Most recently, however, a contemporary of *Pachyrachis* (*Haasiophis*) -- from the same formation -- has been described as a macrostomate (advanced, non-fossorial snake) which had secondarily become aquatic in the manner of modern sea snakes (Elapids) Tchernov *et al.* (2000). The same authors question the previous interpretation of *Pachyrachis* as primitive. The only other well known Cretaceous snake is *Dinilysia*. *Dinilysia* is clearly a terrestrial snake. Its detailed affinities are unclear, but the structure of its skull, as described by Estes *et al.* (1970), suggests aniliid affinities. That is, it has a noticeable "pick" and may well have derived from a fossorial form.

Digging Out from Under. We may now assemble a nice story along the following lines. Snakes did in fact begin as very basal varanids, with whom they share the forked tongue and other characters. However they did not come by sea, but underground as in the classical interpretation. (Possibly the development of a fossorial life was related to the early Cretaceous development of birds and mammals which could effectively prey on small lizards). Originally these lizards had a variety of shovel-type fossorial adaptations, represented today by the weird variation in scolecophidians (see the Kley site). However, some developed the pick-style, aniliid, centrally-supported rostra and a feeding style that coordinated with snake-like locomotion. This freed up the jaw and peripheral skull elements to begin the development of the extreme cranial kinesis seen in all advanced snakes. During the later Cretaceous, these advanced forms became large and strong enough to abandon fossorial life and experiment with terrestrial or marine existence. *Dinilysia, Pachyrachis*, and *Haasiophia* are all examples of this radiation, which resulted in the variety of terrestrial and marine forms we see today.

Nice story, but time -- as always -- will eventually tell. ATW 000429.

Note added in disproof: A great deal has happened in this area since the Note was originally written, and another essay will follow shortly. Pending that, the better story may now be that the scolecophidians are a very early and very derived group who are not closely related to any of the other living groups of snakes. In fact, one may question (not *too* seriously) whether they are snakes at all. But that is a story for another day. ATW 010901

* The use of the dismissive term "degenerate" in 19th and early 20th century biology is itself an interesting subject, and perhaps not at all as simple as it might seem. However, it is well beyond the scope of this essay.

References: Cundall & Rossman (1993); Cundall *et al*. (1993); Estes *et al.* (1970); Greene (1997); Kley (1998); Kley & Brainerd (1999); Tchernov *et al.* (2000). 010227.

Anomalepididae: Medium sized (20-75 cm) fossorial snakes

Range: R of SAm.

Phylogeny: Scolecophidia: (Leptotyphlopidae + Typhlopidae) + *.

Characters: premaxilla without teeth; retroarticular process elongate; vomerine process of palatine narrow; transverse process of pterygoid curved & receives ectopterygoid dorsally; transverse process of premaxilla straight and lateral; postorbital absent; supratemporal process of parietal not developed; supratemporal present; quadrate suspension shifted anteroventrally to near prootic - basisphenoid suture; stapes shaft not straight; stapes shaft thick & shorter than width of footplate.

References: Tchernov *et al*. (2000) [T]

Leptotyphlopidae: Very small to small (10-25 cm) fossorial snakes.

Range: SAm, NAm, Eur, Afr & SW Asia.

Phylogeny: Scolecophidia:: Typhlopidae + *.

Characters: premaxilla without teeth; vomerine process of palatine narrow; transverse process of pterygoid curved & receives ectopterygoid laterally; transverse process of premaxilla straight and lateral; postorbital absent; supratemporal process of parietal not developed; supratemporal absent; quadrate suspension shifted anteroventrally to near prootic - basisphenoid suture; stapes shaft not straight; stapes shaft thick & shorter than width of footplate.

References: Tchernov *et al*. (2000) [T]. 000428.

Typhlopidae: Small to medium fossorial snakes

Phylogeny: Scolecophidia:: Leptotyphlopidae + *.

Characters: premaxilla without teeth; retroarticular process elongate; vomerine process of palatine narrow; transverse process of pterygoid curved & receives ectopterygoid laterally; transverse process of premaxilla straight and lateral; reduced eyes; postorbital absent; supratemporal process of parietal not developed; supratemporal absent; quadrate suspension shifted anteroventrally to near prootic - basisphenoid suture; stapes shaft not straight; stapes shaft thick & shorter than width of footplate.

References: Tchernov *et al*. (2000) [T]. 000428.

