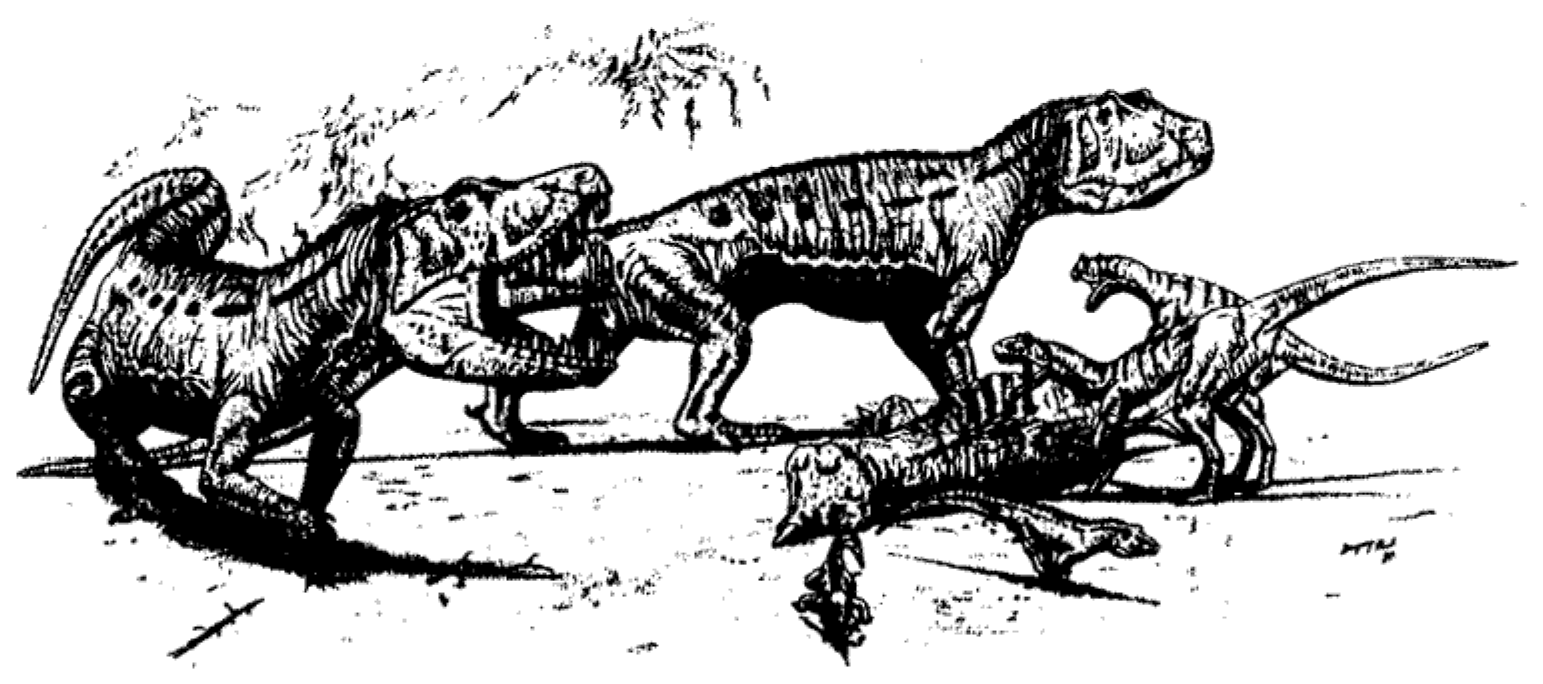
Archosauromorpha: Overview

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

The Archosauromorphs



Triassic Archosauromorphs. A pair of giant predatory prestosuchids (*Saurosuchus galilei*) appropriate a hyperodapedontine rhynchosaur carcass (*Scaphonyx sanjuanensis*), causing small herrerasaurid dinosaurs and ornithosuchids (*Venaticosuchus rusconii*) to flee.

Illustration by Greg S Paul, from K Padian (ed.), *The Beginning of the Age of Dinosaurs*, © Cambridge Univ. Press.

Page Back Unit Home Page Top Page Next

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Archosauromorpha

Protorosaurs

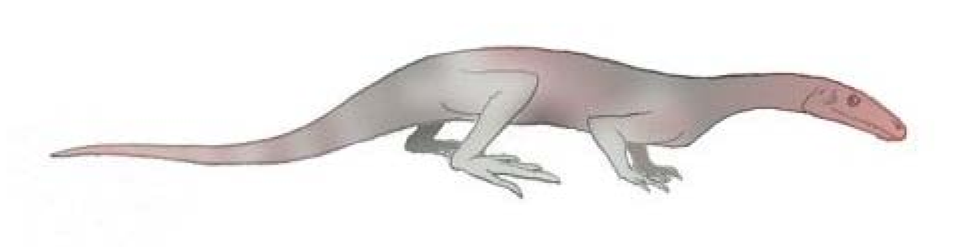
Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--o ARCHOSAUROMORPHA
   |--"Protorosauridae"
   |  |--Czatkowiella
   |  `--Protorosaurus
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

Taxa on This Page

1. Archosauromorpha
2. *Czatkowiella* X
3. "Protorosauridae" X
4. *Protorosaurus* X



Life restoration of *Prolacerta broomi*, an archosauromorph from the Induan of South-west Gondwana. Length about 60 cm. *Protorosaurus speneri* would have been very similar in appearance. The long neck and long hind limbs (for bursts of bipedal running) represent the basal or primitive archosauromorph condition, from which the various more specialised types evolved. Illustration by Ghedoghedo (Wikimedia)

Descriptions

Archosauromorpha: Buzzards > Lizzards

Range: from the Middle Permian.

Phylogeny: Sauria **:** Lepidosauromorpha + * **:** Protorosauridae + (?Choristodera + ?*Helveticosaurus* + ??Chelonia (according to molecular phylogeny, otherwise Anapsida or Lepidosauromorpha) + (Rhynchosauria + (Trilophosauria + (Prolacertiformes + Drepanosauridae + Archosauriformes)))).

Characters: Cervical ribs with 2 heads; concave-convex articulation of astragalus & calcaneum; premaxilla extends dorsally behind nares & excludes maxilla; teeth in sockets; neck with 7-8 vertebrae; centra not deeply *amphicoelous*; *pisiform* usually absent in carpus; primitively, *calcaneal tuber* extends laterally beyond articulating surface of calcaneum (pulley for *gastrocnemius* – more upright position?).

Links: **The Triassic Takeover** (with numerous links); **Reptilian Systematics**. **Archosauromorpha - Wikipedia, the free encyclopedia** has a short discussion, outlining the enormous scope of this group. **Archosauromorpha** has a similar, somewhat fuller discussion, in the same vein, in Spanish. You can get a sense of this diversity directly at **Mikko's Phylogeny** or on the **Taxonomicon**. There is also an on-line (no figures) version of Chris Brochu's review of archosaur systematics and phylogenetic problems at **Journal of Paleontology- Progress and future directions in ...** . Several sites discuss Archosauromorpha as background to the study of dinosaurs; for example **Dinosaur Origins**. **Comparative Anatomy Topic 3 - Archosaurs** and **Archosauria- More on Morphology** have introductions to the anatomy of the group. Some of John Hutchinson's archosaur mechanics papers (destined to be classics) can found here and there, including **here**. ATW051001. (phylogeny MAK101007)

Protorosauridae: (= Archosauromorpha?) *Protorosaurus, Czatkowiella*.

Range: Middle Permian to Early Triassic of Europe.

Phylogeny: Archosauromorpha **:** ?Choristodera + ?*Helveticosaurus* + ??Chelonia + (Rhynchosauria + Trilophosauria + (Prolacertiformes + Drepanosauridae + Archosauriformes)) + * **:** *Czatkowiella* + *Protorosaurus*.

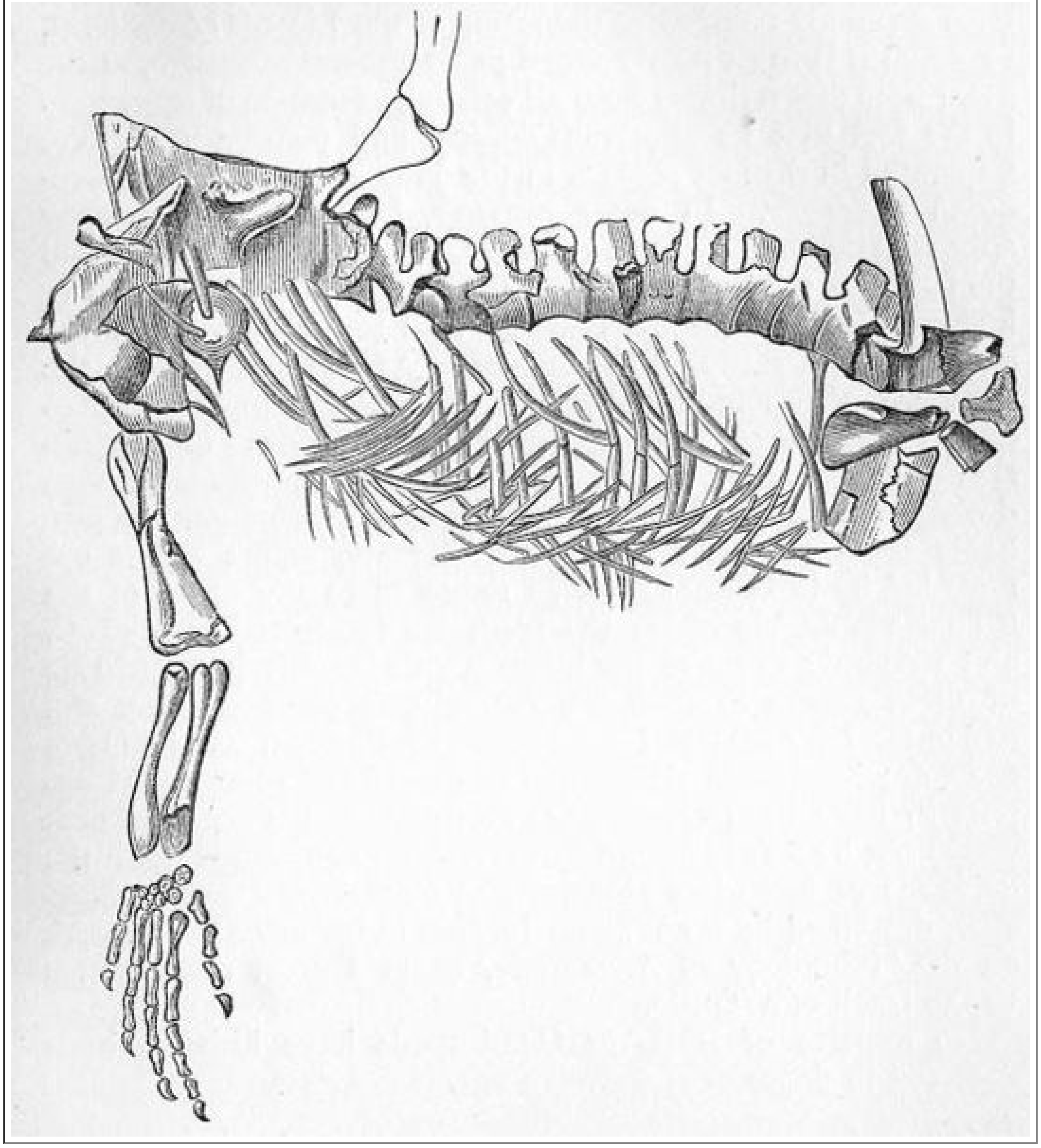
Comments: Although cladograms by Borsuk-Bialynicka & Evans, 2009 unite *Protorosaurus* and *Czatkowiella*, there are few, if any, clear synapomorphies (unique shared features that define a clade as having a common ancestor apart from other related forms) and this is probably a paraphyletic group. MAK101007

Protorosaurus: *Protorosaurus speneri* von Meyer, 1830 .

Synonym: *Proterosaurus* (variant spelling)

Range: Kupferschiefer, late Middle Permian (Capitanian) of East Germany

Phylogeny: Protorosauridae **:** *Czatkowiella* + *.



Protorosaurus speneri. From Henry Alleyne Nicholson, 1876, *The Ancient Life History of the Earth*, Project Gutenberg (public domain). (also on Wikimedia commons)

Characters: From Zittel/Eastman/Woodward 1902 (copyright expired) "Attaining a length of 1.5 m. Vertebral centra completely ossified, and united with their neural arches by suture. Intercentra occur only between the cervical vertebrae, which are elongate, and bear slender ribs. Skull tapering anteriorly, its structure not clearly shown.Hind limb considerably longer than the fore, and distal tarsals less than five in number. Upper Permian (Kupferschiefer) of Thuringia and Hesse, and Magnesian Limestone of Durham, England."

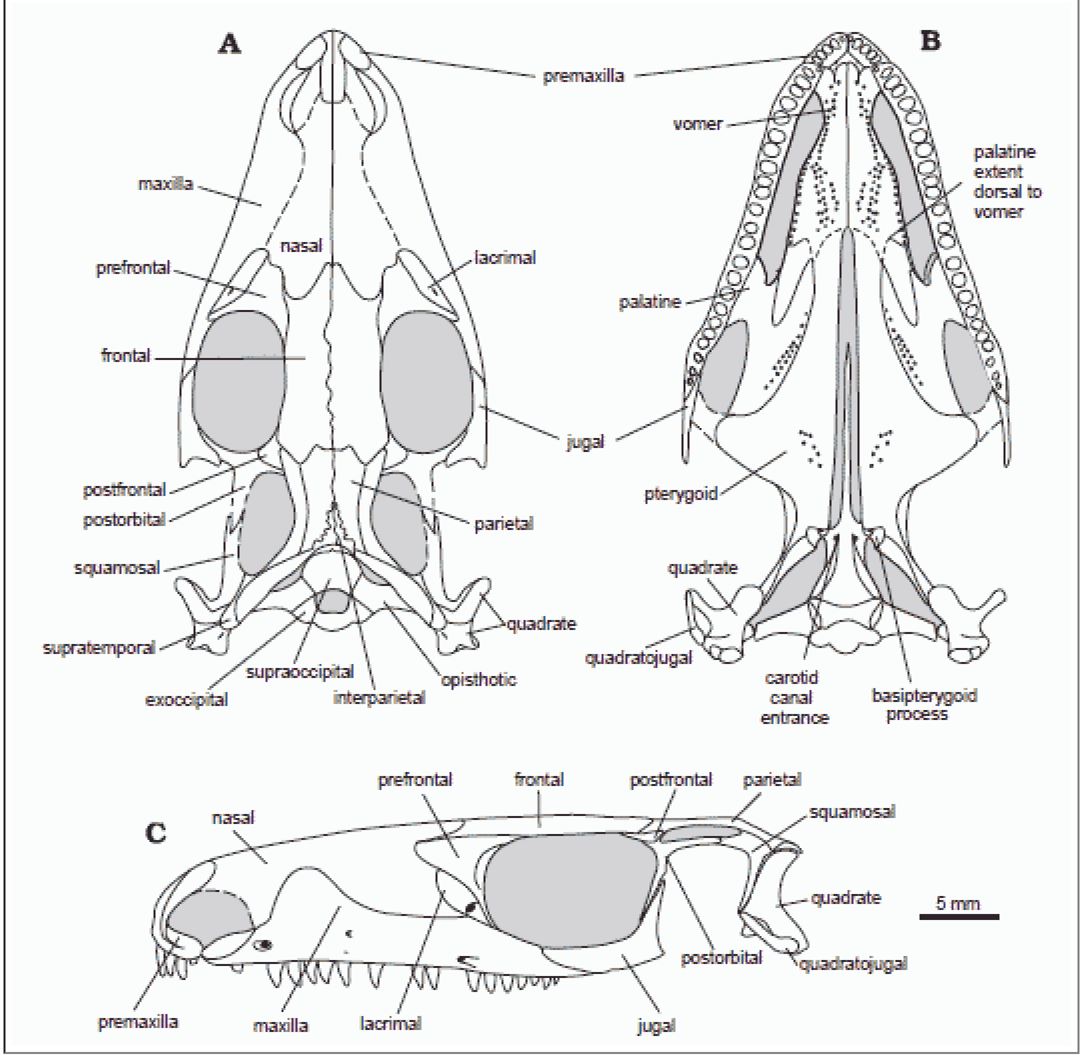
Comments: The earliest known Archosauromorph. Although frequently illustrated as a complete skull and skleleton, or life reconstruction, and often mentioned, this is a poorly known form. Included first in the Euryaspida, later in the Prolacertiformes. Although similar to *Prolacerta*, there are many aspects of its anatomy that are still controversial (Benton 1985), and it may have a more basal position. (Borsuk-Bialynicka & Evans, 2009). Although usually reconstructed as semi-aquatic, these animals were more probably fully terrestrial, very similar in lifestyle and appearance to extant monitor lizards (Varanidae). It is quite likely that the Protorosaurs and Prolacertifomes simlarily used gular pumping of the hyoid skeleton to ventilate the lungs more efficiently. (Dr John Merck - Archosauromorpha). The life- reconstruction of *Prolacerta* at the top of the page could equally apply to *Protorosaurus* or the related *Czatkowiella*.

Links: Wikipedia - Dinocasts com life-sized cast (along with replica fossils and reconstructions of other permian fauna) very nice although the grass spoils the effect (grass didn't appear until the early Tertiary) MAK101008

Czatkowiella: *Czatkowiella harae* Borsuk-Bialynicka & Evans, 2009.

Range: Late Olenekian of Poland

Phylogeny: Protorosauridae : Protorosaurus + *.



The basal archosauromorph *Czatkowiella harae*, Early Triassic of Czatkowice, Poland. Reconstruction of the skull, (length about 4 cm) in dorsal (A), ventral (B), and lateral (C) views. from Borsuk-Bialynicka & Evans, 2009. This was a long necked animal very similar in appearance to, but smaller than, *Protorosaurus* and *Prolacerta*

Characters: long slender neck, three headed ribs on some anterior dorsal vertebrae, and short broad neural spine tips in the dorsal vertebrae.

Comments: resembles *Protorosaurus* but differs enough to justify distinct generic status. Both show diagnostic long-necked “prolacertiform” characteristics (loss of the parietal foramen, distinct transverse processes on the dorsal vertebrae, double-headed ribs), but cladistic analyses does not recover a monophyletic Prolacertiformes. Czatkowiella and Protorosaurus represent basal archosauromorphs with few specialised or common characteristics; the traditional prolacertiforms, like the younginiformes, probably represent a basal assemblage grouped together because of shared primitive (plesiomorphic) characteristics the retention of primitive character states. If ichthyosaurs, sauropterygians, and testuduines are archosauromorphs, they would derive from this early evolutionary assemblage of long-necked lizard-like forms.

References: Borsuk-Bialynicka & Evans, 2009.

Links: Wikipedia MAK101007

Page Back Unit Home Page Top Page Next

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Helveticosauridae

Abbreviated Dendrogram

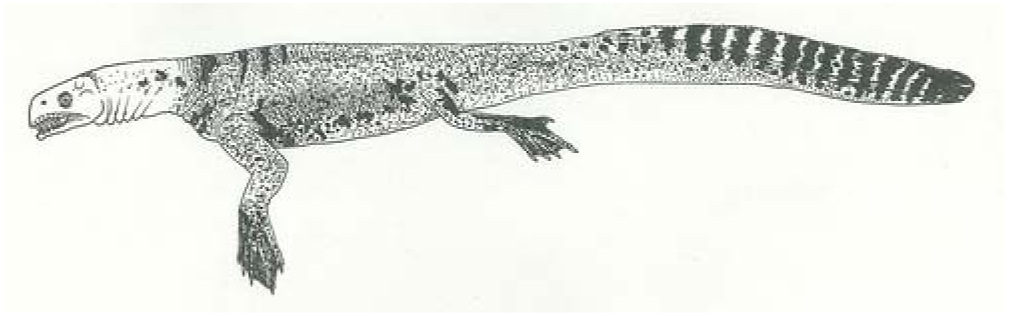
```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosauroidea
      |      |--Helveticosaurus
      |      `--SVT 203 (unnamed genus)
      |
```

`--+--Rhynchosauria `--+--Trilophosauria `--+--Prolacertiformes |--Drepanosauridae `--ARCHOSAURIA

Contents

Taxa on This Page

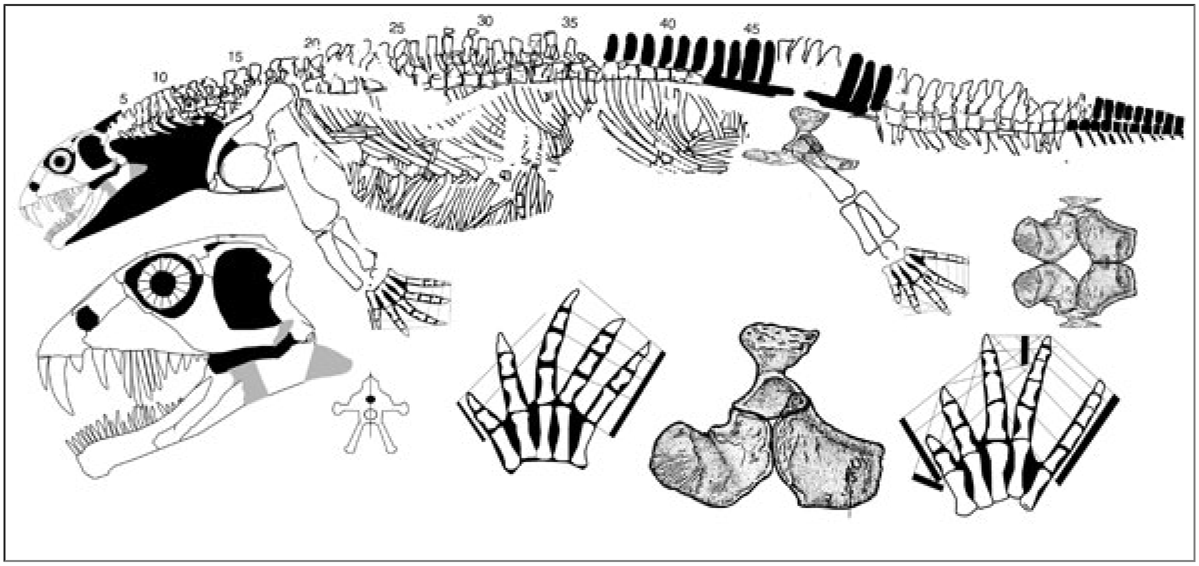
1. Helveticosauroidea X
2. *Helveticosaurus* X
3. SVT 203 (unnamed genus) X



Life restoration of the enigmatic diapsid *Helveticosaurus zollingeri*, Middle Triassic of European Tethys. Illustration copyright © Darren Naish (Flikr)

Introduction

During the Triassic Period, there was a tremendous evolutionary radiation among the diapsid reptiles. Among these, a surprising number of different lineages returned to the sea, where they quickly evolved into a number of specialised forms, superficially resembling the modern marine iguana in size and shape. Many were highly endemic. Among the strangest of these were the Helveticosaurs, whose bizarre appearance is featured in the illustrations on these pages. Whatever the helveticosaurs did for a living, they were reasonably succesful, as they continued for several millions of years of teh Early and Middle Triassic. Perhaps in the end they were out-competed by the turtle and walrus-like placodonts, which they closely but superficially resembled. Or perhaps it was just the changing environment of the Triassic world. In any case, by the start of the Jurassic, all these strange creatures had disappeared, the world was a less diverse place, and the seas were owned by ichthyosaurs, plesiosaurs, and marine crocodiles. In any case, these little known craetures are unique enough to deserve their own Unit on palaeos, at least until future research and phylogenetic anaylsis places them unambiguously among one or another of the better known reptilian groups of the Triassic. MAK110923



Reconstruction of skull and skeleton of *Helveticosaurus zollingeri*. The original animal was about 2 meters long. Drawing copyright © David Peters - Reptile Evolution - original url, reproduced with permission.