Page Back | Unit Home | Page Top | Page Next

checked ATW060222

Palaeos

SQUAMATA

THE VERTEBRATES

PYTHONOMORPHA: ALETHINOPHIDIA

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

Squamata: Pythonomorpha: Alethinophidia

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
Scleroglossa
|
Pythonomorpha
|--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   `--Alethinophidia
      |--Dinilysia
      `--+--Aniloidea
         |  |--Aniliidae
         |  `--+--Cylindrophiidae
         |     `--+--Uropeltidae
         |        `--Anomochilidae
         `--Macrostomata
            |--Boidae
            `--Caenophidia
               |--Acrochordoidea
               `--Colubroidea
                  |--Colubridae
                  `--Viperidae
```

Contents

Taxa on This Page

1. Alethinophidia
2. Aniliidae
3. Aniloidea
4. Anomochilidae
5. Cylindrophiidae
6. *Dinilysia* X
7. Uropeltidae

Descriptions

Alethinophidia:

Phylogeny: Serpentes: Scolecophidia + * **:** *Dinilysia* + (Aniloidea + Macrostomata).

Characters: vomerine process of premaxilla large and broadly in contact with vomers; **$** vomeronasal nerve enters vomer through single large (or 1 large + 1 small) foramen [T[; coronoid present; maxilla not mobile; ascending process of maxilla contacts frontal; rostral region articulated to braincase by naso-frontal articulation; braincase narrow, elongate and tapers anteriorly; postfrontal well-developed and fused to parietal; quadrate short & vertical; footplate of stapes large; facets of zygapophyses slant upward; middle and posterior vertebrae lack hypapophyses.

Note: these are the *primitive* conditions, i.e. characteristics of the paraphyletic Aniloidea.

Links: Lab VII. Snakes (a sampler); S09528369990050 51d 49..58 (taxonomy, feeding biology and evolution); Digimorph - Ramphotyphlops braminus (Brahminy blind snake) - head; Herpetology- Snakes; PII- S1631-0691(02)01510-X.

References: Holman (2000); Tchernov *et al.* (2000) [T] ATW030923

Dinilysia

Range: upK (Coniacian [C&A]) of SAm.

Phylogeny: Alethinophoidia :(Aniloidea + Macrostomata) + *.

Characters: slightly flattened skull [C&A]; palatine does not contact ectopterygoid; pterygoid with teeth; outer orbital (lateral) margin of prefrontal vertical; low medial foot process of prefrontal; supraorbital present(?); quadrate vertical; shaft of stapes not straight; inhabited seasonally (or sporadically?) arid interdune environment with wind-dominated sedimentation [C&A]; terrestrial, semi-fossorial mode of life, with active or ambush predation in loose groundcover [C&A].

Links: BBC Online - Walking with Dinosaurs - Fact Files; Mike Caldwell hunts fossil snakes in Argentina.;

References: Caldwell & Albino (2001) [C&A]; Tchernov *et al*. (2000) [T]

Note: shares almost no derived features with scolecophidians.

Aniloidea: *Anilius* > *Crotalus*.

Range: fr upK of NAm, Eur, SAm, India & SW Asia.

Phylogeny: Alethinophidia ::Macrostomata + * **:** Aniliidae + (Cylindrophiidae + (Uropeltidae + Anomochilidae)). 010901.

Aniliidae:*Anilius, Coniophis, Eoanilius (?)*.

Range: from the Late Cretaceous (Campanian). Currently SAm only (1 sp.)

Phylogeny: Aniloidea :(Cylindrophiidae + (Uropeltidae + Anomochilidae)) + *.

Characters: Robust, tightly knit skull; premaxillary, palatine, and pterygoid teeth present; lower jaw hinged on surangular; palatine has gliding joint on maxilla; m. retractor vomeris present; splenial absent; gape not wide; upper jaw solidly attached to skull; frontal-parietal articulation closed & immobile; reduced eyes lying beneath large, at least semi-transparent head scales; squamosal present, but short; supratemporal present; fovea dentis present in occipital condyle; vertebrae squarish in outline and not longer than broad; zygosphenes flare upward; vertebrae lack prominent neural spine or substantial accessory processes; hemal carina absent; hypapophyses absent on mid-thoracic vertebrae; vestigial hindlimbs and girdle; single bone in pelvic girdle; femur may project as anal spur; small, smooth scales; ventral scales slightly larger than dorsal; ventral scales with black & white checkered pattern; gastrosteges present; liver relatively anterior; heart relatively anterior; 2 lungs, with left lung reduced; kidneys relatively anterior; fossorial; carnivorous; ovoviviparous.

Note: At this level, snake phylogeny is very unclear. Possibly the majority opinion is that the advanced snakes are more closely related to Boids than to *, although both groups are fairly primitive. Most aniliids use defensive display behaviors which attempt to mimic toxic or dangerous organisms. This group may also include Loxocemids. 010609.

Discussion: Aniliids today are represented only by the genus *Anilius* of South America. However, they are perhaps the oldest group of snakes known from reasonably distinctive fossil remains. They have a more or less continuous fossil record from the Upper Cretaceous to the present day.

The distinctive squarish vertebrae of *Coniophis* are known from numerous locations in the Upper Cretaceous, Paleocene and Eocene of North America. Hecht (1959); Holman (2000). Oddly, *Coniophis* is also known from the Cretaceous of South America -- one of several indications that a land bridge existed between the two continents at one or more times in the later Cretaceous. Holman (2000). The early Eocene was apparently a good time for snakes in North America. However, the diversification seems to have been due to the evolution of larger, terresestrial forms. The fossorial aniliids are represented only by the familiar *Coniophis*. In the later Eocene, perhaps as the result of colder climates, many snake species became extinct, including *Coniophis*. *Id.*

Presumably, some relict population survived in South America, since *Anilius*, the False Coral Snake, is known from a number of locations in northern and Western South America today. However, with the exception of a few Miocene vertebrae (*Colombophis*) there does not appear to be any fossil record in the Western Hemisphere after the middle Eocene. It has been argued that *Columbophis* is more likely to be a uropeltid than a true aniliid. Szyndlar (1994). Given that Recent uropeltids are only found in a restricted area of South Asia, it is perhaps more likely yet that *Columbophis* represents some completely extinct branch derived from the the *Coniophis* stem.

About the same time as *Coniophis* was dying out in North America, *Eoanilius* was making its first appearance in Europe. *Eoanilius* is said to be a true aniliid and is a fairly common fossil snake (if any ophidian fossil can be referred to as "common") from the Eocene and Oligocene of England, France and Germany. Europe, like North America, suffered a devastating extinction of snake species during the later Eocene. However, through chance or some difference in circumstances, the aniliids appear to have hung on in Europe for at least some period of time. Szyndlar (1994). In fact, a possible aniliid, *Michauxophis*, has been reported from as late as the Pliocene of France. Bailon (1988).