The enigmatic Helveticosaurs

Helveticosaurus was for some time classified as the most primitive member of the Placodontia (a clade of turtle-like Sauropterygia), in which it was given its own superfamily, the Helveticosauroidea. (Peyer 1955). Olivier Rieppel, an expert on Sauropterygia, rejects the Helveticosaurus is a placodont status of (Rieppel, 1989). Only the dorsal vertebrae of *Helveticosaurus*, which are very similar to those of placodonts, suggest that it is a member of the order; the genus lacks many of the autapomorphies characteristic of sauropterygians and thus evolved from a different ancestor, independently adapting a marine lifestyle. Its affinities with other diapsids remain largely unknown, as it differs greatly from any other known taxa, with no apparent close relatives. It shares some characteristics with archosauromorphs, and may be related to the clade if not a member of it. (Adapted from Wikipedia)

Rieppel argues on cladistic grounds that the Sauropterygia are lepidosauromorphs. But perhaps, if Sauropterygia fall on the archosauromorph side of the fence, then an archosauromorphian *Helveticosaurus* may represent a possible intermediate form. However, most who do support an archosauromorph status of Sauropterygia do so by grouping the Sauropterygia with the Ichthyopterygia (Ichthyosaurs and relatives) as the Euryaspida (Caldwell 1996; Merck 1997). This would make the Thalattosaurs, a group of diapsids of uncertain relationships but increasingly allied with ichthyosaurs, and in any case very unlike *Helveticosaurus*, basal Euryaspida and hence basal archosauromorphs. While David Peters presents a cladistic tree that nests Helveticosaurus in the thalattosauriforms, more derived than *Askeptosaurus*

Descriptions

Helveticosauroidea: *Helveticosaurus zollingeri* Peyer 1955.

Range: Early to Middle Triassic of Europe (north and central Laurasia)

Phylogeny: ???Archosauromorpha **:::** * **:** *Helveticosaurus* + SVT 203

Comments: Originally considered basal placodonts. MAK101008

Helveticosaurus .

Range: Middle Triassic (Anisian/Ladinian boundary) of Monte san Giorgio, Switzerland (Tethys Sea)

Phylogeny: Helveticosauroidea **:** SVT 203 + *.

Reference: Peyer 1955.

Comments: From Wikipedia: "*Helveticosaurus* possessed many features that were adaptations to a marine lifestyle in the shallow-sea environment that existed in Europe at the time when much of the continent was part of the Tethys Ocean. The long, flexible tail is similar to what can be seen in other extinct marine reptiles such as thalattosaurs, and it probably propelled itself through the water by means of lateral undulation. However, Helveticosaurus also possessed a robust pectoral girdle and forelimbs that were well adapted for paddle like propulsion as a supplementary method of locomotion, as seen in secondarily aquatic tetrapods. This unique combination of undulation and paddling is highly unusual for an aquatic reptile."

Links: Wikipedia, Darren Naish - One of so many bizarre Triassic marine reptiles, Art Gallery - Silvio Renesto, David Peters - Reptile Evolution. MAK101008, 110923

SVT 203 (unnamed species) .

Range: Early Triassic of Spitsbergen

Phylogeny: Helveticosauroidea **:** *Helveticosaurus* + *.

Comments: From Wikipedia: Pelvic material from SVT 203, may share similarities with the pelvic material known from Helveticosaurus. (Motani, 2000) However, this is only if the anterior element of the pelvic girdle in Helveticosaurus is interpreted as the pubis. The pubis of SVT 203 also shares similarities with placodonts, although the ischium differs in lacking constriction. SVT 203 was once referred to the ichthyosaur *Grippia longirostris* (Mazin 1981) but the pubis, femur, metatarsals, and phalanges suggest that it is not from an ichthyopterygian, therefore making it more probable that it belongs to a taxon related, and possibly ancestral, to *Helveticosaurus*, although more material is needed to give a definitive confirmation. The small size of material comprising SVT 203 in relation to *Helveticosaurus*, along with the compression seen on both ends of the femur, may indicate that it is a juvenile form of the species to which it belongs, but both temporal and geographical separation of SVT 203 with *Helveticosaurus* makes size comparison as a means of determining immaturity unnecessary, as it is possible that *Helveticosaurus* evolved from an ancestor that was smaller in overall size.

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images not loading? | error messages? | broken links? | suggestions? | criticism?
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page last modified MAK110923

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

Archosauromorpha: Rhynchosauria

Rhynchosaurs

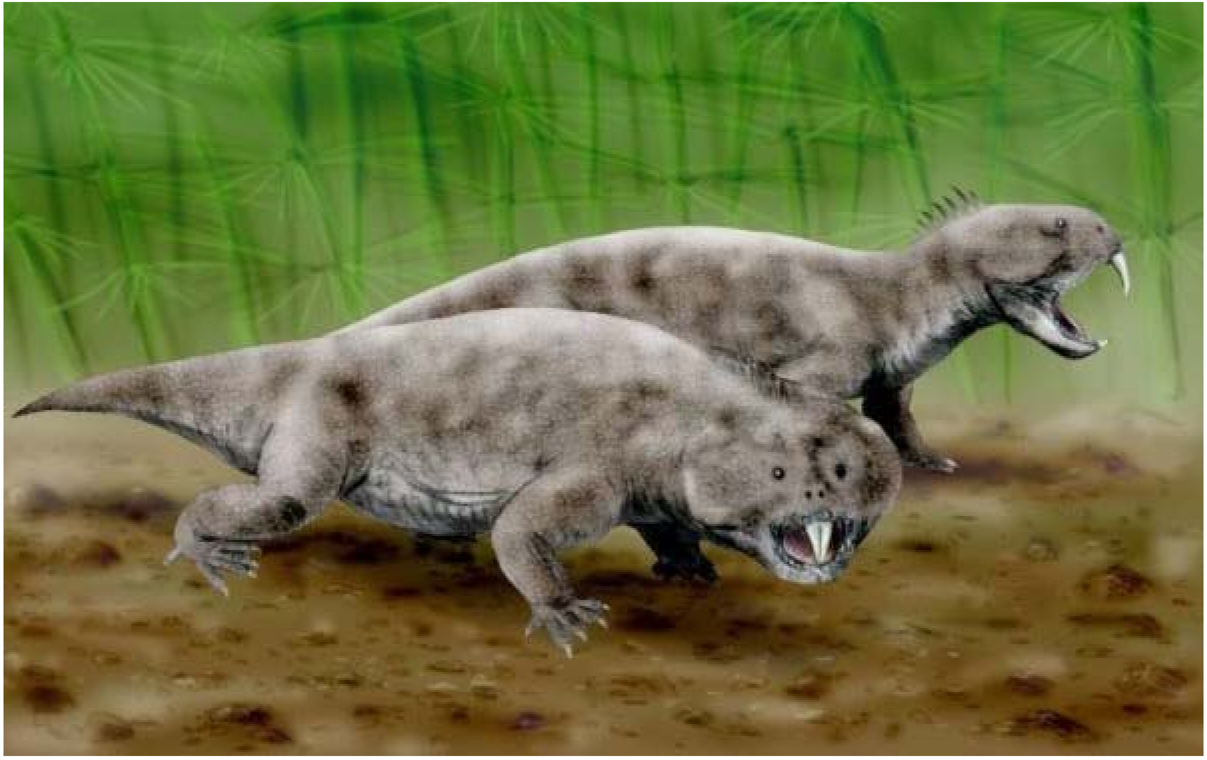
Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

Taxa on This Page

1. Rhynchosauria X

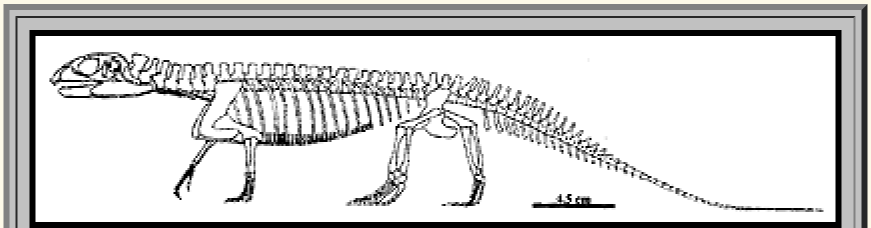


Life reconstruction of the advanced late Triassic rhynchosaur *Hyperodapedon huxleyi*, late Carnian of India
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

The rhynchosaurs are a group of highly distinctive Triassic archosauromorphs. Early forms, like Mosuchus, were quite lizard-like in appareance, but more derived forms like the ubiquitous genus Hyperodapedon became stocky herbivores about 1.5 meters long, with strong digging claws, beaked heads wider than they were long, and remarkable tooth plates for processing tough plant material. During a brief interval in the Late Triassic (the late Cranian, or, in the "Long Norian" chronology, early Norian), they were the most abundant terrestrial herbivores. The sudden and unexpected demise of such successful animals, and their contemporaries the more conventionally lizard-like Trilophosauria and the ox-sized kannemeyeriid dicynodonts, may or may not have been associated with the extinction of the *Dicroidium* flora that had characterised much of the Triassic Gondwanan ecosystem MAK120312

Descriptions

Rhynchosauria:



Mesosuchus browni **reconstruction in left lateral view. From Dilkes (1998)**

Range: Triassic, fl Middle Triassic

Phylogeny: Archosauromorpha :: (Trilophosauridae + (Prolacertiformes + Archosauriformes)) + *.

Characters: Specialized dentition with numerous rows in maxilla & dentary and beak; temporal area greatly expanded latterally (adductor muscles); pig-sized; teeth not replaced, but new rows added. In later forms, rear limbs move under body, astragalus & calcaneum attach & lose articulating surface; tarsus consolidates to simple hinge for fore-and-aft motion. Possible ecological intermediate between dicynodont & dinosaur-dominated faunas.

Links: link (note * are 60% of vertebrates found here); link (ichnology).

References: Dilkes (1998). ATW991008.

Page Back Unit Home Page Top Page Next

checked ATW050908, last modified MAK120312

Archosauromorpha: Trilophosauria

Trilophosaurus

Abbreviated Dendrogram

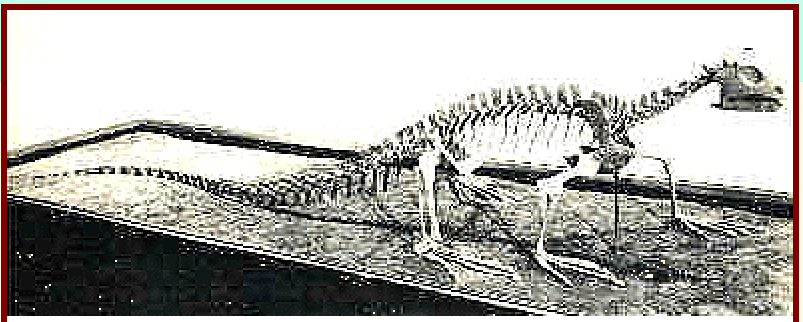
```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauridae
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

Taxa on This Page

1. Trilophosauridae X

Trilophosaurus



Trilophosaurus, from a 1949 Texas Memorial Museum postcard.

There is something a little magical about holding a rare paleontological manuscript, even if it is only a moderately obscure thesis from scarcely thirty years ago. Just for a moment, you can be perhaps the sole possessor of some arcane shard of knowledge which few have seen and all but you have lost or forgotten. For a brief interval you can empathize with the cackling grey-beard medieval alchemist gloating over a treasured, rotting manuscript; or the last, most-favored student of the half-senile musical pandit who has just learned a final and most secret *bandish* from the lips of his dying master.

Its a strange and unique experience, but a really dangerous way to run a science. Recently I was able to obtain Peter Parks' 1969 master's thesis on the cranium of ***Trilophosaurus***. I'm not sure how many copies exist, but the library copy I borrowed, perhaps the only one in general circulation, was poorly bound and lacked a number of important figures. I understand that more work is being done on the beast. However, until that is published, Parks (1969) remains one of the very few sources of detailed anatomical information on this unusual early archosauriform. One of the others, a University of Texas publication from the 1940's, is even more difficult to locate. Gregory, JT (1945), *Osteology and relationships of* ***Trilophosaurus***. **U. Tex. Publ.** No. 4401: 273-359

The gist of Parks' work is that *Trilophosaurus* evolved in such a way that its braincase and cranium had a very strong vertical orientation. Parks reconstructs the jaw musculature in detail and argues that the jaw was capable only of simple orthal (vertical) chomping, with no grinding. The long vertical runs of muscle must surely have permitted a strong, rapid bight which probably aided the presumed beak to clip vegetation efficiently. Parks argues from this data, and from the pattern of wear facets, that *Trilophosaurus* fed primarily on rough, silicate-containing vegetation.

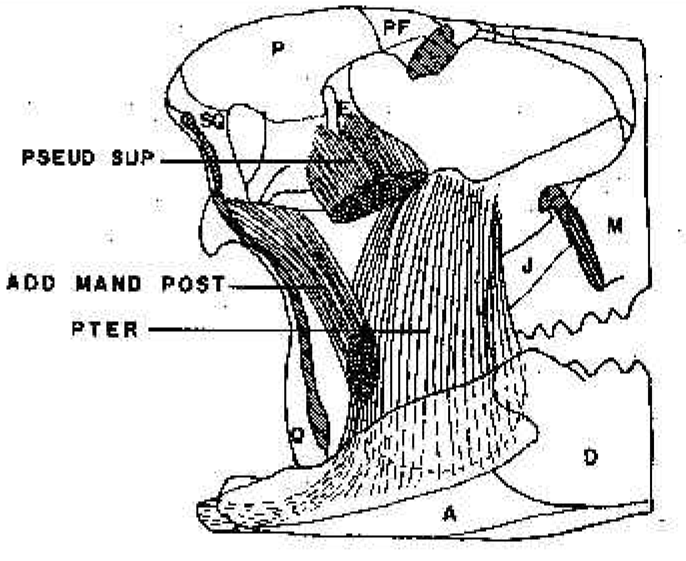


Figure 22. *Trilophosaurus*. Jaw musculature reconstruction, third depth, X1.

In fact, these observations may lend themselves to an alternate interpretation. The wear facets are not notably deep or common. The really striking thing about the skull is its consolidation and height. This was a skull designed to deliver and withstand very sharp, rapid shocks, presumably with a reasonably sharp beak, and then further cut its food rather finely. This suggests perhaps a strongly fibrous food source, or one covered by a hard external layer: a woody fern or something on that order.

Whatever the story may be, we should know more in a few years. --ATW 000618 Revised ATW030808.

Descriptions

Trilophosauridae: *Trilophosaurus*.

Range: ?Early Triassic to Late Triassic of North America.

Phylogeny: Archosauromorpha ::: (Prolacertiformes + Archosauriformes) + *.

Characters: Similar to Rhynchosaurs, 2-3 m. Skull 10-15 cm long; dermal bones smooth; premaxilla and opposite surface of dentary without teeth, possibly with horn beak; snout very narrow; cheek teeth expanded transversely to sharp slicing surfaces; lower temporal fenestra and maxillary fenestra absent; orbits large, high on skull, and closely spaced on the narrow skull; orbits extensively floored by jugals and palatines; lacrimal small, not reaching nares; septomaxilla absent; skull highly consolidated, with sides tall and essentially vertical; dorsal surface of skull table dominated by large, wide fenestrae; high, narrow parietal crest between upper fenestrae; post-temporal bar narrow, overhanging occiput; quadrate tall with a marked posterior notch; tabulars, postparietals and supratemporals absent; wide, somewhat elongated ventral spines; heavy tail with long, heavy chevrons; no suggestion of upright carriage; phalanges very long; herbivorous.

***Trilophosaurus* © 1997 Pamela Gore (Georgia Perimeter College); reproduced by permission.**

Image: *Trilophosaurus* © 1997 Pamela Gore (Georgia Perimeter College); reproduced by permission.

Links: Mesozoic; Reptilian Systematics; Untitled Document; trilophosaurus (Douglas Henderson image); New Page 1; Centre Consolidated School, Geology Page (kids' site, but very well done); IS NOT A PROCOLOPHONID-DATA FROM A ... (abstract); Natural Canvas Fossils - Reptiles 1 (some very nice teeth); Trilophosauria (Mikko); 川崎悟司イラスト集·トリロフォサウルス (Japanese).

References: Carroll (1988); Jalil (1997); Parks (1969). ATW030825.

Page Back Unit Home Page Top Page Next

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Archosauromorpha: Prolacertiformes

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
     `--+--Rhynchosauria
         |--Trilophosauria
         |?--Dinocephalosaurus
         `--+--+--Prolacerta
"Prolacertiformes"
            |  `--Malerisaurus
            |--Macrocnemus
            |--Tanystropheidae
            |--Drepanosauridae
            `--ARCHOSAURIA
```

Contents

Taxa on This Page

1. *Dinocephalosaurus* X
2. *Prolacerta* X
3. Prolacertiformes X
4. Tanystropheidae X
5. *Malerisaurus* X
6. *Macrocnemus* X

Life restoration of *Malerisaurus robinsonae*, a prolacertiform from the Late Triassic of India. The long neck and long hind limbs (for bursts of bipedal running) are primitive archosauromorph features. Illustration by Nobu Tamura (Wikipedia)

The Prolacertiformes - an assemblage of early archosauromorphs

Prolacertiformes or Protorosaurs are an assemblage of mostly lizard like archosauromorphs that, with the exception of the Permian *Protorosaurus*, were limited to the Triassic Period, although during this time they were diverse and widespread. There is a close similarity between *Prolacerta* and *Proterosuchus (Chasmatosaurus)*, and it generally accepted that Prolacertiformes (sensu stricta) and Archosauriformes are sister-groups, or in other words that Archosauriformes ("thecodonts" in older books) evolved from a Archosauriforme-like ancestor. Rhynchosaurs and Trilophosaurs seem to be less closely related.

Prolacertiformes such as *Protorosaurus*, *Prolacerta*, *Macrocnemus*, and *Tanystropheus*, share numerous characteristics and are usually considerd a monophyletic clade (Chaterjee, 1980; Benton 1984; Benton 1985, Chaterjee, 1986, Jalil 1997).

Benton 1984 and Benton 1985 present the following, which was the first cladistic study of basal Diapsida.

```
|--Lepidosauromorpha
`--ARCHOSAUROMORPHA
   |--Pterosauria
   `--+--Trilophosaurus
      `--+-- Rhynchosauria
         |--+--Protorosaurus
         |  `--+--o Prolacertidae
         |      |   |--Prolacerta
         |      |    `--Macrocnemus
         |      `--o Tanystropheidae
         |           |-- Tanytrachelos
         |            `-- Tanystropheus
         `--Archosauriformes
```

Apart from the Pterosauria, which are now considered Ornithodira rather than basal archosauromorphs, this defined the basic approach to the Prolacertiformes. Chaterjee, 1986 who discovered and desceribed *Malerisaurus*, offers a basically similar phylogeny (Protorosauria = Prolacertiformes only):

```
o Protorosauria
| --o Protorosauridae
|   |--Protorosaurus
|   `--+--+--Prolacerta
|      |  `--Kadimakara
|      `--+--Macrocnemus
|         `--+-- Yerrapalli form
```

```
|            `-- Malerisaurus
`--o Tanystropheidae
   |-- Tanytrachelos
   `-- Tanystropheus
```

This phylogeny gives a deeper division between Protorosauridae (= Prolacertidae) and Tanystropheidae, as *Protorosaurus* has been moved up from the base of the tree.

A later study by Jalil 1997, including an analysis of more characters and more taxa, including the newly described *Jesairosaurus*, gives the following, quite different cladogram:

```
--+--Choristodera
  `--+--Rhynchosauria
     `--+-- Trilophosaurus
        |--+--Protorosaurus
        |  `--+--Prolacerta
        |     `--+--+-- Jesairosaurus
        |        |  `-- Malerisaurus
        |        `--+-- Macrocnemus
        |           `--+--Langobardisaurus
        |              `--+-- Boreopricea
        |                 `--+-- Cosesaurus
        |                    `-- Tanystropheidae
        |                       |-- Tanytrachelos
        |                       `-- Tanystropheus
        `--Archosauriformes
```

Here the Trilophosaurs and Rhynchosaurs play musical chairs. Also, in contrast to Benton 1984 and 1985 and Chaterjee, 1986, Prolacertiformes are not divided into Prolacertidae/Protorosauridae and Tanystropheidae, but represent instead a single series.

But that is not the end of the matter. Through analysis of a newly described genus, *Czatkowiella*, Borsuk-Bialynicka & Evans, 2009 broke with the paradigm of a monophyletic Prolacertiformes by defining *Protorosaurus* as a more basal form, and making the Prolacertiformes in general as a grade of basal archosauromorphs rather than a clade .