Unfortunately, as with most areas of snake taxonomy, it is not clear that all workers are speaking about the same thing. The traditional practice was to lump the Cylindrophiidae, Aniliidae, Anomalochilidae, and Uropeltidae under a general heading: usually "Aniloidea," but also frequently "Aniliidae." There is certainly a distinct possibility that the Aniloidea, in this sense, are a clade which diverged early from the boids and their progeny. Cundall et al (1993) make a good case that any "aniloid" group would be paraphyletic. However, their cladistic analysis rests on the combination of skeletal and soft tissue traits. As they are careful to point out, their skeletal data, considered alone, would *support* an aniloid clade. Their soft tissue data, taken only from highly derived extant species, makes almost no sense at all if considered alone. It is only the combination of skeletal and non-skeletal characters which yields the paraphyletic aniloidea as used in these Notes. However, the combined tree is fairly robust, especially for a snake phylogeny. Furthermore, the supposition that all "aniloids" form a separate branch of the family tree requires us to accept an odd, mosaic distribution of traits.

In the last analysis, the apparent similarity of the aniloids is quite possibly due to the fact that all known members of the constituent groups are fossorial to one degree or another. The difficult business of crawling around underground creates some rather severe constraints on biological design. As touched on elsewhere, the pressures of becoming fossorial followed by regaining terrestriality, are likely to result in a radically re-engineered skull. However, the re-engineering is not possible without the initial step of fossorial existence. Thus the unique and radical kinesis of the advanced snakes sets them apart from the "aniloids," but also argues that advanced snakes descended from a fossorial stem group, presumably part of the original aniloid radiation. ATW 010108.

Note added in disproof: The Rieppel people, *e.g.* Tchernov *et al.* (2000), disagree on almost everything in Lee's trees, *e.g.* Scanlon & Lee (2000) -- everything *except* the monophyly of the aniloids. On this subject, they speak with one voice. Accordingly, I grudgingly concede error, with much whining and snarling, and have accordingly restored the Aniloidea to their presumably rightful place.

Links: Aniliidae; Anilius scytale: Media; Lab VII. Snakes; espacio.ya.com - Bienvenido a la página de aligatorjazz; s102110100043.pdf.

References: Bailon (1988); Cundall *et al.* (1993); Hecht (1959); Holman (2000); Scanlon & Lee (2000); Szyndlar (1994); Tchernov *et al.* (2000). ATW 010901.

Cylindrophiidae(= Cylindrophiinae)**:** *Coniophis* (?), *Cylindrophis*.

Range: Recent of SE Asia.

Phylogeny: Aniloidea ::(Uropeltidae + Anomochilidae) + *.

Characters: Small to moderate size; teeth present on palatine & pterygoid; 9-13 maxillary teeth; robust dentary; anterior tips of dentary rounded, with limited, hinge-like mobility [LBC]; prominent mental groove; premaxillary process long, extending between nasals; large ectopterygoid, overlapping maxilla and pterygoid; prefrontal small; spectacle covering eyes present; postorbital present; frontal-parietal articulation closed & immobile; occipital condyle without fovea dentis; vertebrae generally same as in Aniliidae; heart ~30% of snout-to-vent length from snout; vestigial left lung complex present; kidneys relatively far posterior & near vent; scales smooth, with 19-23 rows; semi-aquatic. Many details of superficial characters (e.g. scales & dentition) at Cylindrophis maculatus.

Note: *Eoanilius* (upEc of Eur) has been referred to this taxon, but the assignment is strongly disputed.

Image: *Cylindrophis rufus* from foto-bibliotheek.

Links: Cylindrophiidae; Cylindrophis sp; Lady Di Body Art (Dutch); Cylindrophis maculatus (**Best on the Web**); *Cylindrophis rufus* (Japanese); Herpetofauna of Myanmar (several images); 两栖动物分类 (Chinese).

References: Cundall et al (1993); Cundall & Rossman (1993); Hecht (1959); Lee *et al.* (1999a) [LBC]. ATW040114.

Uropeltidae (= Uropeltinae)**:** "shield-tail" snakes.

Range: R of S Asia.

Phylogeny: Aniloidea :::Anomochilidae + *.

Characters: Skull massive and akinetic; usually pointed snout; upper jaw solidly attached to skull; premaxilla and maxilla closely associated (sutured?); teeth absent from palatine & pterygoid; prefrontal extends between nasal and maxilla and interlocks strongly with maxilla; frontal-parietal articulation partially open; no eye-covering spectacles; small eyes; often have long posterior process on dorsal end of quadrate; quadrate associated directly with otic elements; supratemporal absent; basisphenoid, basioccipitals, prootics, and supraoccipitals all fused; inner centrum of atlas absent; long occipital condyle forms ball and socket joint with axis; fovea dentis present; no hind limb vestiges, but pelvic bone present; keratinous disk-shaped shield at tip of tail which may be specialized for prehensile or mimetic purposes; upper surface of tail with single or series of thickened scutes, often covered with spines; gastrosteges present but reduced, left lung very small; superficial branch of adductor mandibulae externalis originates from temporal tendon and inserts on coronoid process; heart located 30% of snout-to-vent length, liver about 50%; gall bladder near posterior limit of liver; kidney relatively far anterior to vent; carnivorous; fossorial; viviparous (?); mimetic defensive displays.

Links: Docent Webpage; Uropeltidae; espacio.ya.com - Bienvenido a la página de aligatorjazz (Spanish).

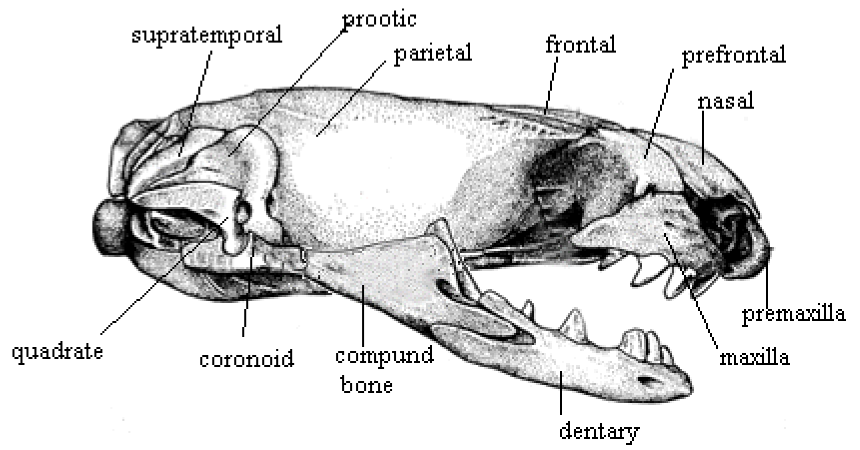
References: Cundall et al (1993); Cundall & Rossman (1993).

Image: *Uropeltis* from foto-bibliotheek. ATW020123.

Anomochilidae: *Anomochilus.*

Range: R of SE Asia.

Phylogeny: Aniloidea :::Uropeltidae + *.



Anomochilus weberi skull in right lateral view. Modified from Cundall & Rossman (1993).

Characters: Small, cylindrical body; head no wider than body; broad, blunt snout; pterygoid, palatine, pterygoid, and premaxillary teeth absent; 3-4 maxillary teeth; teeth short, with stout base; teeth not ankylosed & attachment may be fibrous; robust dentary; ectopterygoid much reduced, entirely incorporated in ligament between pterygoid and maxilla, but does not contact maxilla or pterygoid; mental groove absent; coronoid present & well-developed; nasal process of premaxilla weak and not fixed to nasals; nasals very large and participate in anterior margin of rostrum; prefrontal extends between nasal & maxilla and is supported on maxilla; frontal-parietal articulation partially open; process of parietal ("postfrontal") excludes frontal from margin of orbit; braincase relatively wide, lacking prominent crests or laterally expanded otic capsule; long posterior process on dorsal end of quadrate; separate supra-, ex- & basioccipitals and prootic; occipital condyle with fovea dentis; superficial adductor mandibulae externis originates on braincase only and inserts on coronoid process (?); spectacle scales reduced or absent; eyes reduced; smooth scales with 17 - 19 rows; rectal cecum absent; liver large and posteriorly asymmetrical; gallbladder displaced posteriorly; left lung complex absent; heart and lung relatively far anterior; 2 renal arteries; oviparous.

Links: Anomochilidae.

References: Cundall et al (1993); Cundall & Rossman (1993). 010107.

Page Back | Unit Home | Page Top | Page Next

checked ATW060222

Squamata: Pythonomorpha: Macrostomata

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
Scleroglossa
|
Pythonomorpha
|--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   `--Alethinophidia
      |--Aniloidea
      `--Macrostomata
         |--Madtsoiidae
         `--+--Pachyophiidae
            `--+--Boidae
               `--Caenophidia
                  |--Acrochordoidea
                  `--Colubroidea
                     |--Colubridae
                     `--Viperidae
```

Contents

Taxa on This Page

1. Acrochordoidea
2. Boidae
3. Caenophidia
4. Macrostomata
5. Madtsoiidae X
6. Pachyophiidae X

Descriptions

Macrostomata: *Crotalus* > *Anilius*. snakes with large gapes (boas, cobras, vipers)

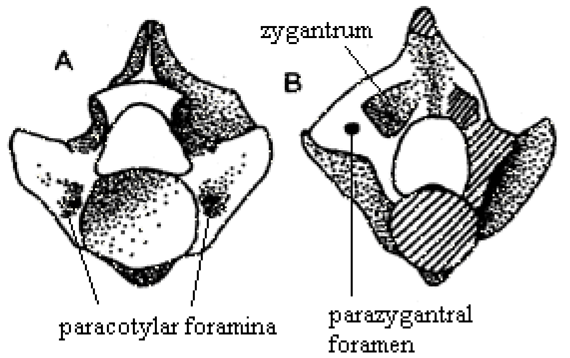
Range: fr upK worldwide.

Phylogeny: Alethinophidia:: Aniloidea + *: Madtsoiidae + (Pachyophiidae + (Boidae + Caenophidia))

Characters: **$** enlorged posterodorsal toothed process of dentary [Z98]; toothed anterior process of pterygoid [Z98]; **$** *basipterygoid processes* reduced, with articulating surface facing ventrally [Z98]; **$** free-ending process of supratemporal [Z98]; **$** dorsal surface of prootic concealed by supratemporal [Z98]; quadrate vertical or posteriorly directed [Z98]; **$** quadrate suprastapedial process absent (except *Xenopeltis*) [Z98];

References: Zaher (1998) [Z98]

Madtsoiidae: *Alamitophis*, *Gigantophis* (~9m! see image at fossili), *Wonambi*. Some very large. Mostly known from isolated vertebrae.



Alamitophis: trunk vertebra in (A) anterior and (B) posterior view. From Albino (2000).

Range: mK-lwPle of Gondwana (SAm, Aus. & Egypt). Latest South American finds are of Ec age.

Phylogeny: Macrostomata: (Pachyophiidae + (Boidae + Caenophidia)) + *.

Characters: generally cylindrical body[C&A]; skull long & low [S&L]; upper jaw tightly fixed to skull [S&L]; palate very broad [S&L]; palatine in extensive contact with vomer [S&L]; small facets on pterygoids for basipterygoid articulation; snout rounded [S&L]; ligamentous maxilla - premaxilla connection [S&L]; prefrontal sutured to maxilla, but movable on frontal [S&L]; frontal - nasal articulation sutured and rigid [S&L]; jugal probably retained [S&L]; supratemporal and/or quadrate projected posteriorly [S&L]; braincase narrow betwen orbits, widening posteriorly [S&L]; paracotylar foramina present; **$** "parazygantral foramina" (i.e. foramina on the vertebrae lateral to the zygantra) [A]; prezygapophyseal processes absent; synapophyses (?!) located low from centrum [A][S&L]; tall, narrow vertebrae with single hypapophyses on anterior trunk [S&L]; vertebrae elongate and become lower more posteriorly [S&L]; trunk ribs curved throughout, with proximal facets slightly constricted between diapophyseal & parapophyseal processes; no limb or girdle elements [S&L].

Links: Faiyum introduction; fossili (Italian); Faiyum 2nd; News in Science 27/01/00 First snakes may have come from the water (*Wonambi*); A twist in the tail of snake evolution (**Best on the Web**); un485.pdf (third page); ABC Online Forum (comment from "eric").

References: Albino (2000) [A]; Caldwell & Albino (2001) [C&A]; Scanlon & Lee (2000) [S&L]

Note: Apparently, the only decently known madtsoiid is *Wonambi*. Thus the characters above are almost all apomorphies of *Wonambi*.

Pachyophiidae: *Haasiophis*, *Pachyophis*, *Pachyrachis*, *Podophis*.

Range: mK-upK of the Middle East & E.Eur.

Phylogeny: Macrostomata:: (Boidae + Caenophidia) + *.

Characters: up to 1.1 cm, with laterally compressed bodies [C&A]; probably wide gape [C&A]; pterygoids with teeth [T]; toothbearing process of dentary long [T]; long, recurved pterygoid teeth [C&L]; mandible not fused; **$** intramandibular joint

Haasiophis terrasanctus: detail of hind limb

anterior (*Pachyrachis*) [C&L]; angular not exposed on medial surface of jaw [C&L]; **$** large rectangular coronoid process (*Pachyrachis*) [C&L]; palatines do not contact ectopterygoid [T]; transverse process of pterygoid gently curved and receives ectopterygoid on lateral surface [T]; lateral edge of ectopterygoid not straight [T]; anterior end of ectopterygoid invades surface of maxilla, approaching posteroventral corner of orbit [T]; reduced *basipterygoid processes* [C&L]; lacrimal absent [C&L]; ventral tip of postorbital contacts (or almost contacts) ectopterygoid, completing orbital margin [T]; postorbital & postfrontal fused (*Pachyrachis* & maybe *Haasiophis*) [C&L]; supratemporal process of parietal not well developed [T]; "free ending" (?) process of supratemporal present [T]; braincase completely encased; prootic fully concealed by supratemporal or parietal in dorsal view [T]; quadrate vertical (cephalic condyle & mandibular condyle at same anteroposterior level) [T]; no or vestigial stapedial process of quadrate cephalic condyle [T]; **$** quadrate anteroposteriorly expanded (*Pachyrachis*) [C&L]; ~140 trunk vertebrae; pachyostotic mid-dorsal vertebrae & ribs [C&L] [C&A]; well-developed hindlimb, with pelvis outside ribs; may have sacrum [C&L]; femur, tibia, fibula and some tarsals present; astragalus & calcaneum not fused [C&L]; inhabited sheltered marine reef environments [C&A].