The following cladogram is from Borsuk-Bialynicka & Evans, 2009, using the data matrix of Müller 2004, with *Czatkowiella* added and *Protorosaurus* updated:

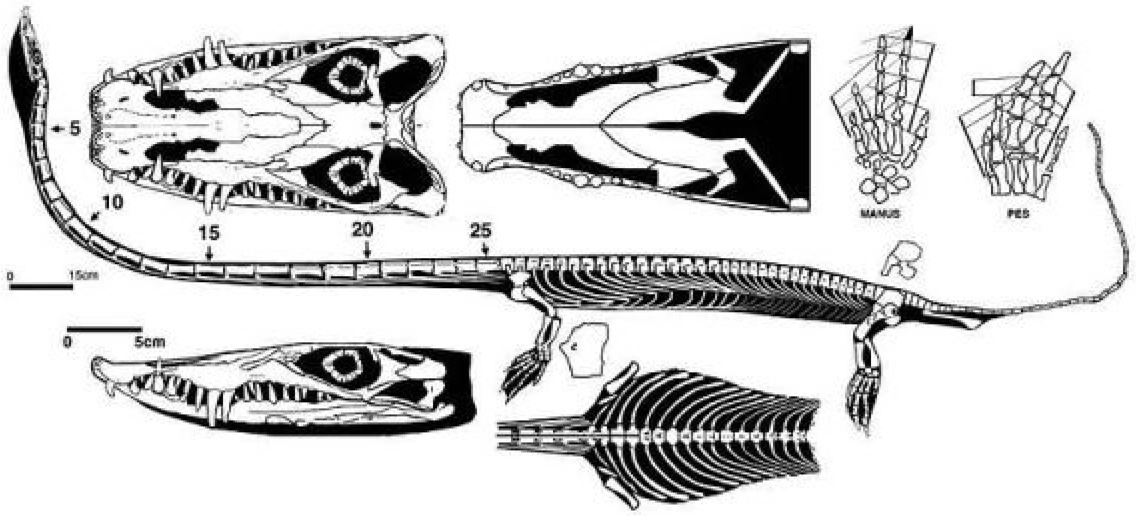
```
--Lepidosauromorpha
`--ARCHOSAUROMORPHA
   |--+--Czatkowiella
   |  `--Protorosaurus
   `--+--Coelurosauravus
      `--+--+--Thalattosauria
         |  `--Ichthyopterygia
         `--+--+--Choristodera
            |  `--+--Sauropterygia
            |     `--Testudines
            `--+--Macrocnemus
               |--Tanystropheus
               `--+--Prolacerta
                  `--+--Rhynchosauria
                     |--Trilophosauria
                     `--Archosauriformes
```

Here traditional Prolacertiformes have been shown in bold. This phylogeny is interesting because it includes some of the various marine Diapsids that seem to appear out of nowhere in the course of the Triassic. The Testudines (turtles) are here shown as basal archosauromorphs, in keeping with molecular phylogeny. *Coelurosauravus* however is more often understood as a basal Neodiaspid. *Macrocnemus* and *Tanystropheus*, rather than representing highly derived Prolacertiformes, constitute distinct parallel lineages. Also, *Prolacerta* is the most derived frather than a fairly basal Prolacertiform (*Malerisaurus* and similar forms are not considered but may perhaps go here as well). Rhynchosaurs and Trilophosaurs are here shown as more derived than "Prolacertiformes", whereas in other cladograms beginning with Benton 1985 the inverse is almost always the case. Quite possibly, Rhynchosaurs, Trilophosaurs, and "Prolacertiformes" represent a general assemblage of early archosauromorphs, which differ only in that the Rhynchosaurs and Trilophosaurs have become more specialised as regards a herbivorous diet, whereas the "Prolacertiformes" have retained their plesiomorphic (primitive) generalised lizard-like shape.

It is somewhat unsettling that, in considering the above cladograms, there does not appear to be a single clear consensus among them all in the series that the various taxxa appear, beyond *Protorosaurus* occupying a basal position, and the close relation between the two specialised and long-necked forms: *Tanystropheus* and *Tanytrachelos*. Were these poorly known and fragmentary forms one could understand, but these are well known animals pof which a number of taxa are known from complete skulls and skeletons.

Other Triassic diapsids that have been associated with the Prolacertiformes over the last three decades or so, but only because there is nowhere else to put them, and making it a sort of "wastebasket taxon". These include a number of unusual arboreal forms, as enigmatic, specialised, and difficult to place in their own way as the various Triassic marine forms. They include the glider *Sharovipteryx*, the chameleon-like drepanosaurs, and *Longisquama*, a small animal with long feather-like scales that would obviously have been used for intra-specific display or perhaps to frighten away predators (by making the animal look larger). While all of these forms are almost certainly archosauromorphs, their exact relationships remain unclear. And with the Prolacertiformes possibly losing their monophyletic status, the way is open for new interpretations and rearrangements of these various taxa. MAK101012

Descriptions



Dinocephalosaurus, traced from the *in situ* fossil. Note how different the neck is from that of *Tanystropheus*. Although both were near-shore marine archosauromorphs, their lifestyle, environment, and food sources would have differed. Original art by David Peters also on Wikipedia

Dinocephalosaurus**:** *D. orientalis* Li, 2003 .

Range: Middle Triassic Guizhou Province, China

Phylogeny: Archosauromorpha **:::** *.

Comments: Although considered a Prolacertiforme, trhere is no reason why *Dinocephalosaurus* should be specifically related to that group, beyond sharing plesiomorphic archosauromorph chracatreistics. One area in which it is very unlike other Prolacertiformes is as regards the 25 cervical vertebrae, which means the neck is very long but also flexible like a plesiosaur (overall length of animal about 2.7 meters, of which the neck makes up 1.7 m),in in contrast to the long but stiff (few vertebrae) neck of *Tanystropheus*. Although similar in appearance, and both marine, the long necks of both taxa evolved independently. The limbs are also more paddle like than those of *Tanystropheus*, and carpal and especially tarsal bones resemble those of nothosaurs as simple rounded bones. It may quite likely represent simply one more aquatic diapsid lineage.

Links: Wikipedia, Dinosaur Mailing List, BBC news, Pharyngula, photos MAK101012

Prolacertiformes: *Prolacerta*, *Malerisaurus*, *Tanystropheus*.

Range: Early to Late Triassic.

Phylogeny: Archosauromorpha ::: Archosauriformes + *.

Characters: Like early Lepidosauromorphs in reduction of temporal bar; squamosal reduced or ventral process that precludes streptostyly; agile terrestrial predators. Also includes *Tanystropheus*, with very long neck composed of only 6-7 vertebrae but twice length of trunk & relatively immobile, limbs poorly ossified; apparantly ate cephalopods.

Links: tanyst; Nuova pagina 1. wikipedia

Skeleton of *Tanystropheus longobardicus*, from the Grenzbitumenzone (middle Triassic, Anisian/Ladinian boundary) of Monte San Giorgio, Switzerland. The extraordinarily long neck consists of 12 elongate cervical vertebrae. Photo by Ghedoghedo, Wikipedia

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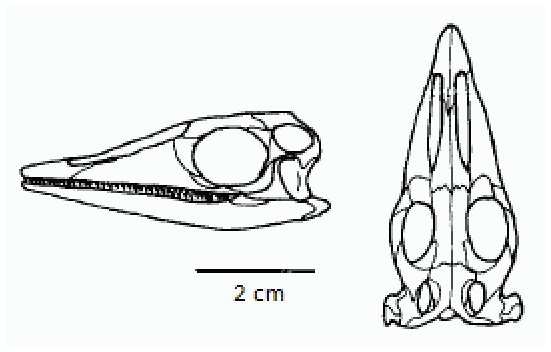
Macrocnemus: *Macrocnemus basanii* (Nopcsa, 1930).

Range: Grenzbitumenzone (middle Triassic) of Monte San Giorgio, Switzerland

Phylogeny: Archosauromorpha/"Prolacertiformes" ::: *.

Comments: shares characteristics both with *Prolacerta* and *Tanystropheus*, may be closer to one or the other, or alternatively represent a third lineage of "Prolacertiformes".

Links: Wikipedia MAK101012



Macrocnemus basanii; skull, in dorsal and lateral view, from Benton 1985

Malerisaurus: *M. langstoni* Chatterjee, 1986; *M. robinsonae* Chatterjee, 1980.

Range: late Triassic Maleri Formation (late Carnian) of India and contemporary Dockum Formation of Texas,

Phylogeny: "Prolacertiformes" **:** *Prolacerta* + *.

Comments: A lightly built lizard-like form with long hind limbs. Originally placed in the Protorosauridae with Protorosaurus by Chaterjee, 1980 on the basis of its apparently closed lower temporal bar and other features. With further material it was realised that the temporal bar was open as with *Prolacerta* which is seen to be a closely related form Chaterjee, 1986

References: Chaterjee, 1980 Chaterjee, 1986.

Links: Wikipedia MAK101012

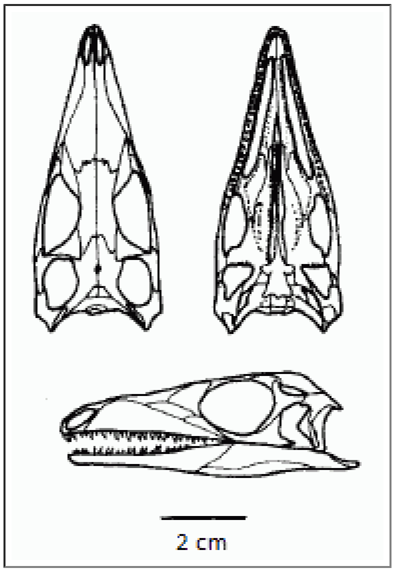
Prolacerta: *Prolacerta broomi* Parrington, 1935.

Range: Lystrosaurus Zone of South Africa and the Fremouw Formation of Antarctica (Induan of South-West Gondwana)

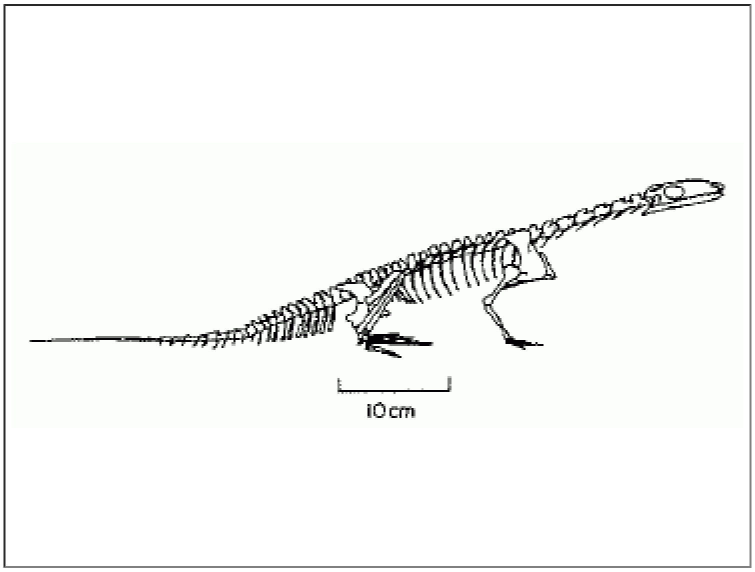
Phylogeny: "Prolacertiformes" : *Malerisaurus* + *.

Comments: Previously regarded as an ancestral lizard, an eosuchian and a proto-thecodont.

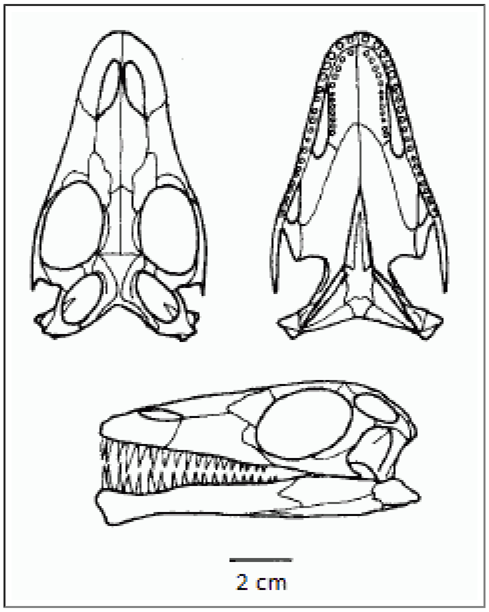
Links: Wikipedia MAK101007



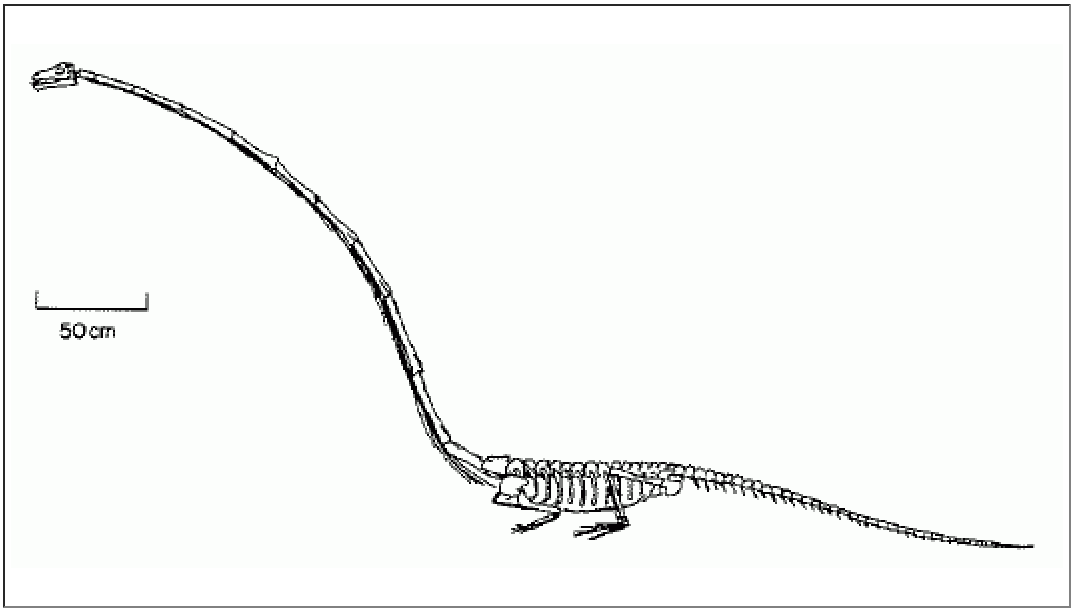
Prolacerta broomi; skull, in dorsal, palatal, and lateral views, from Benton 1985



Prolacerta broomi; skeleton, length of original about 60 cm, from Benton 1984



Tanystropheus longobardicus; skull, in dorsal, palatal, and lateral views, from Benton 1985.



Tanystropheus longobardicus; skeleton, length of original upto 6 meters, from Benton 1984. Apart from the unusual neck, the proportions are very similar to *Prolacerta*

Tanystropheidae: *Tanystropheus, Tanytrachelos*.

Range: early, middle and late Triassic of Western Tethys (central Europe and the Middle East), late Triassic of eastern North America

Phylogeny: Archosauromorpha/"Prolacertiformes" ::: *.

Comments: These are fresh-water to fully marine forms, characterised by the elongation of the neck through 12 elongate cervical vertebrae. This reaches an extremne form in *Tanystropheus longobardicus*. The neck was stiffened by long, slender cervical ribs. Less derived other "Protorosaurs" and Prolacertiformes (including *Protorosaurus*, *Prolacerta*, *Kadimakara*, *Macrocnemus*, *Malerisaurus*, etc) have a moderately long neck, with 8 vertebrae. *Tanystropheus* was classified as a euryapsid by Romer, but is now placed in the Prolacertiformes. *Tanystropheus* was a large animal, which grew upto 5 to 6 m long. Although *Tanytrachelos* is much smaller (20 cm long), and has procoelous vertebrae, the two share a number of unique characteristics

References: Benton 1985, Chaterjee, 1986 .

Links: Wikipedia MAK101012

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

page last modified MAK120312

Archosauromorpha: Drepanosauridae

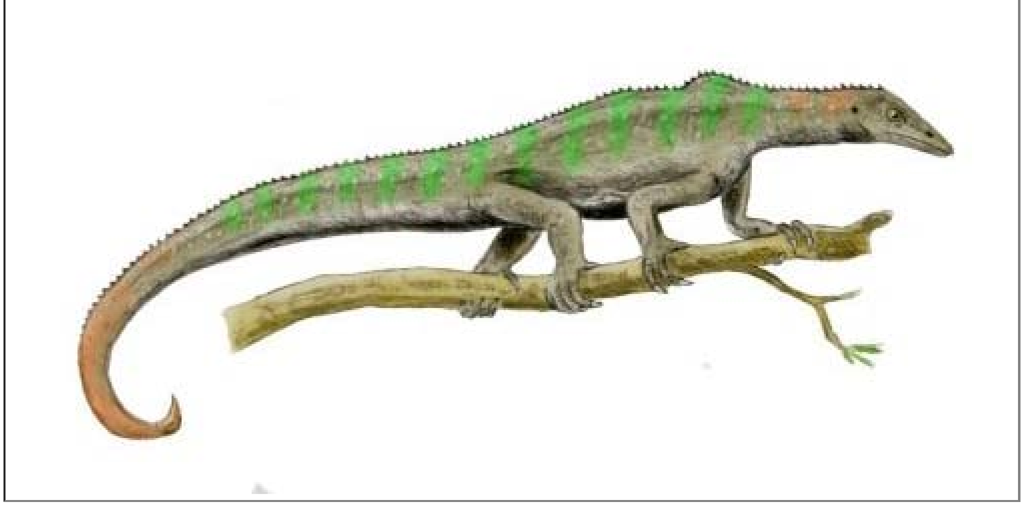
Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauromorpha
               |  |-- Hypuronector
               |  `--Elyurosauria
               |     |-- Vallesaurus
               |     `--Drepanosauridae
               |        |--Dolabrosaurus
               |        `--Megalancosaurinae
               `--ARCHOSAURIA
```

Contents

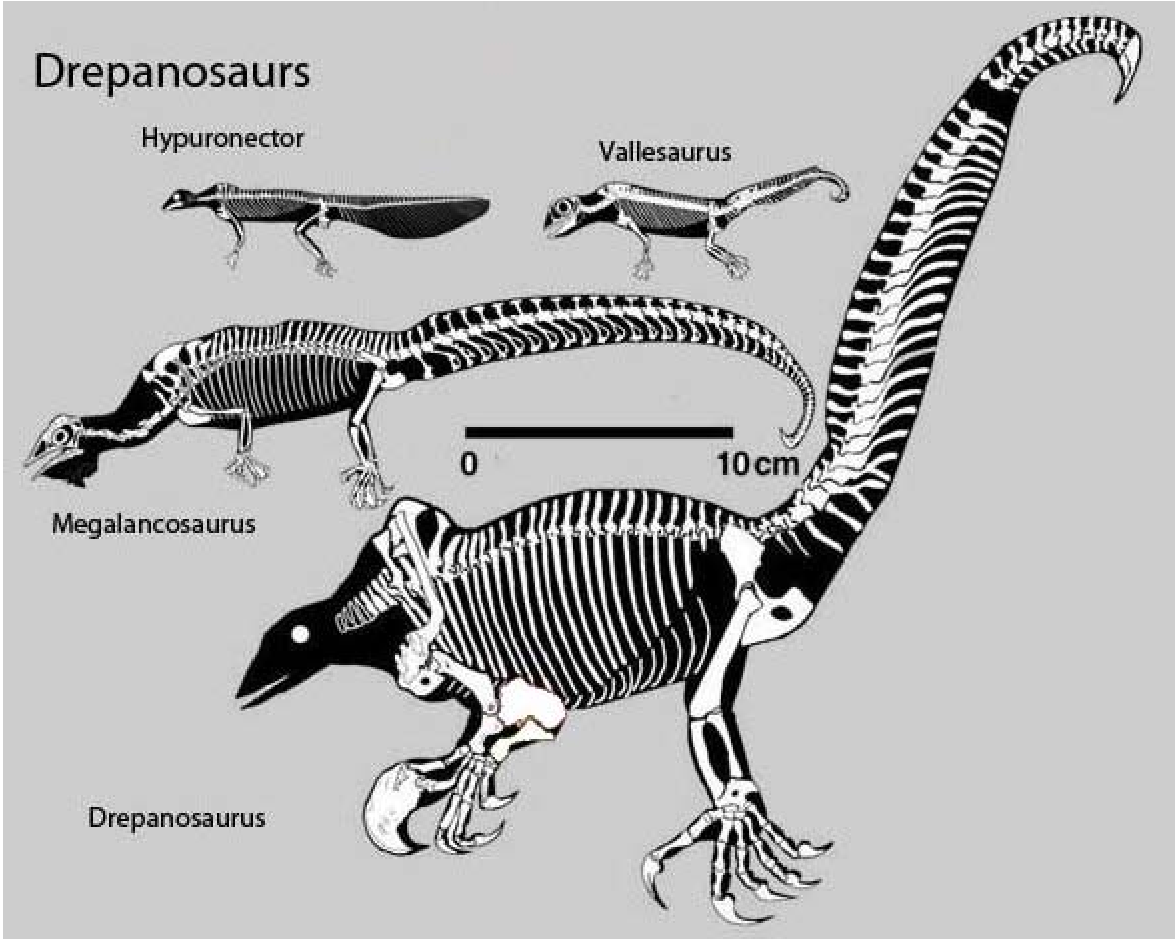
Taxa on This Page

1. *Dolabrosaurus* X
2. Drepanosauridae X
3. Drepanosauromorpha X
4. Elyurosauria X
5. *Hypuronector* X
6. Megalancosaurinae X
7. *Vallesaurus* X



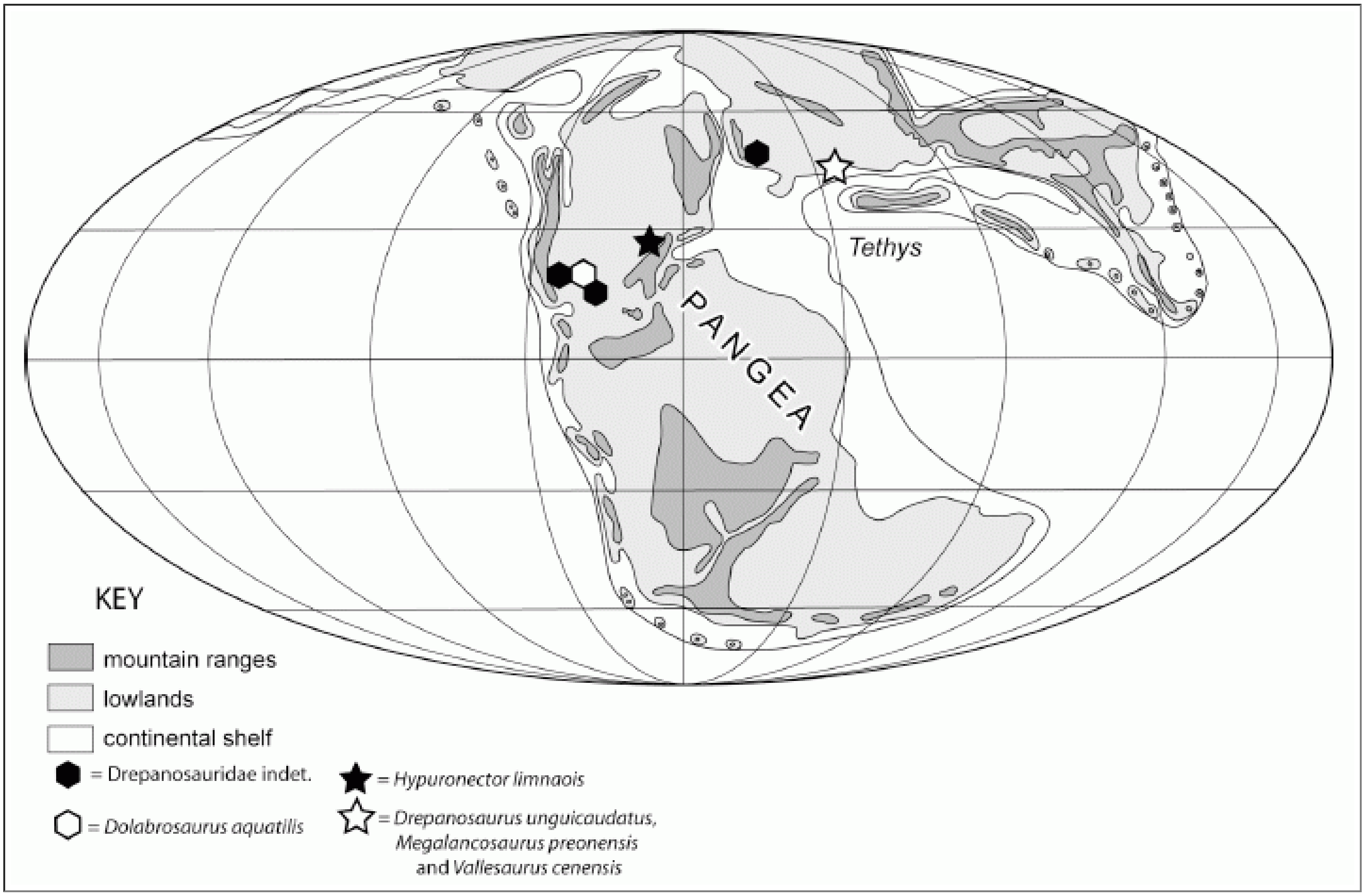
Life restoration of *Megalancosaurus preonensis*, a specialised Drepanosaur from the Late Triassic (Middle Norian) of European Tethys (Northern Italy). Length about 25 centimeters. Illustration by Nobu Tamura (Wikipedia).

The above text is adapted from Wikipedia - MAK



Drepanosaurs drawn to scale; artwork by David Peters

The Drepanosaurs are a group of specialised archosauromorphs notable for their distinctive, triangular toothless skulls, which resemble the skulls of birds. This similarity to birds may have led to the possible mis-attribution of a drepanosaurid skull to the would-be "first bird", *Protoavis*. (Renesto, 2000). In fact, they were more chameleonthan bird-like, featuring a suite of bizarre, almost chameleon-like skeletal features. Above the shoulders of most species was a specialized "hump" formed from fusion of the vertebrae, possibly used for advanced muscle attachments to the neck, and allowing for quick forward-striking movement of the head (perhaps to catch insects). Many had derived hands with two fingers opposed to the remaining three, an adaptation for grasping branches. Some individuals of *Megalancosaurus* (possibly exclusive to either males or females) had a primate-like opposable toe on each foot, perhaps used by one sex for extra grip during mating. Most species had broad, prehensile tails, sometimes tipped with a large "claw", again to aid in climbing. These tails, tall and flat like those of newts and crocodiles, have led some researches to conclude that they were aquatic rather than arboreal. In 2004, Senter dismissed this idea, while Colbert and Olsen, in their description of *Hypuronector*, state that while other drepanosaurs were probably arboreal, *Hypuronector* was uniquely adapted to aquatic life. Colbert & Olsen 2001. However it may also have been arboreal, using the deep tail for intra-specific display



Paleogeographic map of the Late Triassic, with drepanosaurid localities highlighted, from Renesto et al 2009 p.316. Drepanosaurs seem to be predominate in northern Pangea; at the time of writing none have been found South of the equator, although this may simply be an artifact of preservation. So far they are known from the Carnian to Norian (late Triassic) of northern Italy, England, Arizona, New Mexico, New Jersey,

The highly specialised nature has made understanding where they belong on the diapsid family tree difficult. Renesto, 1994 assigned the drepanosaurids and *Longisquama* to the Prolacertiformes. Senter 2004 however found them to form a group with the coelurosauravids, for which he coined the name Avicephala, as a sister taxon to Neodiapsida (the group which includes all modern diapsids and their extinct relatives).

Within Avicephala, Senter created the group Simiosauria to refer to all the species traditionally grouped together within the Drepanosauridae, reserving that name for a more exclusive sub-group. Senter found that *Hypuronector*, originally described as a drepanosaurid, actually lies just outside that clade, along with the primitive drepanosaur *Vallesaurus*. He also recovered a close relationship between the drepanosaurs *Dolabrosaurus* and *Megalancosaurus*. The following cladogram was found by Senter in his 2004 analysis.

```
o Avicephala
|--? Longisquama
|--Coelurosauravidae
|   |--Weigeltisaurus
|   `-- Coelurosauravus
`--Simiosauria
   |-- Vallesaurus
   `--+--Hypuronector
      `--Drepanosauridae
         |--Drepanosaurus
         `--+--Megalancosaurinae
            `-- Dolabrosaurus
```

Renesto et al. 2010 demonstrated that Senter (2004) cladogram was based on poorly defined characters and dataset. The resulting phylogeny was therefore very unusual compared to any other previous study on drepanosaurs or related taxa. The new cladogram proposed in this last study abandoned both Avicephala (because it is polyphyletic) and

Simiosauria, redefining the latter under the PhyloCode as Drepanosauromorpha. Drepanosauromorphs are closely related to the Prolacertiformes, especially genera like Langobardisaurus and Macrocnemus, if not part of the Prolacertiformes. Among the drepanosauromorphs it was defined a more inclusive taxon, Elyurosauria ("lizard with coiled tails"), was erected, in order to include all the drepanosaurs with coiled tails, *Vallesaurus* is thus more derived than *Hypuronector* (as clearly shown by its morphology).*Drepanosaurus* and *Megalancosaurus* are also in a new taxon named Megalancosaurinae. The alternative cladogram presented in Renesto et al. (2010) is followed here.

```
Drepanosauromorpha
`--+-- Hypuronector
   `--Elyurosauria
      |-- Vallesaurus
      `--Drepanosauridae
         |--Dolabrosaurus
         `--Megalancosaurinae
            |-- Drepanosaurus
            `--Megalancosaurus
```

We have adopted this phylogeny and assume that the Avicephala are the result of convergence among Permo-Triassic aboreal or gliding forms.

Descriptions

Drepanosaurus unguicaudatus, from the Museo di Storia Naturale di Bergamo, showing the curled tail that is the defining feature of the Elyurosauria ("lizard with coiled tails"). Photo by Ghedoghedo, Wikipedia

Drepanosauromorpha .

Range: Late Triassic (early Late Carnian to Late Norian) of Europe and North America.

Phylogeny: Archosauromorpha ::: Archosauriformes + * **:** *Hypuronector* + Elyurosauria

Comments: from Wikipedia: specialized adaptation toward climbing, especially on narrow supports such as the twigs of trees (Renesto, 2000). highly modified cervical vertebrae with adaptations that limited lateral mobility. Both structures indicate the presence of powerful muscles and ligaments for the extension of the neck. This possibly suggests a projectile feeding adaptation (Renesto, 2000). The head was suddenly launched forward to catch prey and the limited lateral mobility prevented undesired jerks of the neck which could have dislocated the cervical vertebrae during the quick extension. In smaller drepanosaurids like *Megalancosaurus* and *Vallesaurus*, such adaptations may be related to an insectivorous diet. The teeth of Drepanosaurs such as *Vallesaurus* seem well suited to cut or crush the tough exoskeleton of insects and other arthropods.Renesto & Binelli 2006

Links: Monkey Lizards of the Triassic - An illustrated article on drepanosaurs from HMNH; Images and discussion of *Drepanosaurus* and Images and discussion of *Megalancosaurus* by Silvio Renesto.

Hypuronector: *Hypuronector limnaios* Colbert & Olsen 2001

Range: Latest Carnian (Adamanian) of N Am (New Jersey)

Phylogeny: Drepanosauromorpha **:** Elyurosauria + *.

Comments: The oldest well-known Drepanosaur, although indeterminate remains are slightly older (early Adamanian) Renesto et al 2009. The tail of this genus is very deep and non-prehensile, and may have been used as a swimming organ Colbert & Olsen 2001; the name means "deep-tailed swimmer from the lake". Alternatively and equally or perhaps more plausibly, this may have been an aboreal form (see illustration at right). *Hypuronector* is conventionally placed near the base of the Drepanosaur tree. But it may also be that like some other aquatic forms it may have secondarily taken on more primitive characteristics

Links: Wikipedia MAK101008

Restoration of *Hypuronector limnaios*, showing possible arboreal behavior. Length about 12 centimeters. Artwork by Smokeybjb, Wikipedia

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Elyurosauria .

Range: Known from the Norian of Europe and North America

Phylogeny: Drepanosauromorpha **:** *Hypuronector* + * **:** Drepanosauridae + Vallesaurus.

Comments: chameleon-like arboral forms with prehensile tails. MAK101008

Vallesaurus: *V. cenenis* (type species), *V. zorzinensis*.

Range: Late Triassic (Middle Norian) Zorzino Formation of the Italian Alps

Phylogeny: Elyurosauria **:** Drepanosauridae + *.

Comments: Adapted from Wikipedia: A small drepanosaurid about 15 centimetres (5.9 in) long. It is pentadactyl, with the 4th digit being longest and equal in length to the humerus. Its tarsus has a centrale, or an ankle bone which articulates with the tibia. In addition, Vallesaurus also has modified distal tarsals and metatarsals, and a clawless hallux. Renesto & Binelli 2006.

The hand has no opposable fingers; however, the shape and length of the fingers suggest good climbing abilities. (Unwin et al 2000).

The first specimen of *Vallesaurus cenensis*, MCSNB 4751, was found in 1975 by the staff of the Museo Civico di Scienze Naturali of Bergamo, Italy. The genus was named in respect of professor Valle, the former director of the museum. The species, on the other hand, was named after a local municipality called Cene neighbouring the site where the fossil was excavated. The specimen was given to palaeontologist Rupert Wild to study at the Staatliches Museum of Stuttgart, Germany. Wild named the genus in 1991. Renesto & Binelli 2006

Vallesaurus differs in some characteristics from another drepanosaur, Megalancosaurus. Vallesaurus has a proportionally shorter and higher snout, a thicker and larger maxilla and set of maxillary teeth, and a shorter cervical vertebra. It also lacks the fusion between the neural spines of the second and third dorsal vertebrae. Vallesaurus differs from Drepanosaurus, another drepanosaur, in that it lacks the enormous claw found on the second digit of the manus. It can be distinguished from Drepanosaurus, Megalancosaurus and possibly Dolabrosaurus in the lack of a terminal spine at the end of the tail. In addition, Vallesaurus also differs from Hypuronector, a related drepanosaur, in having anteroposteriorly extended neural spines of the anterior dorsal vertebrae and forelimbs much shorter than the hindlimbs. Renesto & Binelli 2006

Drepanosauridae Berman & Reisz 1992 **:** *Dolabrosaurus*, *Drepanosaurus*, *Hypuronector*, *Megalancosaurus* .

Range: Norian of Europe and North America

Phylogeny: Elyurosauria **:** *Vallesaurus* + * **:** *Dolabrosaurus* + Megalancosaurinae .

Dolabrosaurus: *Dolabrosaurus aquatilis* Berman & Reisz 1992.

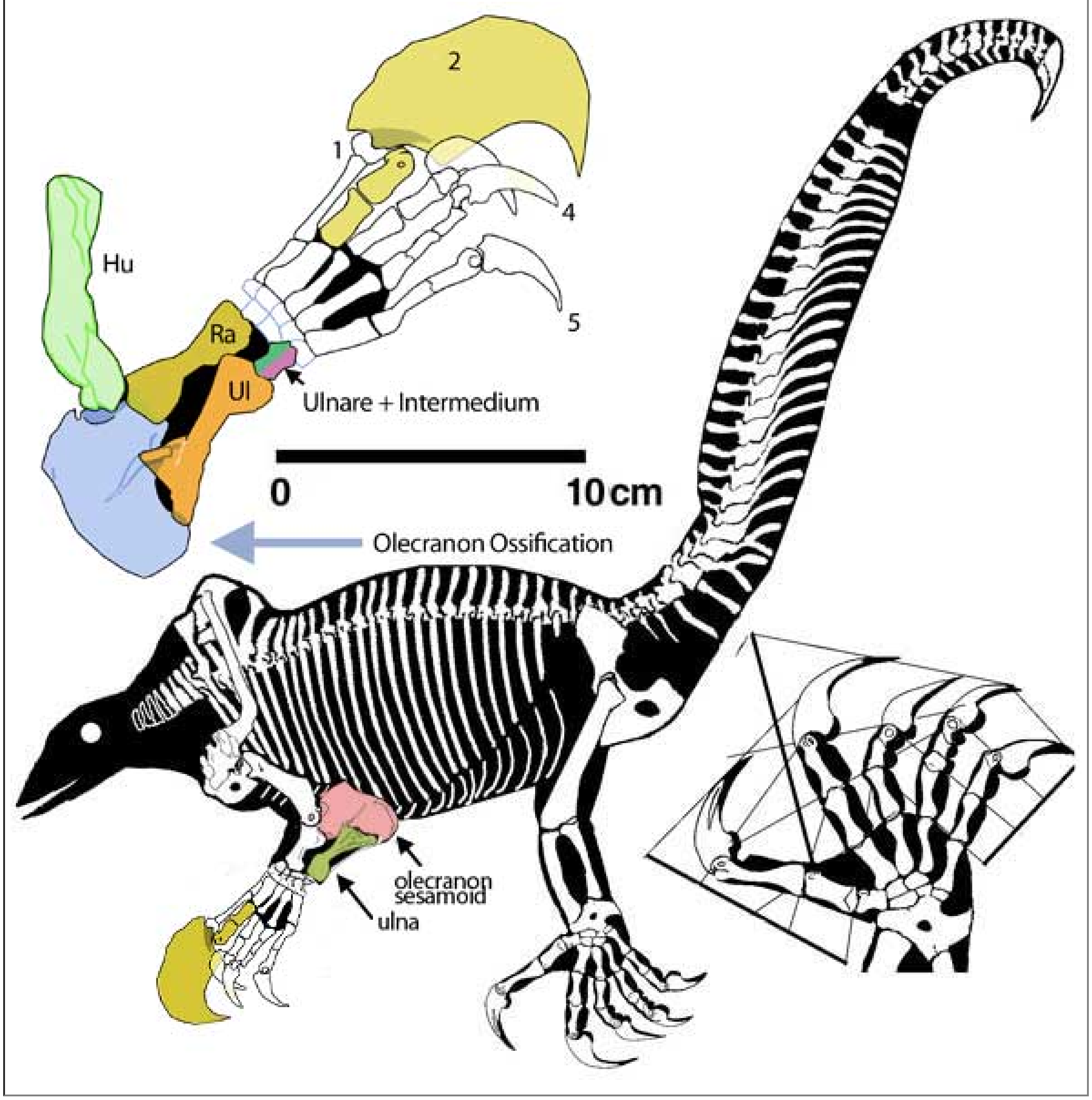
Range: Late Triassic (Middle Norian) Chinle Formation of north-central New Mexico

Phylogeny: Drepanosauridae **:** Megalancosaurinae + *.

Comments: Described on the basis of portions of the vertebral column and partial fore- and hindlimbs of a single specimen and found to be similar to *Drepanosaurus*. The two species were made the basis of the family Drepanosauridae, with Dolabrosaurus more primitive in certain aspects of its vertebral and pedal morphology. Originally considered amphibious or aquatic Lepidosauromorph, now understood to be (like the other drepanosaurs) an aboreal archosomorph.

References: Berman & Reisz 1992.

Links: Wikipedia MAK101008



Drepanosaurus unguicaudatus (Pinna 1980) - The scapula was relatively robust with a 70 degree bend at the bottom. The humerus and radius were short and robust. The ulna was replaced by the ulnare and shifted to the elbow where it became disc-like, unlike any other tetrapod. Apparently this was related to the enlarged ungual on digit II which would have required a large muscle, perhaps for digging through tree bark. Graphic and text by David Peters

Megalancosaurinae: *Drepanosaurus unguicaudatus*, *Megalancosaurus preonensis* .

Range: Late Triassic (Middle Norian) Zorzino Formation of the Italian Alps

Phylogeny: Drepanosauridae **:** *Dolabrosaurus* + *.

Comments: The most highly derived (specialised) drepanosaurs; note the unique climbing claw in *Drepanosaurus* (right).

References: Calzavara et al 1980, Renesto, 1994.

Links: Wikipedia MAK101008

Page Back | Unit Home | Page Top | Page Next

checked MAK101008

Archosauromorpha: Classification

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

This classification is based mainly on Carroll (1988), as the most recent comprehensive linnaean classification of the Vertebrates, with more recent groups added. Each taxon is listed by rank, name, and original author, and followed by a short description. The pages is rather stubby at the moment, but will hopefully be developed further.

For the phylogenetic arrangement, see the dendrogram page MAK120312

Infraclass Archosauromorpha Huene, 1946 Archosaurs and their relatives, one of the two major diapsid clades
  Order Protorosauria Lydekker, 1888 a varied and paraphyletic assemblage of small to large, lizard-like reptiles, Late Perm to Late Trias, cosmopolitan
    Family Protorosauridae Lydekker, 1888 (ancestral archosauromorphs, semiaquatic - Late Perm to Early Trias of Eur)
    Family Prolacertidae Parrington, 1935 (paraphyletic assemblage or watsebasket taxon of medium-long necked lizard-like forms, faculatively bipedal Early to Late Trias, Cosm)
    Family Tanystropheidae Gervais, 1858 long necked, mostly semi-aquatic forms, may be several parallel or only distantly related protorosaurs, Mid to Late Trias, Eur, N Am, & China
      Subfamily Macrocneminae Kuhn, 1946 - shorter neck, may be a distinct family but here re-ranked as subfamily. Monotypal, Mid Trias of Eur
      Subfamily Dinocephalosaurinae (informal) informal monotypal subfamily for *Dinocephalosaurus orientalis* - many neck vertebrae - Mid Trias of China
      Subfamily Tanystropheinae - here used for specialised long-necked forms, length to 6 meters (mostly neck), Mid to Late Trias, Eur & N Am
    Family Drepanosauridae Berman and Reisz 1992 (= Drepanosauromorpha Renesto et al., 2010) small, aboreal, chameleon-like forms, Late Trias, Eur & N Am
  Order Helveticosauria Peyer, 1955 (monotypal)
    Family Helveticosauridae Peyer, 1955 (bizarre aquatic forms, Mid Trias of Eur)

Order Trilophosauria Romer 1956

Family Variodentidae Tatarinov, 1964(monotypal, small lizard-like archosaurs with procolophon-like dentition, *Variodens inopinatus*, Late Trias of Eur)

Family Trilophosauridae Gregory, 1945 (monotypal, large lizard-like herbivores, *Trilophosaurus*, Late Trias of N Am)

Order Rhynchosauria Osborn, 1903 (herbivores with efficient curtting and grinding teeth, four subfamilies constitute a progressive evolutionary series Trias, Cosm.)

Family Rhynchosauridae Huxley, 1887 (only family in order; alternatively the four subfamilies could each be considered a family, although that may be excessive taxonomic inflation)

Subfamily Mesosuchinae Haughton, 1924 (lizard-like basal forms - Early to Early Mid Trias, Sth Afr)

Subfamily Howesiiane Watson, 1917 (monotypal lizard-like primitive form - *Howesia browni* - Earliy Mid Trias of Sth Afr)

Subfamily Rhynchosaurinae Cope, 1870 (= Family: Stenaulorhynchidae, Kuhn, 1933) - intermediate forms, typical rhynchosaurs - Mid Trias of Eur & Afr

Subfamily Hyperodapedontinae Lydekker, 1885; (= Family: Hyperodapedontidae Lydekker, 1885 = Family: Paradapedontidae Huene, 1938) advanced and abundant large (1.5 m) rhynchosaurs with wide skulls and complex dentition, Late Trias, Cosmpol

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Page Back Unit Home Page Top Page Next

Archosauromorpha: Dendrogram

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA ToL
   |--Protorosauridae
   |  |-Czatkowiella
   |  `-Protorosaurus
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosauroidea
      |    |--Helveticosaurus
      |    `--SVT 203 (unnamed genus)
      `--+--Rhynchosauria •X MH
         `--+--Trilophosauridae •X MH
            `--Prolacertiformes •X MH
               |--+-Prolacerta   "Prolacertiformes"
               |  `-Malerisaurus
               |--Macrocnemus
               |--Tanystropheidae
               |--Dinocephalosaurus
               |--Drepanosauromorpha
               |  |-- Hypuronector
               |  `--Elyurosauria
               |     |-- Vallesaurus
               |     `--Drepanosauridae
               |        |--Dolabrosaurus
               |        `--Megalancosaurinae
               `--ARCHOSAURIA MH
```

Page Back Unit Home Page Top Page Next

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Archosauromorpha: References