Links: ScienceDaily Magazine: New Fossil Snake With Legs; Argument About Snake Evolution Rekindled by Fossil; SNAKES.SMU.

Reference: Caldwell & Albino (2001) [C&A]; Caldwell & Lee (1997) [C&L]; Lee *et al*. (1999); Tchernov *et al*. (2000) [T]; Zaher (1998).

Note: [1] The characters above from [T] include only derived features, shared by both known genera. [T] also identify 3 synapomorphies of this group: **$** outer orbital (lateral) margin of prefrontal slanting anteroventrally; **$** ascending process of maxilla well-developed; **$** coronoid process from coronoid bone only. *All 3* are supposed reversals, and one might guess that the first two are correlated. This is indeed a weakly supported group. However, the derived characters *do* include strongly consistent (CI=1) macrostomate synapomorphies, so the paper's central conclusion -- that the 'Ein Yabrud specimens are macrostomates -- is well supported. **[2]** There now appears to have been a thriving and diverse community of Cretaceous marine snakes on both the Northern and Southern margins of the Tethys Sea in Late Cretaceous times. [C&A]. C&A note that the Southern population necessarilly places this group close in time and space to the Gondwanan madtsoiids. 010901.

Boidae: boas & pythons.

Range: fr upK.

Phylogeny: Macrostomata::: Caenophidia + *.

Characters: Squamosal and quadrate lengthened. Few diagnostic features: intermediates between Scolecophidia and advanced snakes.

Links: The Boa Constrictor Subspecies.

Caenophidia: (= Xenophidia = Colubroidea) "advanced," poisonous snakes and relatives

Range: fr Ec?; cosmopolitan

Phylogeny: Macrostomata::: Boidae + *: Acrochordoidea + Colubroidea.

Characters: complete absence of pelvic girdle.

Links: Snakes; Caenophidia after Gravlund, 2001. 011105.

Acrochordoidea: Wart or file snakes, *Acrochordus.*

Range:?

Phylogeny: Caenophidia: Colubroidea + *.

Characters: Like advanced snakes in mobility of jaw; primarily aquatic; scales parallel(?), secondarily(?) reduced ventral scales. ATW991003.

---

checked ATW060222

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

Squamata: Pythonomorpha: Colubroidea

Abbreviated Dendrogram

```
SQUAMATA
|--Iguania
Scleroglossa
|
Pythonomorpha
|--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   `--Alethinophidia
      |--Aniloidea
      `--Macrostomata
         |--Boidae
         `--Caenophidia
            |--Acrochordoidea
            `--Colubroidea
               |--Atractaspididae
               |--Elapidae
               `--+--Colubridae
                  `--Viperidae
                     |--Azemiopinae
                     `--+--Crotalinae
                        `--Viperinae
```

Contents

Taxa on This Page

1. Atractaspididae
2. Azemiopinae
3. Colubridae
4. Colubroidea
5. Crotalinae
6. Elapidae
7. Viperidae
8. Viperinae

Descriptions

Colubroidea: Earliest advanced snakes.

Range: fr Ec.

Phylogeny: Caenophidia: Acrochordoidea + *: Atractaspididae + Elapidae + (Colubridae + Viperidae).

Links: Higher Reptile Taxa.

Atractaspididae:

Range: currently Africa & Asia

Phylogeny: Colubroidea: Elapidae + (Colubridae + Viperidae) + *.

Characters: small to medium-sized snakes; blunt-headed; maxilla is extremely reduced; maxilla with elongated, hollow maxillary fang; maxilla has complex articulation with prefrontal; short tails; fossorial; solenoglyphs; oviparous with clutches of 2-11; feed upon newborn rodents and other fossorial reptiles

Links: Atractaspididae; Atractaspididae

Elapidae:

Phylogeny: Colubroidea: Atractaspididae + (Colubridae + Viperidae) + *.

Characters: Venomous, often marine snakes with hollow, relatively immobile maxillary fangs.

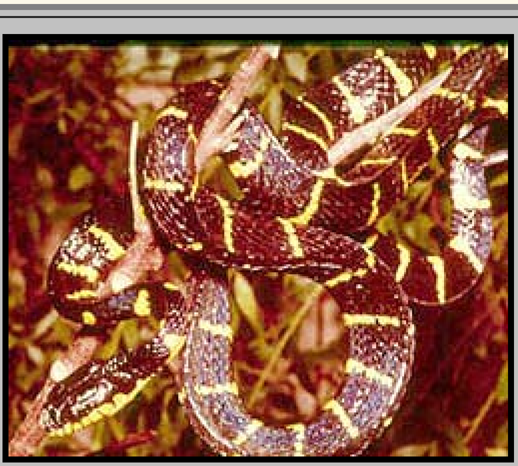
Colubridae:rat snakes, corn snakes, king snakes, garter snakes, indigo snakes, boomslangs, etc.

Range: All continents except Antarctica (and Australia?), in all but coldest latitudes.

Phylogeny: Colubroidea:: Viperidae + *.

Characters: 20-400 cm; frequently venomous but without anterior fangs or hollow teeth; venom, where present, mostly proteases; most have rows of teeth that are of equal size; teeth on premaxillae lost; maxilla elongate; *basipterygoid processes* lost; coronoids lost; pupils round; vertebrae generally lack downward-projecting spines; right common artery lost; pelvic girdle absent; large, strap-like scales in single row down the belly; most terrestrial.

Note: Very speciose taxon, with 85-90% of living species. May be a catch-all taxon for advanced snakes of multiple lineages. ATW021012.



***Boiga dendrophila*, the mangrove snake. From the Virtual Museum of Natural History, by permission.**

Links: Family Colubridae; Flying snake home page (Colubridae: Chrysopelea); Reptilia, Squamata, Ophidia, Colubridae, Nattern (German); Colubridae, (Italian); Predacao de anuros pela serpente (Portugese); ????????? ????? ? (Colubridae). ????: Colubrids. (Russian); Colubridae; I Colubridi, Colubridae (Italian); APUS.RU - Colubridae (Russian); SERPENTS (also in Russian); Advanced Snakes (pictures & lots of references); Colubridae.html (pictures). ATW030128.

Viperidae: adders, vipers, & copperheads.

Range: from the Early Miocene.

Phylogeny: Colubroidea:: Colubridae + *: Azemiopinae + (Crotalinae + Viperinae).

Characters: Large, triangular heads & stout bodies; maxilla short, with one tooth; maxillae rotates so that fangs folded during feeding (distinguishes from Elapids); venom teeth are closed tubes (*solenoglyph*) without visible seam; quadrates flared outward and highly mobile skull; venom common. Largely ambush predators of mammals, injecting venom, then following scent trail.

Image:*Agkistrodon contortrix laticinctus* from Viperidae.

Links: Encyclopedia Entry; Viperidae; Family- Viperidae (ADW); Reptilia, Squamata, Ophidia, Viperidae - Vipern (German); Viperidae.html (just pictures); Viperidae Familyasi (Turkish); I Viperidi, Viperidae (Italian: very thorough coverage); Viperidae (Mikko). ATW030121.

Azemiopinae: (= Azemophinae): *Azemiops* (Fea's viper).

Range: R of China, Tibet, northern parts of SE Asia.

Phylogeny: Viperidae: (Crotalinae + Viperinae) + *.

Characters: <82 cm long; head somewhat flattened & slightly triangular; fangs short; venom sacs comparatively small; loreal (infra-red sensitive) pit-organs absent; moderately sturdy body, with short tail; no tracheal lung; head with with large plates (colubridlike head scales); head scales orange; smooth body scales, body has widely spaced orange rings on a background of deep blue-gray to black; feeds on small mammals and lizards; vibrates tail against vegetation when threatened; hibernates in winter; oviparous.

Image:*Azemiops* from **Viperidae.**

Links: Viperidae; NCBI; ??? - ???? Azemiops feae (Chinese). ATW030503.

Crotalinae:

Phylogeny: Viperidae:: Viperinae + *.

Viperinae: *Adenorhinos, Atheris, Bitis, Cerastes, Daboia, Echis, Macrovipera, Vipera*. "Pitless vipers."

Phylogeny: Viperidae:: Crotalinae + *.

Links: Viperinae; Viperidae; Viperinae2001; The World Of Atheris; Biochem. J. - Bile acids of Viperinae; Viper's; Snake Basics 2 - Simon's Snake Website. ATW020817.

Page Back | Unit Home | Page Top | Page Next

checked ATW060222

Squamata: Dendrogram

Abbreviated Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
|
SQUAMATA
|--Iguania
|  |--Tropiduridae
|  |--Acrodonta
|  |  |--Priscagamidae
|  |  `--+--Agamidae
|  |     |  |--Amphibolurinae
|  |     |  `--Draconinae
|  |     `--Chamaeleonidae
|  `--Iguanidae
`--Scleroglossa
   |--Gekkota
   `--Evansauria
      `--Autarchoglossa
         |--+--Scincomorpha
         |   `--Amphisbaena
         `--+--Anguimorpha
            |   |--Anguoidea
            |   `--Varanoidea
            |      |--Monstersauria
            |      `--+--Necrosauridae
            |         `--+--Varanidae
            |            `--Lanthanotidae
            `--Pythonomorpha
               |--+--Aigialosauridae
               |  `--Mosasauroidea
               `--Serpentes
                  |--Scolecophidia
                  `--Alethinophidia
                     |--Aniloidea
                     `--Macrostomata
                        |--Boidae
                        `--Caenophidia
                           |--Acrochordoidea
                           `--Colubroidea
                              |--Colubridae
                              `--Viperidae
```

Contents

Dendrogram

```
LEPIDOSAUROMORPHA
|--SPHENODONTIA
`--o SQUAMATA MH, ToL, Tax
   |--Huehuecetzpalli
   `--+--Iguania (gross morphology) ToL, MH, Tax
```

```
      |     |--Tropiduridae � Tax
      |     |--Acrodonta MH
      |     |  |--Priscagamidae �X
      |     |  `--+--Agamidae MH, Tax
      |     |     |  |--Amphibolurinae
      |     |     |  `--Draconinae �
      |     |     `--Chamaeleonidae � MH, Tax
      |     `--Iguanidae  � MH, Tax
      `--Scincogekkonomorpha
         |-- Eichstaettisaurus
         `--+-- Ardeosaurus
            `--+-- Liushusaurus
               `--Scleroglossa
                  |-- Dibamidae
                  |--Gekkota
                  `--Autarchoglossa /Scincomorpha  MH
                     |--Scincoidea
                     |  |--Paramacellodidae
                     |  `--+--Scincidae
                     |     `--Cordyloidea
                     |--Xantusiidae
                     `--+--Lacertiformes
                        |  |--+--Teiioidea  MH
                        |  |  |  |--Teiidae  MH
                        |  |  |  `--Gymnophthalmidae  MH
                        |  |  `--Boreoteiioidea
                        |  |       |--Polyglyphanodontinae MH
                        |  |       `--Gilmoreteiidae MH
                        |  `--+--Lacertidae
                        |     `--Amphisbaena
                        `--Toxicofera
                           |?--Iguania (molecular phylogeny, see above for subgroups)
                           |--Anguimorpha
                           |  |--Anguoidea
                           |  `--Varanoidea
                           |     |--Monstersauria
                           |     `--+--Necrosauridae
                           |        `--+--Varanidae
                           |           `--Lanthanotidae
                           `--Pythonomorpha MH
                              |--+--Aigialosauridae �X
                              |  `--Mosasuroidea �X MH
                              `--Serpentes MH
                                 |--Scolecophidia
                                 |  |--Anomalepididae � MH
                                 |  `--+--Typhlopidae � MH
                                 |     `--Leptotyphlopidae � MH
                                 `--Alethinophidia
                                    |--Dinilysia �X
                                    `--+--Aniloidea MH
                                       |  |--Aniliidae �
                                       |  `--+--Cylindrophiidae �
                                       |     `--+--Uropeltidae �
                                       |        `--Anomochilidae �
                                       `--Macrostomata MH
                                          |--Madtsoiidae �X MH
                                          `--+--Pachyophiidae �X
                                             `--+--Boidae �
                                                `--Caenophidia MH
                                                   |--Acrochordoidea �
                                                   `--Colubroidea �
                                                      |--Atractaspididae � MH
                                                      |--Elapidae � MH
                                                      `--+--Colubridae � MH
                                                         `--Viperidae MH
                                                            |--Azemiopinae �
                                                            `--+--Crotalinae � MH
                                                               `--Viperinae � MH
```

Page Back | Unit Home | Page Top | Page Next

Checked ATW060219, ATW030719

Squamata: References

Abbreviated Dendrogram