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
|
`--ARCHOSAUROMORPHA
   |=="Protorosauridae"
   `--+?--CHORISTODERA
      |??-CHELONII (molecular phylogeny)
      |?--Helveticosaurus
      `--+--Rhynchosauria
         `--+--Trilophosauria
            `--+--Prolacertiformes
               |--Drepanosauridae
               `--ARCHOSAURIA
```

Contents

References

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Prolacerta, Tanystropheidae

Benton M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97-164.
The Prolacertiformes, *Prolacerta*, *Malerisaurus*, Tanystropheidae

David S. Berman and Robert R. Reisz, 1992, *Dolabrosaurus aquatilis*, a Small Lepidosauromorph Reptile from the Upper Triassic Chinle Formation of North-Central New Mexico *Journal of Paleontology* Vol. 66, No. 6 (Nov., 1992), pp. 1001-1009
Dolabrosaurus

Borsuk-Bialynicka, M, & Evans, S.E. (2009). A long-necked archosauromorph from the Early Triassic of Poland. *Paleontologica Polonica* 65: 203-234. pdf
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of Friuli". *Gortania*, 2. pp. 49-63.
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Trilophosauridae.

Chatterjee, S. (1980) *Malerisaurus*, a new eosuchian reptile from the Late Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London* B 290: 219-258.
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The Prolacertiformes, *Malerisaurus*, Tanystropheidae

Colbert, E. H., and Olsen, P. E. (2001). "A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup)." *American Museum Novitates*, 3334: 1-24.
Drepanosaurs, Hypuronector

Dilkes, DW (1998), *The Early Triassic rhynchosaur **Mesosuchus browni** and the interrelationships of basal archosauromorph reptiles*. **Phil. Trans. R. Soc. Lond. B** 353: 501-541.
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SVT 203 (unnamed Helveticosaur)

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The enigmatic Helveticosaurs

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SVT 203 (unnamed Helveticosaur)

Müller, 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, München.
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Peyer, B. (1955). Die Triasfauna der Tessiner Kalkalpen. XVIII. *Helveticosaurus zollingeri*, n.g. n.sp. *Schweizerische Paläontologische Abhandlungen* 72:3-50.
The enigmatic Helveticosaurs, *Helveticosaurus*

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Drepanosaurs, Megalancosaurinae

Renesto, S. (2000). "Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile Megalancosaurus from the Late Triassic of northern Italy." Rivista Italiana di Paleontologia e Stratigrafia, 106: 157-180.
Drepanosauridae

Renesto, S., Spielmann, J.A., and Lucas, S.G. (2009). "The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian Placerias Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae." *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 252(3): 315-325. doi: 10.1127/0077-7749/2009/0252-0315. pdf,
Hypuronector

Silvio Renesto, Justin A. Spielmann, Spencer G. Lucas, and Giorgio Tarditi Spagnoli. (2010). The taxonomy and paleobiology of the Late Triassic (Carnian-Norian: Adamanian-Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). New Mexico Museum of Natural History and Science Bulletin. 46:1-81
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Rieppel, O. (1989). Helveticosaurus zollingeri Peyer (Reptilia, Diapsida): skeletal paedomorphosis; functional anatomy and systematic affinities. Palaeontographica A 208:123-152.
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Vallesaurus

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.
Protorosaurus

Page Back | Unit Home | Page Top | Page Next

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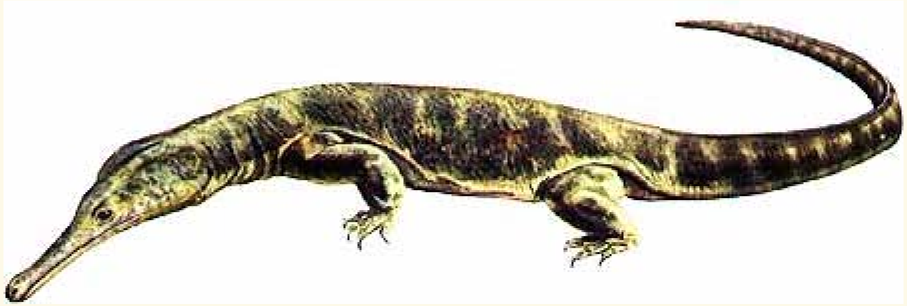
Choristodera

Abbreviated Dendrogram

```
DIAPSIDA
|?-CHORISTODERA
|   |--Cteniogenys
|   `--+--Monjurosuchus
|      `--Neochoristodera
|         |--Simoedosauridae
|         `--Champsosauridae
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
```

Contents



The Choristodera are one of those highly specialised Mesozoic groups that don't seem to be easily placed on the diapsid family tree. Although generally considered a minor group, they include a diverse range of morphotypes, including lizard, crocodilian, and even sauroptyerygian mimics. They were unaffected by the end Cretaceous extinction, and survived well into the Cenozoic. Had they continued only another twenty million years or so, we would have had five rather than four extant orders of reptiles. MAK120708

Image: *Champsosaurus*, from *The Simon and Schuster Encyclopedia of Dinosaurs and Prehistoric Creatures*

Choristodera

Champsosaurs (Neochoristodera)

Abbreviated Dendrogram

```
DIAPSIDA
|?-CHORISTODERA
|   |--Lazarussuchus
|   `--+--Cteniogenys
|      `--+--Hyphalosaurus
|         |--Monjurosuchus
|         `--Neochoristodera
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
```

Contents

Taxa on This Page

1. Choristodera X
2. *Cteniogenys* X
3. *Hyphalosaurus* X
4. *Lazarussuchus* X
5. *Monjurosuchus* X

Descriptions

Choristodera: .

Range: Late Triassic (Rhaetian) to early Miocene of North America, Asia, and Europe

Phylogeny: Younginformes or Archosauromorpha **:** * **:** *Cteniogenys* + (*Monjurosuchus* + Neochoristodera)

Links: Wikipedia ATW010715 and MAK101008

Lazarussuchus: *L. inexpectatus Hecht, 1992 (type species), L. dvoraki Evans and Klembara, 2005*

Range: *late Oligocene and early Miocene of France and the Czech Republic. .*

Phylogeny: Choristodera **:** (Cteniogenys + (Hyphalosaurus + Monjurosuchus + Neochoristodera)) + *.

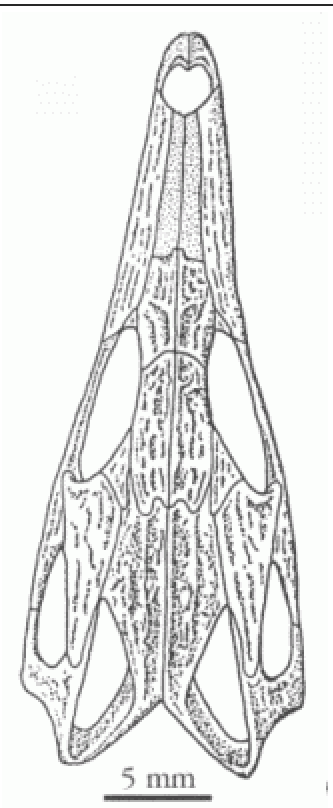
Comments: *a small lizard-like animal, the most basal choristoderan, as well as the most recent. Assuming morphology based cladistic analysis is correct, and also assuming no reversals (secomdary loss of advanced characteristics) this implies a long* ghost lineage*. The name refers to the biblical Lazarus, who rose from the dead, just as this species existed long after the last choristoderans became extinct in the Eocene; hence,* "lazarus taxon"*. MAK120707*

Cteniogenys*: Cteniogenys antiquus Gilmore, 1928.*

Range: *Middle (Bathonian) to Late (Kimmeridgian-Thithonian) Jurassic of Western Laurasia (Europe and North America)*

Phylogeny: Choristodera **:** Lazarussuchus + ((Hyphalosaurus + Monjurosuchus + Neochoristodera) + *).

Characters: *short snout, elongated and laterally (sideways) facing orbits.* Matsumoto et al 2007 *p.344*



Cteniogenys antiquus from the Bathonian of England. Illustration from Evans & Milner 1994

Comments: *a small bodied, lizard like animal, the most primitive Choristoderan (the status of the late surviving Lazarussuchus, sometimes considered the most primitive, is unclear). The same species, Cteniogenys antiquus, is given for both the Bathonian (*Evans & Milner 1994*) and Kimmeridgian-Thithonian species. Since it is unlikely that a single species would persoist unchanged for so long, these probably are two distinct but very similar forms*

Links: Wikipedia *MAK101008*

Hyphalosaurus*: H. lingyuanensis Gao, Tang & Wang, 1999 (type), H. baitaigouensis Ji et al., 2004*

Horizon: *Jehol Biota - Yixian Formation; Mid Cretaceous (Aptian) of China.*

Hyphalosaurus lingyuanensis, on display at the Paleozoological Museum of China. Photo © Captmondo, Wikipedia

Phylogeny: *Choristodera : Lazarussuchus + (Ctenіogenys + (Monjurosuchus + Neochoristodera + *)).*

Comments: *A choristoderan mimicking a sauropterygian, this small freshwater reptile is distinguishe dby the astronishingly long neck. It is known from thousands of specimens representing a complete growth seqyuence. H. baitaigouensis seems to have lived slightly later, and is distinguished by the larger number of neck vertebrae 26 instead of 19. This implies an anagenetic series (straight line evolution), with the animals developing progressively more flexible necks over time. In other respects the two species are identical, and both reach a length of 80 cm. The related and more or less contemporary Shokawa ikoi from Japan was very similar, but more about twice as long*

Links: *Wikipedia (detailed coverage)*

Monjurosuchus splendens, Yixian Formation, Early Cretaceous (Hauterivian–Barremian) of western Liaoning, China; from the Beijing Museum. Wikipedia

Monjurosuchus: *Monjurosuchus splendens, Monjurosuchus sp.*

Range: *Early Cretaceous (Berriasian to Barremian) of Japan and China.*

Phylogeny: *Choristodera : Lazarussuchus + (Ctenіogenys + (Hyphalosaurus + Neochoristodera + *)).*

Characters: *relatively short neck (cervical vertebral count of eight rather than the usual nine), short rounded snout (or preorbital region to give the technical term), narrow, fused frontal bones, closed lower temporal fenestrae, large dorsally (upward) directed orbits*

Comments: *A small (skull 8 cm long and 5 wide), semi-aquatic form. Hyphalosaurus, Lazarussuchus, and Monjurosuchus have a similar head type, but Lazarussuchus is originaruily or secodnarily) more primitive and Hyphalosaurus is a specialised form distinguished by its very long neck.*

References: *Matsumoto et al 2007.* MAK101008

Links: *Wikipedia*

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Choristodera

Champsosaurs (Neochoristodera)

Abbreviated Dendrogram

```
DIAPSIDA
|?-CHORISTODERA
|   |--Cteniogenys
|   `--+--Monjurosuchus
|      `--Neochoristodera
|         |--Simoedosauridae
|         `--Champsosauridae
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
```

Contents

Taxa on This Page

1. Champsosauridae X
2. Neochoristodera X
3. Simoedosauridae X

The Champsosaurs

The phylogenetic position of the Choristodera generally is still fairly vague. Current estimates place them somewhere between basal Diapsida and basal Archosauromorpha. (In fact, one well-known web site has them in *both* places) Here, they are placed as the sister group to Archosauromorpha, consistent with deBraga & Rieppel (1997). This paper does seem to contain some probably minor errors in scoring the Choristodera. For example, the pterygoid flange is scored as having a single row of teeth along the posterior margin, rather than a *shagreen* of small denticles, as might be more appropriate. It is unlikely that these significantly affect the result. However, it remains entirely possible that the Choristodera are more nearly basal diapsids than near - Archosauromorphs. Internal relationships within Choristodera are described according to Gao & Fox (1998). The Choristodera in general, and particularly the Champsosauridae, are plagued with bad names -- junior synonyms of unrelated genera and the like. Gao & Fox do a very careful job of trying to straighten out this confusion, and their paper is strongly recommended.

The Champsosaurs are the "classic" Choristoderans: very crocodile-forms with highly elongated snouts, looking very much like living gharials. Much of the similarity is illusory. The orbits, for example, are placed well forward of the archosaur position. The rear of the skull is not flat and strongly consolidated, like a crocodile. Instead it is rounded, hugely expanded and consists to a considerable degree of complex bony arches surrounding empty space. In life, this space was presumably occupied by massive jaw muscles. However, the fossils look a bit like a lizard skull in a carnival mirror, the anterior drawn out into a long, thin pisciverous rostrum and the posterior blown up like a balloon. However, champsosaurs lack the complex quadrate of lizards as much as they lack typical archosaurian features.

One of the striking results of deBraga & Rieppel's study is the number of presumably convergent features the choristoderes share with placodonts. Some examples (all apomorphies of both groups) include (a) the transverse process of the pterygoid extends below the maxillary tooth row; (b) the mandibular joint lies posterior to the level of the occiput; (c) the maxilla does not extend to the level of the posterior margin of the orbit; and (d) the post-orbital skull is longer than the pre-orbital skull. One might suspect that these odd convergences in jaw structure are derived from a common lifestyle. Specifically, it seems quite possible that the choristoderes were originally shellfish-eaters like placodonts and only secondarily became long-snouted fish eaters. Interestingly, choristodere families more primitive than champsosaurs do tend to have shorter, broader snouts.

The limbs are very well developed for basically aquatic animals. It appears from their architecture that the entire distal limb, not just the hands and feet, was used as a paddle. This is also consistent with the relatively short limbs that may have allowed these animals some mobility on land, and the straight, unbowed ulna. The limbs are relatively gracile. Champsosaurs would not have been ambush amphibious predators like crocs since they seem to have lacked the ability to leap to attack in the amazing fashion of modern crocodiles, who can often jump 1.5 times their length. In addition, champsosaur ribs are thickened and short in the manner of other aquatic reptiles, such as some pachypleurosaurs.

Choristoderans do share one other feature with crocs. They survived the KT boundary. They became extinct only in the Eocene, possibly even the Oligocene. Their ultimate extinction may have been the result of any number of factors: falling temperatures and the evolution of whales come to mind. In this connection, it may be relevant that their last redoubt may have been the non-marine waters abutting the cooling remnants of the Western Interior Sea, rather than the whale-infested waters of the Tethys and Atlantic. ATW000716.

Descriptions

Neochoristodera:

Range: Middle Jurassic to Eocene.

Phylogeny: Choristodera : *Cteniogenys* + (*Hyphalosaurus* + *Monjurosuchus* + * : Simeodosauridae + Champsosauridae)

Characters: **$** Basal infolding of tooth enamel; **$** vomer does not contact premaxilla (snout elongated); **$** palatal foramen (?) opens between pterygoid & palatine without contribution from vomer; **$** lacrimal foramen opens between lacrimal, prefrontal and palatine -- not penetrating lacrimal; **$** pterygoids with long medial contact; **$** *interpterygoid vacuity* medial, small & near posterior margin of suborbital fenestra; **$** orbits small & directed dorsally; nasals long and fused; **$** upper temporal fenestra flared posteriorly and much larger than orbit; dorsal process of squamosal slender & elongate to mid-level of lower temporal fenestra; **$** pterygoid process of quadrate horizontal, reduced & slender; **$** presacral vertebral centra short & spool-like; **$** "ventromedial crest" of dorsal vertebrae reduced or absent; bones *pachyostotic* in adults.

References: Gao & Fox (1998); Tarduno *et al*. (1998). ATW010715.

Simoedosauridae:

Phylogeny: Neochoristodera **:** Champsosauridae + *.

Champsosauridae: *Champsosaurus*.

Range: lw(?)K-lwEc.

Phylogeny: Neochoristodera **:** Simoedosauridae + *.

Characters: Crocodile-like aquatic forms. Single fused nostril at tip of greatly elongated snout, exceeding 1/2 of skull length; mandibular symphisis extended to over 1/2 length of tooth row; splenial strongly involved in symphisis; secondary palate for air-breathing; premaxilla does not contact vomer; small interpterygoid foramen; suborbital fenestra short & kidney-shaped; pterygoid fused to parasphenoid (?); craniomandibular joint anterior to occipital condyle; internarial present; interorbital width narrower than diameter of orbit; postorbital excluded from orbit; lacrimal reduced to small triangle; neomorphic bone forms ventral border of post-temporal fenestra; paroccipital process strongly deflected ventrally; temporal bars extended laterally to accommodate very large jaw muscles; limbs poorly ossified (but full development of all limbs). No sternum, but not relevant for aguilliform movement.

Links: Evolutionary Relationships of Archosaurs (basal archosauromorphs); Archosauria: More on Morphology; Theodore Roosevelt National Park Champsosaur; Welcome to FS-Today!; usda.gov article5; utoronto champsosaurus; champsosuarus gigas; tucsonshow tgms2000_p9; Introduction to the Diapsids; Champsosaur Bones in the Arctic; Brown Coulee - Champsosaur Vertebrae; Champsosaurs - Suite101.com; Ghost lineage; Fossil Find Above the Arctic Circle. ATW000531.

References: deBraga & Rieppel (1997); Gao& Fox (1998)

Page Back | Unit Home | Page Top | Page Next

checked ATW050908

Choristodera: Dendrogram

Abbreviated Dendrogram

```
DIAPSIDA
|?-CHORISTODERA
|    |--Cteniogenys
|    `--+--Monjurosuchus
|       `--Neochoristodera
|          |--Simoedosauridae
|          `--Champsosauridae
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
```

Contents

Dendrogram

```
DIAPSIDA
|?-CHORISTODERA MH
|    |--Lazarussuchus
|    `--+--Cteniogenys
|       `--+--Hyphalosaurus
|          |--Monjurosuchus
|          `--Neochoristodera
|             |--Simoedosauridae
|             `--Champsosauridae
|--ARCHOSAUROMORPHA
```

`--LEPIDOSAUROMORPHA

Page Back	Unit Home	Page Top	Page Next

Choristodera: References

Abbreviated Dendrogram

```
DIAPSIDA
|?-CHORISTODERA
|   |--Cteniogenys
|   `--+--Monjurosuchus
|      `--Neochoristodera
|         |--Simoedosauridae
|         `--Champsosauridae
|--ARCHOSAUROMORPHA
`--LEPIDOSAUROMORPHA
```

Contents

References

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Champsosauridae,.

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

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
Cteniogenys.

Gao, K & RC Fox (1998), *New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of Choristodera*. **Zool. J. Linnean Soc.** 124: 303-353.
Champsosauridae; Neochoristodera.

Matsumoto, R., Evans, S.E., and Manabe, M. 2007. The choristoderan reptile *Monjurosuchus* from the Early Cretaceous of Japan. *Acta Palaeontologica Polonica* 52 (2): 329-350. pdf
Monjurosuchus

Tarduno, JA, DB Brinkman, PR Renne, RD Cottrell, H Scher, & P Castillo (1998), *Evidence for extreme climatic warmth from Late Cretaceous arctic vertebrates*. **Science** 282: 2241-2244.
Neochoristodera.

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Palaeos
ARCHOSAURIA
VERTEBRATES
OVERVIEW

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

Archosauria: Overview

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
`--ARCHOSAUROMORPHA
   |
   `--ARCHOSAURIA
      |--Proterosuchidae
      `--+--Erythrosuchidae
         `--+--Euparkeriidae
            `--+--Proterochampsidae
               `--Crown Group Archosauria
                     |--Ornithodira
                     |  |--PTEROSAURIA
                     |  `--DINOSAUROMORPHA
                     `--Crurotarsi
                        |--Phytosauridae
                        `--Rauisuchiformes
                           |--Rauisuchia
                           |  |-
-Ornithosuchidae
                           |  `--+-
-Prestosuchidae
                           |     `-
-Rauisuchidae
                           `--Suchia
                              |--Aetosauridae
                              `-
-CROCODYLOMORPHA
```

Contents

The Archosauria

Life reconstruction of the large rauisuchian *Prestosuchus*, based on the skeleton cast on display at the American Museum of Natural History
Artwork by Nobu Tamura , via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

The name Archosauria means "ruling reptiles" and these are the creatures that dominated the world during the Mesozoic era. This great group of animals includes dinosaurs, birds, crocodiles, pterosaurs (flying reptiles) and many other groups of creatures. The archosaur skeleton has several anatomical characteristics that distinguish it from other groups of animals, such as an extra opening on each side of the skull in front of the eyes (the preorbital fenestra), and teeth set in sockets ("thecodont" teeth) which anchors them, and makes them less likely to be lost during feeding. Some archosaurs differ from other reptiles in their more upright posture which eliminated the sinuous lateral flexure of the skeleton when moving, such as is found in lizards. Archosaurs also differ from more primitive sauropsids in practice of parental care of the young and in a four-chambered heart (for more efficient distribution of oxygenated blood to the rest of the body). Some archosaurs, such as birds and coelurosaurian dinosaurs also developed large brains, indicating a higher level of intelligence. It has even been speculated that if a bolide had not seen out the dinosaurs, then they would have eventually evolved into a human-grade intelligent species, a "dinosauroid." Just because intelligent life on planet Earth is presently mammalian is no reason to suppose that it has to be necessarily so. We are truly accidents of history.

Most of the more derived archosaurs are covered in separate sections relating to crocodylomorphs, dinosaurs, birds, and pterosaurs. This unit deals with the basal forms historically known as "thecodonts", along with several of their more primitive and less well-known lizard-like cousins, generally grouped under the assemblage of "basal archosauromorphs". We have synonymised this rank-free cladistic term with the cladistic-linnaean rank based Paraorder (= paraphyletic Order) Thecodontia, which updates Olshevsky (1991)'s "Superorder Thecodontia"

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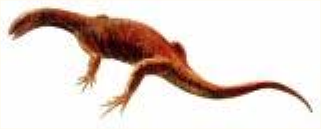
Metabolism

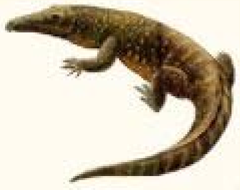
The early ("thecodontian") Archosaurs were for the most part were armoured scaly animals, probably ectothermic, which flourished during the warm dry desert conditions of the Triassic. The only truly ectothermic archosaurians that persisted beyond the Triassic and still survive today are the Crocodylia. The Dinosauria were or include some representatives that were at least partial endotherms (warm blooded) which also flourished during the Mesozoic and which still flourish as the fully endothermic birds (Aves). Many scientists still reject the endothermic dinosaur hypothesis, although Bob Bakker (who started the whole warm-blooded dinosaur thing) says that many thecodonts were also warm-blooded. However, Triassic thecodonts were much like crocodiles except they were fully terrestrial. As descendents of the crurotarsan thecodonts, crocodiles are ectothermic. Since it is unlikely that a large warm-blooded animal will loose this metabolic characteristic and become cold-blooded, there is a solid case that Triassic thecodonts were also ectotherms. In fact, the supremacy of the archosaurian thecodonts over the certainly partially endothermic proto-mammalian therapsids during the Triassic can be seen as the result of the superiority the reptilian metabolism has in hot dry conditions, such as characterized much of Pangea during the Triassic. In fact, for much of Australia's Plio-Pleistocene history, where conditions were probably similar, the largest terrestrial predators were not mammals but gigantic varanid lizards (*Megalania*) and land crocs, (and possibly also, as in South America, giant flightless birds)

Birds however, which are the descendents of dinosaurs, are warm-blooded; and theropod dinosaurs are extremely similar to birds. Several advanced types (protobirds) have even been found fossilized with a coating of feathers or feather-like structures. It can be assumed therefore that some dinosaurs (especially the small advanced coelurosaurs) were basically like modern-day birds, i.e. warm-blooded.)