```
Scleroglossa
|
Pythonomorpha
|--Mosasauroidea
`--Serpentes
   |--Scolecophidia
   `--Alethinophidia
      |--Aniloidea
      `--Macrostomata
         |--Boidae
         `--Caenophidia
            |--Acrochordoidea
            `--Colubroidea
               |--Colubridae
               `--Viperidae
```

Contents

References

Albertetal2009
Episquamata

Albino, AM (2000), *New record of snakes from the Cretaceous of Patagonia (Argentina)*. **Geodiversitas** 22: 247-253.
Madtsoiidae

Alifanov, V. R. 2000 Macrocephalosaurs and the early evolution of lizards of Central Asia. *Tr. Paleontol. Inst.*272, 1�126. [In Russian.]
Tuberocephalosaurus

Bailon, S (1988), *Un aniliid� (Reptilia, Serpentes) dans le Plioc�ne Sup�rieur Europ�en*. **C.R. Acad. Sci. Paris (Ser. II)** 306: 1255-1258.
Aniliidae.

Benton, M.J. 2000, Vertebrate Paleontology, Blackwell, 2nd Ed.

Paramacellodidae

Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica* 46: 5�105. pdf
Bainguidae

Caldwell, MW (1999), *Squamate phylogeny and the relationships of snakes and mosasauroids*. **Zool. J. Linnean Soc.** 125: 115-147.
Agamidae, Anguoidea; Lanthanotidae; Monstersauria; Pythonomorpha; Serpentes; Varanoidea.

Caldwell, MW & MSY Lee (1997), *A snake with legs from the marine Cretaceous of the Middle East*. **Nature** 386: 705-709. Squamata.

Caldwell, MW (2000), *On the phylogenetic relationships of* ***Pachyrachis*** *within snakes: a response to Zaher 1998).* **J. Vert. Paleontol.** 20: 187-190.
Serpentes

Caldwell, MW & AM Albino (2001), *Paleoenvironment and paleoecology of three Cretaceous snakes:* ***Pachyophis***, ***Pachyrachis***, *and* ***Dinilysia***. **Acta Palaeontol. Pol.** 46: 203-218.
Dinilysia; Madtsoiidae; Pachyophiidae.

Caldwell, MW, RL Carroll, & H Kaisar (1995), *The pectoral girdle and forelimb of* ***Carsosaurus marchesetti*** *(Aigialosauridae), with preliminary phylogenetic analysis of mosasauroids and varanoids* **J. Vert. Paleontol.** 15: 516-531.
Pythonomorpha.

Caldwell, MW & MSY Lee (1997), *A snake with legs from the marine Cretaceous of the Middle East*. **Nature** 386: 705-709.
Serpentes; Pachyophiidae.

Camp, C. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. 48:289-481.
Lacertiformes

Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. Freeman
"Teiioiformes", Xantusiidae.

Conrad, J. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology.*Bulletin of the American Museum of Natural History*, 310, 1�182 abstract and pdf
Scincogekkonomorpha

Cundall, D & DA Rossman (1993), *Cephalic anatomy of the rare Indonesian snake* ***Anomochilus weberi***. **Zool. J. Linnean Soc.** 109: 235-273.
Anomochilidae; Cylindrophiidae; Scolecophidia; Uropeltidae.

Cundall, D, V Wallach & DA Rossman (1993), *The systematic relationships of the snake genus* ***Anomochilus***. **Zool. J. Linnean Soc.** 109: 275-299.
Aniliidae; Anomochilidae; Cylindrophiidae; Scolecophidia; Serpentes, Uropeltidae.

deBraga, M & O Rieppel (1997) *Reptile phylogeny and the interrelationships of turtles*, **Zool. J. Linnean Soc.** 120: 281-354.
Squamata; Pythonomorpha.

Dixon, D. (2008) *The World Encyclopedia of Dinosaurs and Prehistoric Creatures*. Lorenz Books
Polyglyphanodontinae

Estes, RD, TH Frazzetta, & EE Williams (1970), *Studies on the fossil snake* ***Dinilysia patagonica*** *Woodward: part I. Cranial morphology*. **Bul. Mus. Comp. Zool.** 140: 25-73.
Scolecophidia.

Estes, R. 1983 Sauria Terrestria, Amphisbaenia. In *Handbuch der Palaeoherpetologie* 10A (ed. P. Wellnhofer), pp. 1�245. Stuttgart, Germany: Gustav Fischer Verlag.
Adamisaurus, *Gilmoreteius*, *Polyglyphanodon*

Estes, R.; de Queiroz, K. & Gauthier, Jacques (1988): Phylogenetic relationships within Squamata. In: Estes, R. & Pregill, G. (eds.): *The Phylogenetic Relationships of the Lizard Families*: 15-98. Stanford University Press, Palo Alto. pdf
Lacertiformes, "Teiioiformes", Teiioidea

Evans, S.E. 2003, At the feet of the dinosaurs: the early history and radiation of lizards. *Biol. Rev*. (2003), 78, pp. 513�551.
Huehuecuetzpalli, Paramacellodidae

Evans, S. E. & Barbadillo, L. J. 1998. An unusual lizard (Reptilia, Squamata) from the Early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, 124, 235�266.
Scandensia

Evans, S.E., Raia, P., and Barbera, C. 2004. New lizards and rhynchocephalians from the Lower Cretaceous of southern Italy. *Acta Palaeontologica Polonica* 49 (3): 393�408. pdf
Eichstaettisaurus

Evans, Susan E. and Wang, Yuan(2010) 'A new lizard (Reptilia: Squamata) with exquisite preservation of soft tissue from the Lower Cretaceous of Inner Mongolia, China', *Journal of Systematic Palaeontology*, 8: 1, 81 � 95
Huehuecuetzpalli,

Greene, HW (1997), **Snakes: the Evolution of Mystery in Nature.** U. Calif. Press, 351 pp.
Scolecophidia.

Hecht, MK (1959), *Amphibians and reptiles,* in PO McGrew (ed.), *The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming*. **Bull. Amer. Mus. Nat. Hist.** 117: 130-146.
Aniliidae; Cylindrophiidae; Serpentes.

Hedges, S.B. & Vidal, N. (2009). Lizards, snakes, and amphisbaenians (Squamata). In: S.B. Hedges & S. Kumar (Eds.). *The timetree of life* Oxford University Press, pp. 383-389.