Early Archosauromorph Evolution

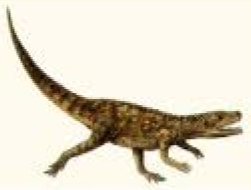


The Permo-Triassic Archosaurs represent a wonderful evolutionary succession. At one end, appearing in the late Permian period, there are reptiles that in appearance, habits, and metabolism were probably indistinguishable from modern lizards. There are the **Basal Archosauromorphs**, represented by unspecialized animal like *Protorosaurus* and the **Prolacertiformes**, which superficially resembled from large modern lizards (say 50 cm to 2 meters in length), differing in certain anatomical details (the most obvious being the large hind legs, but many differences in the skull and skeleton show that these were not the animals that gave rise to modern lizards. Obviously there were other forms too, which lived in arid desert regions where the likelihood of fossilization was very poor (*Protorosaurus* was actually apparently aquatic, or at least partially so).)



From these lizard-like forms evolved a whole assemblage of reptiles, including several archosauromorph herbivore lineages, and more importantly, the **Basal Archosauriformes**. The Archosauriformes (as opposed to the Archosauromorphs) include somewhat more advanced forms, but not the more primitive lizard-like ones. These are thecodonts, and the most basal Archosauriformes (historically, the Suborder **Proterosuchia** of the Order Thecodontia) first appear during latest Permian time. Their most primitive, ancestral members include the late Permian *Archosaurus* and the better known early Triassic *Proterosuchus*, whose name resembles *Protorosaurus* as much as Archosauriformes does Archosauromorphs. With all this resemblance of names, it is surprising anyone is not confused. But of more interest here is the fact that *Proterosuchus* and its relatives are much more advanced animals than *Protorosaurus*. Of especial interest is the presence of an extra opening on each side of the skull in front of the eyes, the *preorbital fenestra* (which perhaps originally housed some sort of gland), and is a distinguishing characteristic in almost all archosaurian skulls since (although some have secondarily lost it).)

If *Protorosaurus* looked superficially like a large stocky lizard (a modern-day varanid might be a good analogy, at least in build), *Proterosuchus* was rather like a small crocodile, especially with its squat build and long toothy jaws. It would easily have been distinguished however by the lack of armoured scutes; these only came later on the evolutionary tree.)



Proterosuchus was replaced in turn by even more advanced forms, such as *Erythrosuchus* and *Euparkeria*, which constituted even further evolutionary succession, including further modification of the skull, and improved posture. Again, all these characteristics were carried on to their descendents.)

Euparkeria was a small active animal with a double row of bony scutes along its back. In time its descendents formed a new monophyletic clade, the **Archosauria** proper or **Crown Group Archosauria** (or at least the most basal and ancestral members of the taxon), which have the same relation to the Archosauriformes as the Archosauriformes do to the Archosauromorphs (think of it as like Russian dolls, each more basal or "primitive" clade includes the next more advanced clade as among its members) Archosauriformes does Archosauromorphs)

The early crown group archosaurs (the post-Proterosuchian thecodonts) were a diverse group of Triassic reptiles that dominated the land during the Middle and Late Triassic. They included small, agile two- and four-legged forms, large four-legged carnivores, armored herbivores, and crocodile-like aquatic reptiles. They eventually gave rise to crocodiles, dinosaurs, and two quite different breeds of flying reptiles (pterosaurs and, through dinosaurs, the birds).)

At a very early stage, these basal crown group archosaurs split into two major evolutionary lineages, the crurotarsian line, which includes crocodiles and a number of other groups, and the ornithodiran line, which includes the ancestors of dinosaurs, birds, and pterosaurs.)

The forms that evolved from early Crurotarsian ancestors included the phytosaurs, large semi-aquatic crocodile-like **phytosaurs**; the terrestrial

carnivorous prestosuchids; the armoured herbivorous **aetosaurs**; the ctenosauriscids, strange sail-backed forms; and other little known types. This pseudosuchian or crocodile-related line constituted the dominant branch of thecodontian archosaurs. Among their members they included, along with the small bird-/dinosaur-like crocodile-ancestors and similar forms, three other lines, all of which, although soon becoming extinct themselves curiously presaged later evolutionary lines.)

Lagosuchus

Whereas the Crurotarsi quickly diversified and evolved, the ornithodires remained small, bird-like forms, which tended more and more towards total bipedality. This cursorial, or agile running tendency, was continued further in *Marasuchus* (= *Lagosuchus*, late Ladinian; mid-Triassic), the slim, long-legged ancestors of the dinosaurs, and possibly of the Pterosaurs as well.)

The highest development of the Thecodontia was represented by the late Triassic **Rauisuchia**, advanced Crurotarsian types like the large carnivorous rauisuchids and poposaurs which replaced the prestosuchids, and a number of small running forms, which included the direct ancestors of the crocodiles. They represent a diverse but poorly known assemblage; active, fully terrestrial, with upright dinosaurian and mammalian type stance. The difficulty of determining evolutionary relationships among them is the result of mostly incomplete material. Hopefully this will be resolved in the future as more complete specimens are studied.)

By the late Triassic then, the thecodontian archosaurs had reached their maximum diversity. They included both large and small dinosaur-like bipeds (long tailed animals that ran on their hind legs), armored aetosaur herbivores, several lines of large terrestrial carnivores, the large predatory ornithosuchids, capable of running on either their hind legs or on all fours, and crocodile-like semi-aquatic predators (phytosaurs and proterochampsids), and active little four-legged runners (the Sphenosuchia, variously considered to be crocodiles and thecodonts). The ornithodire line meanwhile had already produced the first dinosaurs and pterosaurs, but these early ornithodires, although common, for the most part remained in the shadow of the large archosaurs.)

End of a dynasty

Just as the terminal Permian mass extinction paved the way for the archosaur revolution by eliminating most of the therapsids, so the terminal Triassic extinction killed off all the basal archosaurs except for a few sphenosuchids, allowing their fellow archosaurs, the dinosaurs, to take over as the dominant life-form. The dinosaurs and pterosaurs would continue to dominate terrestrial and aerial niches until the end of the Mesozoic, while the small terrestrial sphenosuchids lineage evolved the large semi-aquatic crocodilians that would share the dinosaurs' world, and ultimately outlive them. (MAK 991003 & 030730, updated MAK101007 and 120311)

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

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Archosauria: Archosauriformes

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
`--ARCHOSAUROMORPHA
   |
   `--ARCHOSAURIA (= Archisauriformes)
       |--Proterosuchidae
       `--+--Erythrosuchidae
          `--+--Euparkeriidae
             `--+--Proterochampsidae
                `--Crown Group Archosauria
                   |--Ornithodira
                   |  |--PTEROSAURIA
                   |  `--DINOSAUROMORPHA
                   `--Crurotarsi
                      |--Phytosauridae
                      `--Rauisuchiformes
                         |--Rauisuchia
                         |  |--Ornithosuchidae
                         |  `--+-
-Prestosuchidae
                         |      `--Rauisuchidae
                         `--Suchia
                            |--Aetosauridae
                            `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

1. Archosauriformes
2. Erythrosuchidae X
3. Euparkeriidae X
4. Proterochampsidae X
5. Proterosuchidae X

The Archosauriforms

The **Archosauriformes** evolved as sprawling semi-aquatic archosaurian predators (**Proterosuchidae**) in Pangea during the late Permian. For some fifteen million years they remained rare, undergoing very little evolutionary change. The terminal Permian catastrophe, which killed off 95% of all types of life, cleared the world of all large therapsids and allowed the proterosuchids to take center stage as the top carnivore. Within the space of five million years the proterosuchids had evolved into a wide variety of terrestrial and semi-aquatic carnivores.

Early Triassic archosauriforms like ***Euparkeria*** were the source of a further evolutionary radiation. These animals, which are historically referred to as "thecodonts", are characterized by certain shared primitive or ancestral features, such as the *antorbital fenestra* (an opening on each side of the skull between the eye sockets and the nostrils) and teeth in sockets. The name *Thecodont* is actually Latin for "socket-tooth," referring to the fact that thecodont teeth were set in sockets in the jawbones; an archosaurian characteristic that was inherited by the dinosaurs. Thecodontia therefore is an evolutionary grade of animals, rather than a clade. They represent a "grab-bag" taxon for any archosaur that wasn't a crocodilian, a pterosaur, or a dinosaur. (MAK 991003 & 030730)

The fine details of archosauriform evolution are still uncertain. In particular, *Euparkeria* and the **proterochampsids** continue to switch places as the sister group of Archosauria every few years. What is clear is that *Euparkeria*, Proterochampsidae, and Archosauria are a natural group and differ from other archosauriforms in a number of ways. The items on the list of synapomorphies of this unnamed group vary a bit from one study to another. We may take Paul Sereno's work as representative. Sereno (1991) includes:

1) Dorsal body armor (specifically, at least one row of bony plates flanking the vertebrae down the middle of the back).
2) Interclavicle with reduced, tab-like lateral processes (as with most derived tetrapods, the structural integration of the two arms gradually decreases).
3) S-shaped femoral shaft (this one is a bit tricky, since the degree of bend in the upper leg bone is quite variable).
4) Loss of bony astragalocalcaneal canal (but it is possible that erythrosuchids have this character and proterochampsids do not -- *see* Chatterjee, 1982).
5) absence of ossification of distal tarsals 1 & 2
6) digit IV on the foot is markedly shorter than I.

In the 1970's and 1980's it was common to classify archosauriforms on the basis of their ankle morphology. This practice has been soundly criticized -- not least by Sereno himself. However, it is obvious from Sereno's list that there was a core of truth to the "ankle phylogenies" Sereno (1991: 2). Four of Sereno's six synapomorphies concern the structure of the hind limb. What's going on here is that both the front and hind legs are being reorganized. Conventionally, this is expressed in terms of a trend toward dinosaur-style locomotion: upright carriage with the legs held under the body and a simplified, hinge-like ankle joint. However, crocodiles do not walk in that fashion today, and basal archosaurs certainly didn't. A little later on, we will take up the matter of the archosaurian ankle in more detail. The point here is that we remain a bit uncertain exactly how the early archosauriforms, including basal archosaurs, were getting around -- just as we are unsure how the therapsids of about the same period used their legs.

Since Sereno's seminal paper, others have shown that other parts of archosauriform anatomy were also undergoing change. Gareth Dyke has gone so far as to construct archosaur phylogenies deliberately omitting ankle characters. Dyke (1998). These faithfully reproduce the main lines of descent worked out with ankle characters. From this result, Dyke argues that ankle morphology has no special significance in archosaur evolution. Itmay be too soon to say. Until we have a better understanding of early archosaur locomotion from a mechanical perspective, the significance of the lumps and bumps on the archosaur tarsus are difficult to evaluate.

Perhaps we should leave well enough alone with that agnostic comment. However, it may also be worth pointing out two factors which inform our uncertainty:

1. The first half of the Triassic was a period of strongly seasonal climates. In the broader context of Earth's history, this is unusual and might easily have had rather significant implications for locomotion. Survival in a strongly seasonal environment usually requires some combination of migration, torpor, and adaptability to varying substrates. Migration and broad adaptability have obvious (and different) implications for locomotion. Torpor usually requires the ability to store significant fat reserves, which has yet a third implication for locomotion. Thus, there are some *a priori* reasons for thinking that locomotor styles may have been under strong selective pressure -- and a type of pressure that could push in several different directions.

2. The idea that locomotor ability "improved" obscures a multitude of different adaptive strategies. Some of these strategies involve anatomical changes which are quite similar, if one simply adds up character changes, but are entirely different and incompatible in overall effect. For example, moving the legs under the body may be an adaptation for the long-distance strider who needs the speed and elevation for efficient hunting. However, the same trait may also signify adaptation for the slow-moving flat-footed walk of extremely heavy armored herbivores. The difference may show up in the foot. The strider will be *digitigrade*, while the plodder will be *plantigrade*. But a

digitigrade foot may also represent a sprawling, low-slung animal adapted to sloping or uneven surfaces.

The problem with mixing similar characters which reflect incompatible locomotor designs can be seen in Sereno's synapomorphy #6: digit IV on the foot is markedly shorter than I. This wrongly lumps together animals adapted for three-toed, bipedal running with stiff-legged sprawlers **[1]**. There is no reason to believe that this character is homologous in all archosaurs. To the contrary, the bipedal runner is only known from the Ornithodiran lineage of archosaurs. The stiff-legged sprawler (so far as we are aware) is only known among Crurotarsi. *No* taxon smaller than Archosauria itself contains both types. Thus, there is no reason to suppose that this character is a true synapomorphy -- or that it even represents a single character, much less a one-time change both unique and common to the archosaur heritage.

Accordingly, we need to understand much more about the Triassic environment and early archosaur locomotion, before we can make much phylogenetic sense out of early archosaur limb characters. ATW040117.

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[1] Many primitive sprawlers rotate the foot outward during *stance phase*. The outer digits (like digit IV) in this case end up bearing significant weight. A more stiff-legged sprawler keeps the foot pointed more or less forward, so that the weight is disproportionately carried on the inner digit (digit I).

The Braincase of *Euparkeria*: the Anatomy of the Mesozoic Mind

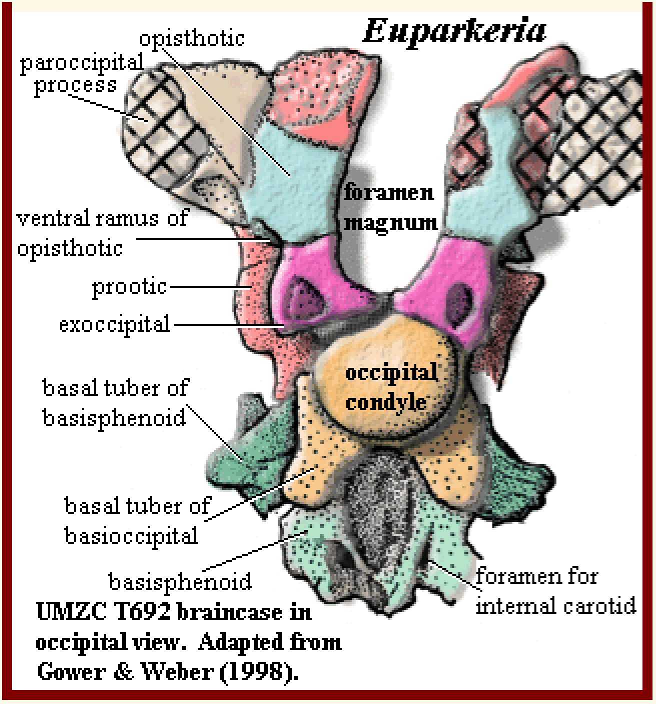
There are about half a dozen specimens of *Euparkeria*, all from the *Cynognathus* Assemblage Zone (probably Early Anisian) in South Africa. One of these, UMCZ T692, resides at Cambridge, and its braincase has recently been described in detail by Gower & Weber (1998) [GW98]. The specimen has an interesting history. It was originally part of the private collection of DMS Watson, who did most of his field work before 1930. It was described by Rosalie Ewer in 1965, but she prepared only a portion of the braincase. In the 1970's, the braincase was extensively prepared by Arthur Cruickshank, using both acid and mechanical techniques. Shortly afterward, further mechanical preparation was performed by Alick Walker. Cruickshank is a prolific scientist. However, he was apparently interested in *Euparkeria* largely for comparative purposes and has never published a detailed description. Walker, we are told, chose not to publish much of his work, although he didn't mind discussing it. Benton & Gower (2002). (As a peculiar result, "A.D. Walker, personal communication" is one of the more important references in this field.)

Perhaps in consequence of this long history of preparation, the specimen seems to have literally fallen apart when Gower & Weber started to examine it in the 1990's. However, it fell apart in a most interesting and convenient way, allowing G&W an unprecedented look directly into the endocranial cavity. We will not follow G&W into these inner recesses. **[2]** However, we will generally follow this same pattern of deconstruction. In addition, we have the happy advantage of access to Gower's later paper, Gower (2002) [G02]. Here he lists a large number of braincase characters which may be phylogenetically significant. These characteristics will be emphasized. For those who are not braincase *aficionados*, it may be a good idea to review the Schematic Guide to the Mind of Bob before venturing further.

The Occipital Face

The first figure, in occipital view, is probably close to what Ewer saw in 1965. The supraoccipital and most of the dermal bones are absent. The distal parts of the paroccipital process and the most dorsal sections of the prootic are also missing. However, the remaining parts of the occiput are relatively undistorted and undamaged.

Its a nice braincase, but not that unusual. The occipital condyle (the part that connects the skull to the back bones) is formed almost entirely by the basioccipital. The exoccipitals, which normally



UMZC T692 braincase in occipital view. Adapted from Gower & Weber (1998).

cooperate closely in this important enterprise, appear to be only loosely engaged. Instead they meet each other on the midline and selfishly exclude the basioccipital from the *foramen magnum* [G02: 5/0] **[1]**. The lateral edges of the exoccipitals are smoothly rounded, lacking a vertical crest [G02: 2/0]. G&W assign the large "hole" in the exoccipital to the exit of the hypoglossal nerve, the XIIth cranial nerve. That's unexpected, but not impossible. The supraoccipital is absent, but it clearly also played a major role in the foramen magnum, since the foramen is open at the top in the absence of the supraoccipital [G02: 19/0].

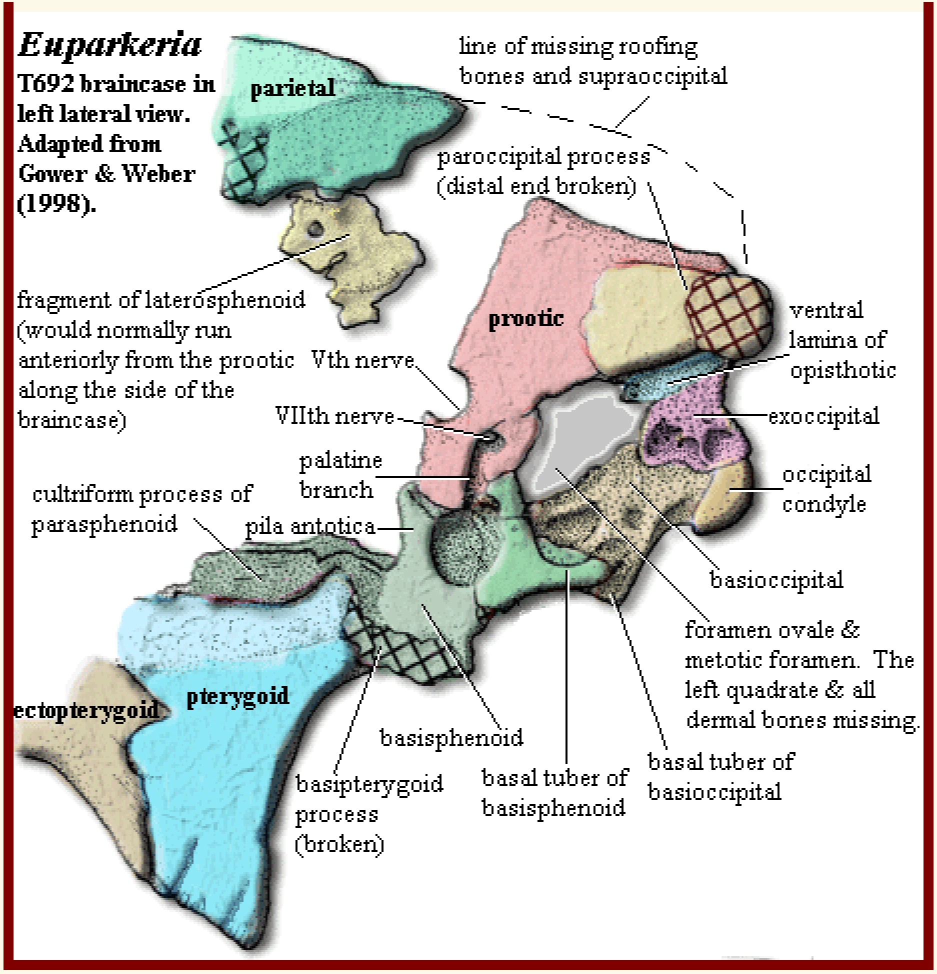
The opisthotic is relatively small, and is closely confined by the prootic, exoccipitals and paroccipital process. However, the ventrolateral corner is free, and a small ventral ramus descends at this point, lateral to the exoccipitals [G02: 3/0]. The ventral ramus fails to contact the prootic at any point [G02: 12/0], doubtless causing the prootic no end of worry and anxiousness.

Below the occipital condyle the basioccipital produces two substantial basal tubera. As in archosaurs, the basisphenoid attempts to confuse the issue by producing tubera of its own. In the midline, the basisphenoid also bears a large and important-looking depression which, despite appearances, is a primitive character of no known function. Of far more actual important is the location of the foramina for the internal carotid arteries. These plainly enter the braincase on the posterior face of the basisphenoid, rather than approaching from the side as in all crown group archosaurs [G02: 1/0].

The Lateral Face

The second figure represents the prepared lateral face of the braincase -- approximately what Cruickshank and Walker saw during the 1970's. Preparation of this area revealed that the braincase had fallen (posteroventrally) away from the skull table. A fragment of laterosphenoid was attached to the parietal, but the remainder had disintegrated, as had the lateral covering of the otic capsule. Thus, in this image, we look right into the floor of the inner ear and, beyond that, into the metotic foramen between the otic capsules.

One critical feature is that there does not appear to be any well-defined (or even poorly defined) lagenar recess. This probably tells us that *Euparkeria* lacked perfect pitch -- or any pitch, for that matter. Mammals, crocodilians and



Euparkeria
T692 braincase in left lateral view. Adapted from Gower & Weber (1998).

dinosaurs independently evolved acute, pitch-sensitive hearing by elongating the *lagena* (called the *cochlea* in mammals). We will omit the details, some of which may be found here. However, this form of hearing requires that a distinct perilymphatic duct receives the compression waves at the *fenestra ovalis* and carry them along one side of an elongate lagena in a rather specific way. In reptiles, this normally means that the inner ear must be divided into at least two compartments: (1) the *scala vestibuli* where the signal is received through the *fenestra ovalis* and in which one side (and only one side) of the lagena is open to the perilymphatic duct; and (2) a *scala tympani* in which the remaining energy in the compression wave carried by the perilymphatic duct is dissipated wave. There is no sign of such a system in *Euparkeria* and certainly no obvious recess for an enlarged lagena [G02: 9/0].

The *trigeminal notch* is large. A very small *crista prootica* is present over the facial (VII) foramen. A well-marked fossa for the palatine branch of the facial nerve trails down from the facial foramen into a large lateral depression. The anterior margin of the depression is formed by the *pila antotica*, and the posterior margin by a dorsal process of the basisphenoid. Anterior to this process is a "semi-lunar depression" [G02: 8/0] which G&W believe is adjacent to the *fenestra ovalis*. Again, this is a bit unexpected. One might expect the *fenestra ovalis* to be located more posterodorsally, nearer the base of the paroccipital process. In any event, the semilunar depression is a hallmark of archosauriforms, but is unknown in crown group archosaurs.

The other features of interest are mostly absence characters. The basisphenoid is not dorsoventrally tall [G02: 17/0]. The *basipterygoid processes* are not enlarged [G02: 18/0]. There is no horizontal ridge on the prootic below the trigeminal notch [G02: 24/1]. The basal tubera of the basisphenoid are not separated by a plate [G02: 27/1].

Lessons

Euparkeria is not as typical of archosauriforms as we might want, but it does give us a basic idea of braincase geography at the base of the archosaur radiation. The otic region is longitudinally somewhat spread out by the standards of later archosaurs, and correspondingly very narrow from side to side. The walls of the capsules are not well ossified, particularly the internal (medial) face. The otic capsules of crocodilians, in particular, are highly ossified and appear to be very tightly organized -- with a form-fitting bony recess for every soft tissue element, like one of those pointless gift sets of household tools. This kind of tight spatial organization is needed for pitch-sensitive hearing because this sense depends on very precise topology. Finally, the braincase is (by croc standards) relatively unmarked by various bumps and flanges for the attachment of muscles and tendons.

If we might oversimplify -- and who can stop us? -- *Euparkeria* represents a sort of a plastic intermediate stage. In basal tetrapods, the braincase was as much a bony anchor for the other cranial structures as it was a convenient box for the brain. This is also true of the crocodilians, although the precise arrangements are very different. However here, at the base of the archosaurs, the braincase is relatively plastic and unconstrained. It lacks (a) an internal need to accommodate pitch-sensitive hearing through the lagena (b) an intimate relation to the dermal bones of the skull and (c) a mechanical need to anchor muscles and tendons. These are matters of degree, of course; but the relative lack of constraint may have helped set the stage for the rapid development of archosaurs in so many different directions during the critical years of the Middle Triassic. ATW031212.

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[1] G&W state that the exoccipitals of *Euparkeria* do not meet at the midline [GW98:374]. By the time of [G02], Gower seems to have changed his mind.

[2] A variety of factors suggest that perhaps this particular specimen is too distorted to carry all the anatomical freight with which it has been loaded. We have great respect for Dr. Gower's extensive experience and observations on archosaur braincases. Perhaps because we lack that experience, the degree of crushing and distortion seems, to us, too extreme to allow a confident reconstruction of the anatomical fine points. G&W do not attempt a reconstruction, and the topographical relationships in the published figures suggest that it might be quite difficult to determine the original relationships inside the otic capsule.

Descriptions

Archosauriformes: *Archosaurus* (probably a proterosuchid).

Range: from the Lopingian [P97]

Phylogeny: Archosauromorpha **::** Prolacertiformes + * **:** Proterosuchidae + Erythrosuchidae + (Euparkeriidae + (Proterochampsidae + Archosauria)).

Characters: Antorbital fenestra; orbit shaped like inverted triangle; teeth laterally compressed & serrated; widespread bipedalism; presence of 4th trochanter (Crown group only?) as attachment point for major tail muscles, the caudofemoralis group of thigh retracting muscles; astragalar facets for tibia and fibula separated by flat, non-articular surface [S91]; double row of bony scutes running along the line of the backbone; elaboration of keratin integumentary structures (e.g. feathers).

Links: link.

Reference: Jones *et al.* (2000), Parrish (1997) [P97], Sereno (1991) [S91]. ATW040117.

Proterosuchidae: *Archosaurus, Chasmatosaurus, Kalisuchus*. Generalized primitive Archosauriforms.

Archosaurus

Range: Late Permian to Early Triassic of Russia, South Africa & Australia -- possibly South America.

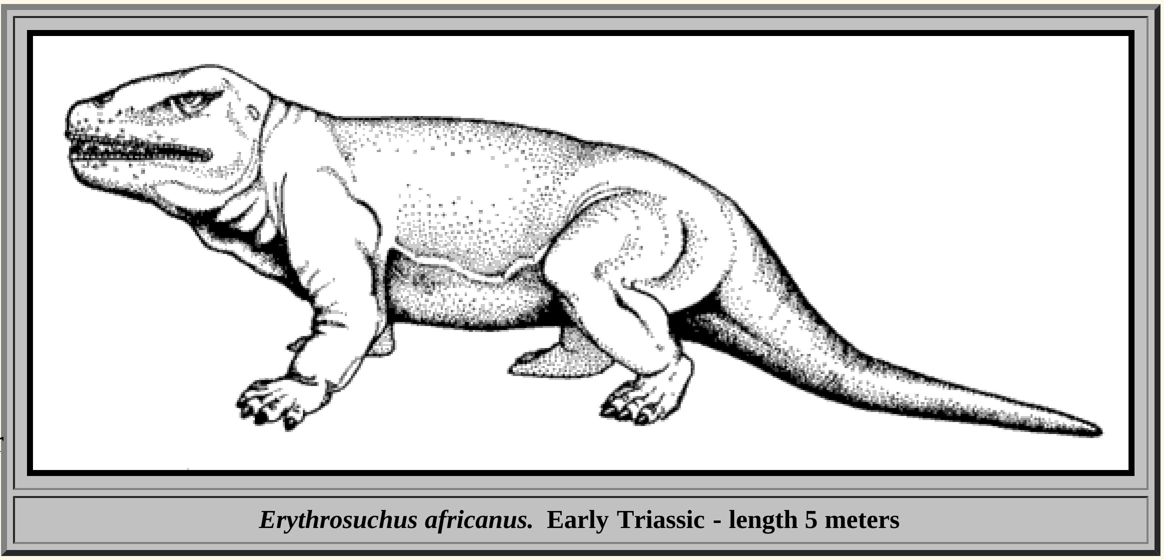
Phylogeny: Archosauriformes **:** Erythrosuchidae + (Euparkeriidae + (Proterochampsidae + Archosauria)) + *.

Characters: **$** marked down-turn of premaxilla; supratemporal and postparietal, pineal opening, all retained; mandibular fenestra absent; shoulder girdle clearly divided as scapula & coracoid (*compare* Lepidosaurs); flat pelvis without *thyroid fenestration*; sprawling gait: head of femur terminal and directed horizontally to *acetabulum*.

Links: Archosaurus; Nathis Archosauriërs (Dutch); Dinosaur Origins; Chasmatosaurus (German); Unterordnung

Proterosuchia (German -- elementary, but good); Proterosuchidae (Mikko's Phylogeny); Archosaurus; Arcosauromorfa. ATW040206

Erythrosuchidae: *Erythrosuchus*, *Vjushkovia*.



Erythrosuchus africanus. **Early Triassic - length 5 meters**

Range: Early Triassic to Middle Triassic

Phylogeny: Archosauriformes : Proterosuchidae + (Euparkeriidae + (Proterochampsidae + Archosauria)) + *.

Introduction: During the later part of the Early Triassic, the first thecodonts, such as *Protorosuchus*, gave rise both to gigantic forms (Erythrosuchids) and tiny ones (euparkeriids).

Erythrosuchus africanus was five metres in overall length, with a stocky body and an enormous head a metre in length. This creature, known from the Cynognathus Zone of South Africa (similar relatives have been found in contemporary rocks in European Russia and in China) represented the culmination of early Thecodont evolution. It was obviously the largest creature of its day, being the size of a large crocodile, and must have been a fearsome predator on contemporary large herbivores, such as the abundant, bullock-sized Kanneymeriid dicynodonts.

There is a strong similarity between the Erythrosuchids of the early Triassic and the dinocephalian (primitive therapsid) anteosaurs of the Mid- Permian. In both there was a strong growth in body size, but also an even greater corresponding growth in head-size, which became fully half the length of the body excluding the tail. As with the early tetrapods, the head becomes truly enormous relative to the body. But whereas the labyrinthodonts had weak jaw and neck muscles, and had to support the weight of their great heads by the buoyancy of water, these great carnivores held their heads aloft on massive necks, and their huge teeth and tremendous jaws would have enabled them to feed easily on other animal prey.

Yet these animals, the largest predators of their time, were too heavy and clumsy to be able to actively pursue and run down prey. Like the modern crocodile or Komodo dragon, they may have been ambush-predators, lying in wait for prey behind thick vegetation, then rushing out in a short burst of speed, and quickly overwhelming the helpless victim with their tremendous jaws. (MAK 991018)

Characters: Largest terrestrial vertebrate of the Early Triassic. Dorsoventrally elongate orbit; deep maxilla beneath antorbital fossa (antorbital fossa not prominent ventral to fenestra); articulating surfaces at carpus & tarsus poorly ossified (amphibious); heavily built, to 5m; triradiate pelvis (upright?).

Links: BPI Palaeontology Fossil Picture Gallery; Paleontology and Geology Glossary: E. ATW010407.

Euparkeriidae: *Dorosuchus, Euparkeria*. The occiput of *Dorosuchus*, as figured in [GS00], is strikingly similar to *Euparkeria*.

Range: Early Triassic of South Africa; Middle Triassic (Anisian) of Russia.

Phylogeny: Archosauriformes :: (Proterochampsidae + Archosauria) + *.

Discussion: If the tendency to gigantism was represented by *Erythrosuchus*, then the opposite, tendency towards the small light agile bird-like form was expressed by its cat-sized relative *Euparkeria*, which at 65 centimeters (26 inches) from snout to tail-tip was only an eighth the linear dimensions. This was a small, long-legged, and agile, with a more erect stance, and capable of bipedal gait. Something similar to *Euparkeria*, in turn, gave rise to two evolutionary branches: the psuedosuchians and crocodiles on the one hand, and ornithodires and dinosaurs on the other. Both began as small agile forms, but the pseudosuchians quickly reverted to the standard lizard-like form, although these were lizards of great size, e.g. the phytosaurs, Aetosauridae, and Crocodylia, all of which reached 3 metres or more in length. Most interesting of all were the great rauisuchians, which although roughly lizard/crocodile-like in form had a fully erect dinosaurian and mammalian posture. MAK991018.

Characters: Small (0.5+ m); slender; facultative bipeds (?); large skull; maxillary and mandibular fenestrae present; no parietal (pineal) foramen or fossa [P93]; for braincase, see essay; foramina for internal carotids posterior to *basipterygoid process* [P93]; palatal teeth present [P93]; teeth laterally compressed, serrated, *thecodont*; vertebral intercentra present [P93]; posterior limbs 1.5x anterior, but joint surfaces etc. not specialized as biped;*fourth trochanter* present; *mesotarsal* joint (like dinosaurs) between proximal & distal tarsals (compare croc *crurotarsal joint* between astragalus & calcaneum) [P93]; astragalar facets for tibia and fibula separated by flat, non-articular surface [S91]; calcaneum with hemi-cylindrical facet for astragalus [P93]; calcaneal tuber convex on both sides [P93]; calcaneal tuber with some posterior deviation from lateral projection [P93]; calcaneal tuber taller than broad [P93]; calcaneal facet for fibula continuous with facet for distal tarsal IV [P93]; foot symmetrical, with elongated digit III.; dorsal row of dermal ossicles on vertebral column & tail [P93].

Links: Introduction to Euparkeria; Lecture 8 - Tetrapods (skeletal anatomy); Triassico (Italian); ???????; Archosauria: More on Morphology; Archosaurs - A new wave of Invadors; 1 Meeting of the EAVP (see Borsuk-Bialynicka abstract -- new Polish form); · (Euparkeria); Euparkeria; Euparkeria capensis (images of fossil); Title; Dino Web - How dinosaurs moved.

References: Gower (2002) [G02], Gower & Sennikov (2000) [GS00], Gower & Weber (1998) [GW98], Parrish (1993) [P93], Sereno (1991) [S91]. ATW030825.

Proterochampsidae: *Cerritosaurus, Proterochampsa*.

Range: Middle Triassic (Ladinian) to Late Triassic (Carnian).

Phylogeny: Archosauriformes **:::** Archosauria + *.

Characters: Broad, low skull with small dorsal fenestra; no parietal (pineal) foramen or fossa [P93]; postorbital with strong, dorsally rugose, horizontal crest [S91]; foramina for internal carotids lateral to *basipterygoid process* [P93]; vertebral intercentra absent [S91] [P93]; primitive plate-like pelvis; calcaneal tuber with some posterior deviation from lateral projection [P93]; astragalar facets for tibia & fibula adjacent [S91]; calcaneal tuber taller than broad [P93]; calcaneal facet for fibula continuous with facet for distal tarsal IV [P93]; calcaneum with hemicylindrical facet for astragalus [P93]; dermal armor present [P93]; aquatic predators from West Gondwanaland.

Links: link (treats as crocodylomorph?)

References: Parrish (1993) [P93]; Sereno (1991) [S91]. ATW040118.

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

checked ATW050702

Archosauria: Crown Group Archosauria

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

1. Archosauria

Sorting Archosaurs

Archosaurian systematics have sometimes been a contentious area. It would be unproductive to relate the entire history of the field. However, it is important to have a rough understanding of the systematic frame of reference used by many of the older papers.

The Classical View

By the middle years of the last century, The term "archosaur" had come to include crocodiles, dinosaurs, pterosaurs and a wide variety of "primitive" Triassic reptiles. Generally speaking, it would include what we would now call Archosauriformes, except for birds. The more basal

archosauromorphs were not recognized as part of this lineage. At that time, rhynchosaurs, for example, were thought to be part of the "Lepidosauria," which encompassed some basal Diapsida ("Eosuchia") as well as Lepidosauriformes. Other archosauromorphs were classified with the "Euryapsida," a vague group which swept in most of the Mesozoic marine reptiles as well as others, such as *Trilophosaurus*, which were thought to be related. The recognized higher orders of Archosauria were Crocodilia, Pterosauria, Saurischia and Ornithischia (the monophyly of dinosaurs was not well established). This left a large number of Triassic species in a paraphyletic group of basal archosaurs, the "Thecodontia." The thecodonts, in turn, were divided into three suborders -- essentially perceived as evolutionary grades on the way to the crocodiles: Proterosuchia (basal Archosauriformes), Pseudosuchia (Crurotarsi except Phytosauridae and Crocodylomorpha), and Parasuchia (Phytosauridae). While it was believed that dinosaurs and pterosaurs derived from the thecodonts, no one had a good idea of where the divergence had occurred. Perhaps the most popular theory was that the dinosaurs and pterosaurs were the result of multiple radiations from several different thecodont lines. See, for example, Walker (1964).

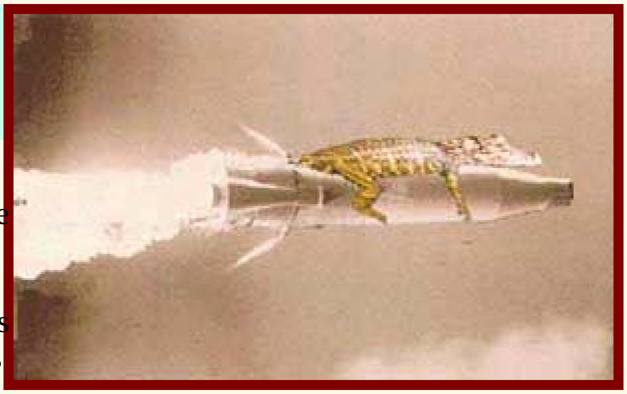
Methods and Madness in the Age of Disco

During the 1970's and 1980's, two developments took place that made a fair mess of the old system and fractured the paleontological community: the advent of cladistic methods and the early anatomical and locomotor studies on the archosaur tarsus (ankle) by Krebs, Cruikshank, Chatterjee, and others. Now, a generation later, younger scientists are writing review articles which seem to wonder what the fuss was all about. See, for example, Brochu (2001) and Gower & Wilkinson (1996). From today's point of view, it appears that everyone was reaching about the same conclusions at about the same time. For example, by the mid- or late 1980's almost everyone agreed that: (a) there was a single main split between the croc lineage and the dino-pterosaur line; (b) *Euparkeria* was very close to that split; (c) forms we now consider to be basal archosauromorphs were just that; (d) *Scleromochlus* was on the dinosaur branch; (e) almost all of the other known "thecodonts" beyond *Euparkeria* were on the croc side of the split; and (e) ornithosuchids and phytosaurs were fairly basal archosaurs. That's obviously very broad agreement. Why all the hard feelings? Perhaps it isn't science, but the question deserves an answer.

The hard feelings were generated precisely by differences in methodology. The traditional taxonomist says "I have studied these bones for 30 years. I have the judgment, experience and wisdom to see patterns and distinctions which you cannot, and so you should listen to me." The cladist says: "I have concentrated on point by point comparisons of dozens of specimens. My conclusions are the result of truly objective computer-based analysis -- not mere intuitions, and so my view is the only scientific one." The anatomist says: "All of you ignore these animals as living organisms. I have studied the detailed relations between the bones. Only I consider how the animal worked as a living organism, and this is the only way one can understand the evolutionary mechanisms at work."

Of course, all three of these hypothetical folks are correct -- except for their claims to exclusivity. Thus, it is not surprising that all three groups were reaching the same conclusions. However, notice that each group's attitude could be perceived as not just disagreeing with some trifling discrepancy in the others' results, and not just disagreeing on methodology, but as attacking the others personally. The taxonomist is heard to question the judgment and maturity of the cladist and anatomist. The cladist may be implying that the others are not objective -- and not even scientific. The anatomist may be implying that the cladist and traditionalist don't really know anything useful. Scientists being no better and no worse than other human beings, sometimes they *did* mean to engage in personal attacks. Mostly they did not. However, the three methodologies of that generation represented very different world views, and the inevitable philosophical conflicts sometimes overshadowed scientific agreement.

The Code War: the Clash of the Cladograms



As the Cold War was ending, the Code War was just heating up. The first serious attempts at cladistic analysis were made by (as usual) Prof. Jacques Gauthier. Gauthier redefined the Archosauria as a crown group, the last common ancestor of birds and crocodiles and all of its descendants: crocs + rocs. Generally speaking, this nomenclature has stuck. Above Archosauria were the Erythrosuchidae and other forms previously referred to as "Proterosuchia." Gauthier used the term Archosauriformes to describe the clade uniting these forms with Archosauria.

A variety of names have been given to the two stem clades within Archosauria. Perhaps the most common are the Ornithodira (rocs > crocs) and Crurotarsi (crocs > rocs). The Ornithodira were originally the Ornithosuchia -- named after the Ornithosuchidae -- until it was learned that the Ornithosuchidae were more likely crurotarsans, which caused a certain amount of embarrassment all around. In any event, the Ornithodira are now believed to include *Scleromochlus*, pterosaurs, dinosaurs, and birds. Crurotarsi is believed to include crocs and all other "thecodonts" within the Archosauria: phytosaurs, aetosaurs, rauisuchians, ornithosuchids, and many strange and poorly-known beasts like *Doswellia*.

Unfortunately, the branching order within Crurotarsi has been, so far, impervious to cladistic analysis. Successive analyses by Benton & Clark (1988), Sereno (1991), Parrish (1993), Juul (1994), Benton (1999), and Benton & Walker (2002) have yielded rather discordant results, as shown in the table below (cladograms simplified and nomenclature standardized to promote comparison).

Benton & Clark (1988)

```
Archosauria
|--Ornithodira
|  |--Ornithosuchidae
|  `--+--Pterosauria
|     `--Dinosauria
`--Crurotarsi
   |--Phytosauridae
   `--+--Gracilisuchus
      `--+--+--Aetosauridae
         |  `--Prestosuchidae
         `--+--Rauisuchidae
            `--Crocodylomorpha
```

Sereno (1991)

```
Archosauria
|--Ornithodira
|  |--Pterosauria
|  `--Dinosauria
`--Crurotarsi
   |--Phytosauridae
   `--+--Ornithosuchidae
      `--+--Aetosauridae
         |--Gracilisuchus
         |--Prestosuchidae
         |--Rauisuchidae
         `--Crocodylomorpha
```

Parrish (1993)

```
Archosauria
|--Ornithodira
|  |--Pterosauria
|  `--Dinosauria
`--Crurotarsi
   |--Ornithosuchidae
   `--+--Phytosauridae
      `--+--Prestosuchidae
         `--+--Aetosauridae
            `--+--Rauisuchidae
               `--+-
-Gracilisuchus
                  `--
Crocodylomorpha
```

Juul (1994)

```
Archosauria
|--Ornithodira
|  |--Pterosauria
|  `--Dinosauria
`--Crurotarsi
   |--+--Prestosuchidae
   |  `--Aetosauridae
   |--Phytosauridae
   `--+--Ornithosuchidae
      `--+--+--Gracilisuchus
         |  `--Rauisuchidae
         `--Crocodylomorpha
```

Benton & Walker (2002)

```
Archosauria
|--Ornithodira
|  |--Pterosauria
|  `--Dinosauria
`--Crurotarsi
   |--Phytosauridae
   `--+--Aetosauridae
      `--+--+--Ornithosuchidae
         |  `--Prestosuchidae
         `--+--Gracilisuchus
            `--+--Rauisuchidae
               `--
Crocodylomorpha
```

Palaeos Best Guess (2003)

```
Archosauria
|--Ornithodira
|  |--Pterosauria
|  `--Dinosauria
`--Crurotarsi
   |--Phytosauridae
   `--+--+--Ornithosuchidae
      |  `--+--Prestosuchidae
      |     `--Rauisuchidae
      `--+--Aetosauridae
         `--+--Gracilisuchus
            `--Crocodylomorpha
```

Each of these studies has its strengths and weaknesses. For example, Sereno's study may have too few characters to resolve the number of taxa in the study. Parrish seems to have too many ankle characters. Indeed, the "ankle phylogeny" has taken on a whole new life through this study. Parrish probably set out deliberately to test the ankle phylogenies by cladistic methods. At any rate his data is overwhelmingly weighted with ankle characters. Benton

(1999) and Benton & Walker (2002) begin with Parrish's data matrix and add further characters. However, the effect of tarsal characters is still very strong. As Dyke (1998: 561) has noted: "[A]nkle characters do not contribute significantly to the broad shape of archosaur phylogeny. Indeed, their considered importance to the classification of the group is probably counter-productive."