Cordyloidea, Lacertiformes, Xantusiidae.

Holman, JA (2000), **Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology**. Indiana Univ. Press, 359 pp.
Alethinophidia; Aniliidae

Kley, NJ (1998), *Kinematics and mechanics of prey transport in scolecophidian snakes*. **Amer. Zoologist** 38: 202A (abstract).
Scolecophidia.

Kley, NJ & EL Brainerd (1999), *Feeding by mandibular raking in a snake*. **Nature** 402: 369-70.
Scolecophidia.

Langer, M.C. 1998. Gilmoreteiidae new family and *Gilmoreteius* new genus (Squamata Scincomorpha): replacement names for Macrocephalosauridae Sulimski, 1975 and *Macrocephalosaurus* Gilmore, 1943. *Comunicacoes do Museu de Ciencias e Tecnologia* 11: 13-18. (UBEA/PUCRS) pdf
Gilmoreteiidae

Lee, MSY (1997), *Pareiasaur phylogeny and the origin of turtles*. **Zool. J. Linnean Soc.**, 120: 197-280.
Pythonomorpha.

Lee, MSY (1997a), *The phylogeny of varanoid lizards and the affinities of snakes*. **Phil. Trans. R. Soc. Lond. B** 352: 53-91.
Anguoidea; Monstersauria; Pythonomorpha; Serpentes; Varanidae; Varanoidea.

Lee, MSY (1998). Convergent evolution and character correlation in burrowing reptiles : toward a resolution of squamate phylogeny. Biological Journal of the Linnean Society 65, 369�453.
Xantusiidae.

Lee, MSY, GL Bell Jr. & MW Caldwell (1999a), *The origin of snake feeding*. **Nature** 655-659.

Cylindrophiidae, Mosasauroidea, Pythonomorpha, Squamata.

Lee, MSY, MW Caldwell & JD Scanlon (1999), *A second primitive marine snake:* ***Pachyophis woodwardi*** *from the Cretaceous of Bosnia-Herzegovina*. **J. Zool. London** 248: 509-520.
Serpentes, Pachyophiidae.

Macey, JR, JA Schulte II & A Larson (2000),*Evolution and phylogenetic information content of mitochondrial genomic structural features illustrated with acrodont lizards.* **Syst. Biol.** 49: 257-277.
Acrodonta

Macey, JR, A Larson, NB Ananjeva & TJ Papenfuss (1997), *Replication slippage may cause parallel evolution in the secondary structures of mitochondrial transfer RNAs*. **Mol. Biol. Evol.** 14: 30-39.
Anguimorpha

Macey, JR, JA Schulte II, A Larson, NB Ananjeva, Y Wang, R Pethiyagoda, N Rastegar-Puyani, & TJ Papenfuss (2000a), *Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics.* **Syst. Biol.** 49: 233-256.
Acrodonta, Agamidae, Amphibolurinae, Draconinae.

Mo JY, Xu X, Evans SE. 2009, The evolution of the lepidosaurian lower temporal bar: new perspectives from the Late Cretaceous of South China. *Proceedings of the Royal Society B: Biological Sciences* Vol. 277(1679): 331-336 html/pdf
Boreoteiioidea

Nydam, RL (2000), *A new taxon of helodermatid-like lizard from the Albian-Cenomanian of Utah* **J. Vert. Paleontol.** 20: 285-294.
Anguimorpha; Monstersauria.

Nydam, R.L. and Cifelli, R.L. (2005) New data on the dentition of the scincomorphan lizard Polyglyphanodon sternbergi. *Acta Palaeontologica Polonica* 50 (1): 73�78
Polyglyphanodontinae

Nydam, R. L.; Gauthier, J.A.; and Chiment, J.J. (2000) The mammal-like teeth of the Late Cretaceous lizard Peneteius aquilonius Estes 1969 (Squamata, Teiidae). *Journal of Vertebrate Paleontology* 20: 628�631
Polyglyphanodontinae

Nydam, R. L., J. G. Eaton, and J. Sankey. 2007. New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary historyof Teeids. *J. Paleont*., 81(3), 2007, pp. 538-549
Boreoteiioidea, Polyglyphanodontinae

Rieppel, O & H Zaher (2000), *The braincases of mosasaurs and* ***Varanus,*** *and the relationships of snakes*. **Zool. J. Linn. Soc.** 129: 489-514.
Varanoidea.

Scanlon, JD & MSY Lee (2000), *The Pleistocene serpent* ***Wonambi*** *and the early evolution of snakes*. **Nature** 403: 416-420.
Aniliidae, Madtsoiidae, Serpentes.

Schultze, H-P (1994), *Comparison of hypotheses on the relationship of sarcopterygians*. **Syst. Biol.** 43: 155-173.
Varanoidea.

Sulimski, A. 1972 Adamisaurus magnidentatus, n. gen., n. sp. (Sauria) from the Upper Cretaceous of Mongolia. *Palaeontol. Polon*. 27, 33�40. pdf
Adamisaurus

Szyndlar, Z (1994), *Oligocene snakes of southern Germany*. **J. Vert. Paleontol.** 14: 24-37.
Aniliidae

Tchernov, E, O Rieppel, H Zaher, MJ Polcyn & LL Jacobs (2000),*A fossil snake with limbs.* **Science** 287: 2010-2012.
Aniliidae, Anomalepididae, Alethinophidia, *Dinilysia*, Leptotyphlopidae, Macrostomata, Pachyophiidae; Scolecophidia; Serpentes, Typhlopidae.

Vidal, N. & Hedges, S.B. (2005). The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *C. R. Biologies* 328 (2005) 1000�1008
Episquamata, Lacertiformes, Unidentatan

Wiens, J. J., C. A. Kuczynski, T. M. Townsend, T. W. Reeder, D. G. Mulcahy, and J. W. Sites, Jr. (2010). Combining phylogenomics and fossils in higher-level squamate phylogeny: molecular data change the placement of fossil taxa. *Systematic Biology*. 59 (6): 674-688.
Huehuecuetzpalli

Zaher, H (1998), *The phylogenetic position of* **Pachyrachis** *within snakes (Squamata, Lepidosauria)*. **J. Vert. Paleontol.** 18: 1-3.
Macrostomata, Pachyophiidae, Serpentes.

Page Back | Unit Home | Page Top | Page Next

checked ATW030408, ATW030719, ATW050706,