Gower (2002) has shown that braincase characters, used alone, generate a rather different pattern. Interestingly, when Gower's characters are combined with the Parrish - Benton data set, the resulting phylogeny may be much closer to Gower's result. This, in any case, was the basis of our "best guess" phylogeny. Further details are given with the cladogram at the end of this unit.

Finally, it has become *de rigueur* in reviews of archosaur phylogeny to add a few words about molecular phylogenies. Molecular phylogenies can add absolutely nothing to our understanding of basal archosaur evolution because all of the taxa of immediate interest are extinct. But, then again, who are we to depart from such a well-established scientific and literary tradition?

Accordingly, and merely by way of example, we include the enlightening cladogram of Hedges & Polling (1999):

```
Reptilia
|--Squamata
`--Archosauria
   |--Aves
   `--+--Rhynchocephalia
      `--+--Testudines
         `--Crocodylia
```

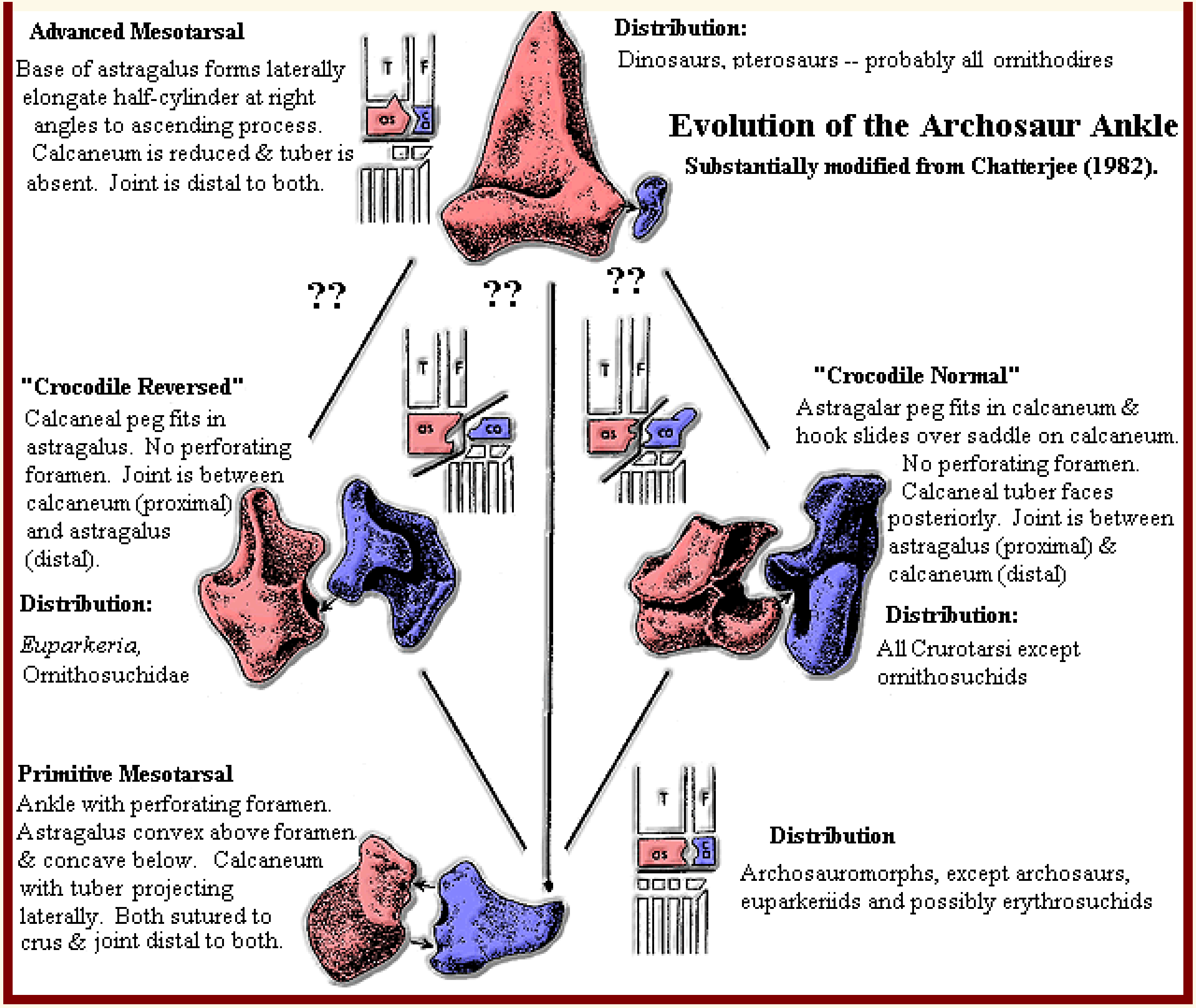
These authors (with truly stunning arrogance) note: "determining how the many groups of extinct reptiles of the late Paleozoic and early Mesozoic fit into this molecular phylogeny will be a challenge to paleontologists."

Yes, indeed .... ATW040123.

A Footnote on Ankles

Considering the historical importance of the archosaur tarsus, we would be remiss if we failed to provide at least some information on the structures in question. The diagram at right was adapted from Chatterjee (1982) and has been somewhat modified from the original in light of later discoveries. It is more or less self-explanatory.

The basal



archosauriform tarsus consisted of an astragalus and calcaneum sutured to the lower leg bones. the two proximal tarsals articulated by means of reciprocal peg and socket joints above and below a large perforating foramen. The functional ankle joint was between the proximal and distal tarsals, *i.e.* below the astragalus and calcaneum. The calcaneum bore a large, projecting tubercle which stuck straight out to the side.

Most Crurotarsi (the croc lineage of archosaurs), modify this arrangement. They have the "crocodile normal" tarsus. Here, the lower peg on the astragalus still articulates with a socket on the calcaneum. However, the upper articulation has been transformed into a sliding, rotary contact in which a "hook" on the astragalus rotates around a hemispherical saddle on the calcaneum. The ankle joint is thus between the astragalus, which is still sutured to the lower leg bones, and the calcaneum, which is now functionally part of the foot. The perforating foramen has disappeared, and the calcaneal tuber projects to the rear.

In theory, the "crocodile reversed" tarsus involves the converse arrangement, in which the calcaneum functions as part of the crus and the astragalus joins the foot. However, there is some uncertainty about the existence of this morph. The ankles of living ornithosuchids and *Euparkeria* may have had rather complex topologies with alternate functional modes.

The "advanced mesotarsal" joint is placed once again between the proximal tarsals and the metatarsals. Here, the calcaneum is reduced to a minor element. The astragalus is very large, with strong sutural connections to the lower leg bones reinforced with an ascending process which follows the shaft of the tibia. In Chatterjee's diagram, this hinge-like joint is shown as being derived from one or the other crurotarsal form. This need not have been the case. We know so little about the basal radiation of ornithodires that nearly anything is possible.

ATW040124.

Descriptions

Archosauria: birds + crocs.

Range: from the Early Triassic

Phylogeny: Archosauriformes **:::** Proterochampsidae + * **:** Crurotarsi + Ornithodira.

Characters: No parietal (pineal) foramen or fossa [P93]; foramina for internal carotids lateral to *basipterygoid process* [P93]; no palatal teeth on pterygoid, palatine or vomer [$S91] [$**p**03]; vertebral intercentra absent [$P93]; calcaneum with hemicylindrical facet for astragalus [P93]; calcaneal tuber with at least some posterior deviation from lateral projection [P93]; calcaneal tuber taller than broad [P93]; calcaneal tuber projects posteriorly at 90° to long axis of articulation between crus & proximal tarsals [$P93]; calcaneal tuber deflected >45° posterolaterally [$S91] [$**p**03]; calcaneal tuber flares such that it is laterally concave & medially convex [$P93]; calcaneal facet for fibula continuous with facet for distal tarsal IV [$S91] [P93] [$**p**03]; dermal armor present [P93].

Notes: "[**p**03]" refers to our own analysis of published data.

Links: link.

References: Parrish (1993) [P93], Sereno (1991) [S91]. ATW040117.

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

checked ATW050702

Archosauria: Archosauria: Ornithodira

Scleromochlus

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--Scleromochlus
            |  `--+--PTEROSAURIA
            |     `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

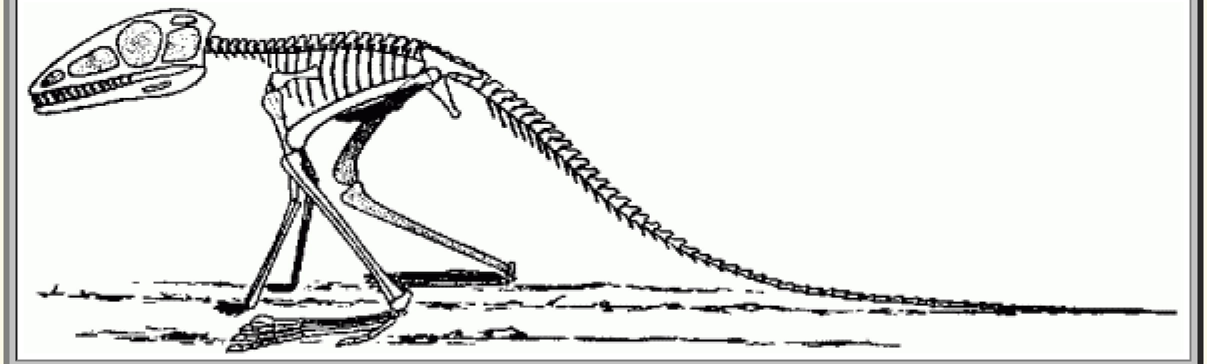
Contents

Taxa on This Page

1. Crurotarsi
2. Ornithodira
3. *Scleromochlus*

The Stem Groups: Ornithodira

and Crurotarsi



Scleromochlus ***taylori*****, a basal ornithodire from the Late Carnian Lossiemouth Beds of Elgin, Scotland. Reconstructed skeleton, length about 25 cm. Illustration in Krebs (1976) after Huene (1914). According to Benton (1999), Huene's reconstruction has the torso too short, the coracoid too small, and perhaps the feet a bit large.**

By definition, the Archosauria (rocs + crocs) are comprised of the **Ornithodira** (rocs > crocs) and the **Crurotarsi** (crocs > rocs). The ornithodires went on to produce pterosaurs and dinosaurs, including the birds. Today, the Crurotarsi are represented only by the Crocodylia. However, the crurotarsans were responsible for most known reptile diversity in the Early and Middle Triassic. The only known basal ornithodire is the ***Scleromochlus*** from the Carnian of Scotland.

Scleromochlus and the Ornithodires

Ornithodires are supposed to share a number of characteristics, many of which are listed in the main entry below. Generally, ornithodires have moderately large heads with numerous fenestrae. In fact the ornithodire head often resembles a complex series of bony arches, rather than a box with holes. The neck has only 7 vertebrae -- sometimes a few more. The interclavicle is absent and the forelimbs are usually markedly shorter than the hindlimbs. The femur is bowed over most of its length, and the legs are generally located under the body. Reduction of the femoral fourth trochanter shows up as a synapomorphy in our analysis, which is surprising and possibly wrong. However, the structure of the limb bones is certainly simpler, with cleaner lines than in more basal archosauriforms. Likewise the ankle joint is strong, but simple and hinge-like. The foot is functionally tridactyl, with digits II - IV bound together and largely functioning as a single unit. The limb bones are quite often hollow, and there was primitively no body armor.

This body plan is one well-adapted for extended (or frequent) locomotion. It is very light, but strong. It is not particularly flexible. Rather, it's the sort of body an engineer might design to perform a series of kinetic and complex, but stereotyped, motions under a wide range of environmental conditions: tasks like running, jumping, or flying. But only one such task, and generally without much variation.

Scleromochlus makes an interesting example of that kind of body plan because it is not really very much like the only other two examples we have: dinosaurs and pterosaurs. *Scleromochlus* was small, about the size of a smallish cat, but much lighter. The head is somewhat like a pterosaur in general form but lacks any of the specializations of that clade. However, it is not merely a generalized ornithodire skull. *Scleromochlus* had its own suite of unique cranial specializations such as the broad nasal bones extending like an awning over the nostrils, and the conspicuously raised rim of the maxilla around the antorbital fossa. One might speculate that these anchored flaps of integument to protect exposed tissues from abrasion. That would be consistent with the low, triangular skull -- almost like a snake's head. However, the rest of the body looks like a leaping form: fairly short arms, long, simplified legs with a strong pelvis and heavily reinforced acetabulum, relatively compact torso and a long tail.

The object is not to reconstruct the lifestyle of *Scleromochlus*. Some of the very best minds of the last century have tried and failed to determine how these characteristics fit together. The lesson is rather that it is clearly an ornithodire, but is quite unlike either of the other ornithodire groups. The valid conclusion we may draw is that the Middle Triassic may well have contained a wealth of hidden ornithodire diversity. With three such disparate forms built on a body plan well-designed for occupying specialized niches, one suspects that the hot, dry inland areas of the Middle Triassic were home to any number of small, strange ornithodires, hopping, flapping, leaping and sprinting from one scarce resource to another.

Crurotarsi

The crurotarsans were made of sterner, if less athletic, stuff. Since the fossil record of basal Crurotarsi is reasonably good, we will not spend much time on a theoretical morphotype. They were generally large, and sometimes huge. The skull, although often strongly fenestrated, is usually far more massively constructed than the ornithodire norm. Basal Crurotarsi have a wide variety of specializations of the premaxilla. While this does not appear on anyone's list of synapomorphies, this feature is -- one might say -- as plain as the nose on their faces. The snout is typically very narrow and variably elongate, and the premaxilla is partially separated from the maxilla and/or forms a long anterior extension. This is difficult to pin down as a morphological character. However, it may well represent a developmental synapomorphy in which the premaxilla and maxilla develop quite separately, with less developmental interaction than is the case in most tetrapods. The cheek bones have a marked tendency to be laterally convex, often to the point of forming a sort of shelf around the side of the skull.

The crurotarsan neck is usually short and massive, with short, stout cervical ribs anchoring the musculature needed to move the massive head and neck. Not surprisingly, crurotarsans are much more likely to be obligate quadrupeds than are ornithodires. The limbs tend to be complex, with the tarsus and foot retaining many small bones and a fuller complement of functional digits. The limb posture may be sprawling or nearly vertical. However, Crurotarsi with vertically-oriented legs normally accomplish this posture by angling the acetabulum to face ventrally, rather than by bending the femur or developing a distinct femoral neck and head.

As noted on a previous page, crurotarsan phylogeny is poorly understood. Thus, it is hazardous to point to one feature or another as basal or derived except in the context of particular lineages. These will be surveyed on the following pages.

ATW040124

Descriptions

Ornithodira: Rocs > Crocs (not the same as Ornithodira *sensu* Benton = dinosaurs + pterosaurs)

Range: from the Middle Triassic.

Phylogeny: Archosauria **:** Crurotarsi + * **:** *Scleromochlus* + (Pterosauria + Dinosauromorpha).

Characters: Anterior cervical vertebrae longer than mid-dorsals [$S91]; "incipient" third sacral is either fully incorporated into sacrum or lost [$**p**03]; no interclavicle [$S91]; clavicles reduced or absent [$S91]; deltopectoral crest rectangular [S$91]; femoral shaft bowed anteriorly for at least 80% of length [$S91]; femoral 4th trochanter absent [$**p**03]; tibia > femur [S$91] [$**p**03]; astragalus without posterior groove [$S91]; astragalus & calcaneum fused to *crus*, *mesotarsal* ankle; calcaneal tuber small or absent [$S91]; calcaneal tuber does not flare (reversal) [P93]; distal tarsals 3 & 4 of similar width [$S91] [$**p**03]; metatarsals bunched [$S91] [$**p**03]; metatarsals II-IV elongate; metatarsals II-IV longer than 50% tibia length [$S91] [$**p**03]; digitigrade on pes II-IV; dorsal body osteoderms absent [S$91] [$**p**03].

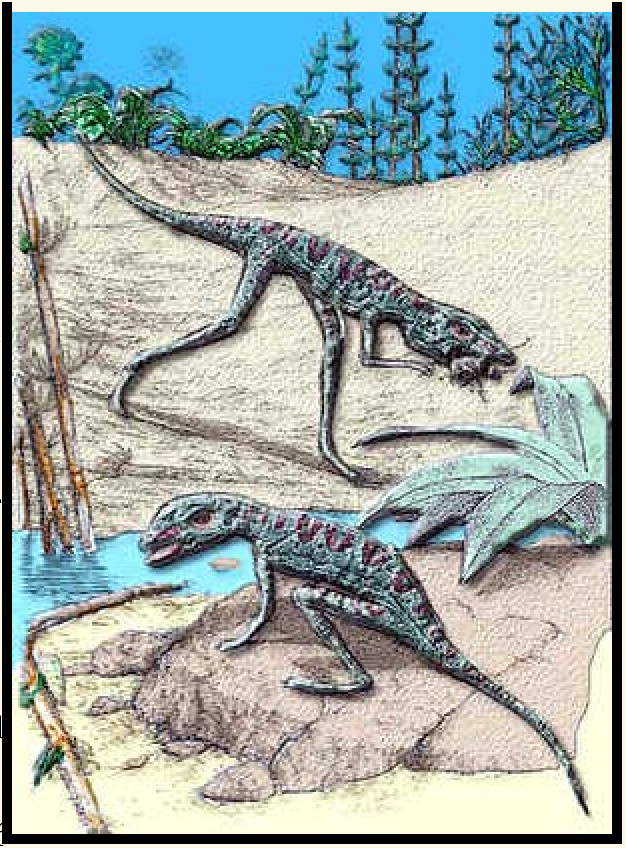
Notes: [1] "[**p**03]" refers to our own analysis of published data. **[2]** The image seems to be based in part on Huene's reconstruction which underestimates the length of the dorsal vertebral column [B99].

Links: link

References: Benton (1999) [B99]; Parrish (1993) [P93], Sereno (1991) [S91], Unwin (1999). ATW040118.

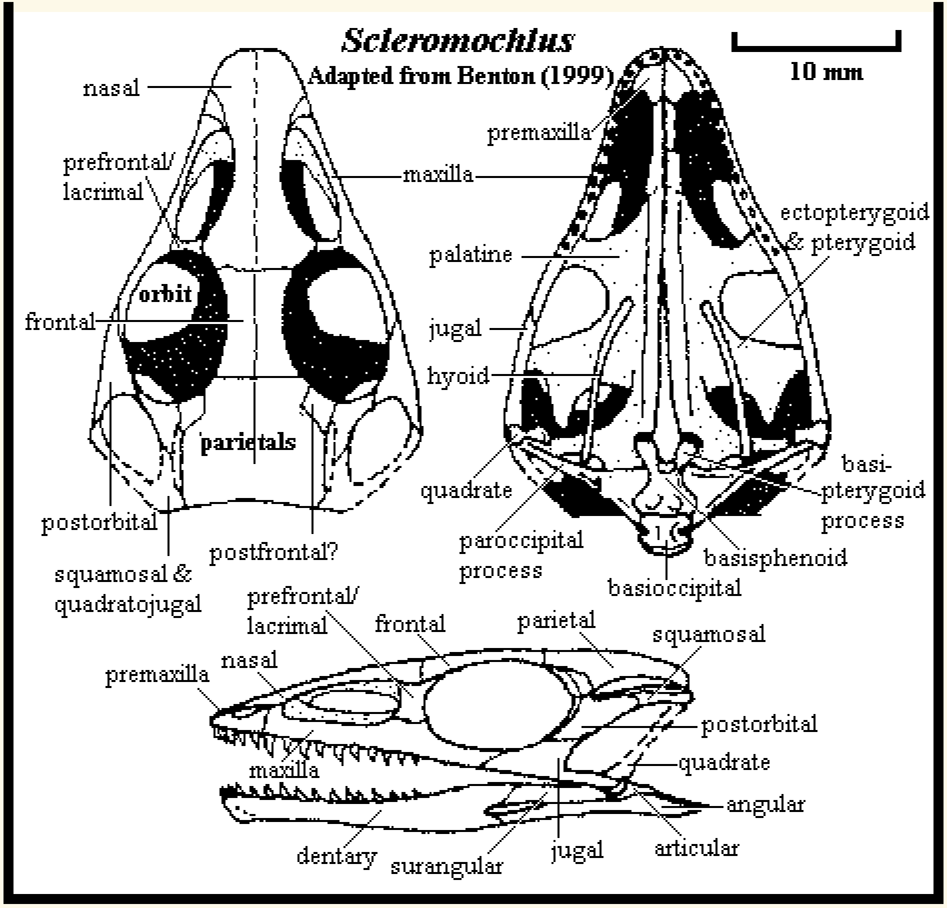
***Scleromochlus*:** *S. taylori* Woodward, 1907 [B99].

Range: Late Triassic (Carnian) of Europe (Scotland).



Phylogeny: Ornithodira **:** (Pterosauria + Dinosauromorpha) + *.

Characters: length ~18cm [B99] **[3]**; skull low & triangular, twice as broad across orbits as deep [**$**S91] [B99]; skull more than 50% length of presacral vertebral column [**$p**03] **[2]**; premaxilla elongate [B99]; maxilla with narrow process to nasal anterior to antorbital fossa & forming most of interior of fossa [B99]; maxilla forming raised anterior margin of antorbital fossa [**$**S91]; maxilla meets lacrimal - prefrontal between orbit & antorbital fossa & meets jugal posteriorly [B99]; expanded nasal forms anterior plate hiding nares & premaxilla in dorsal view [B99]; nasal descending flange forms dorsal wall of antorbital fossa [B99]; frontals form most of dorsal orbit [B99]; parietals broad, expanding behind orbits, with straight posterior margin [B99]; small postfrontal may be present [B99]; *UTF* present as a narrow slit between parietal and postorbital - squamosal [B99]; lacrimal & prefrontal fused, forming bar between orbit & antorbital fossa [B99]; orbit large & nearly circular [B99]; jugal with broad dorsal process meeting postorbital behind orbit and narrow posterior process meeting quadratojugal in long, diagonal suture [B99]; quadratojugal with quadrate facet well forward, at about level of basipterygoid process [B99]; braincase long [B99]; basipterygoid processes long & massive [B99];*sella turcica* narrow [B99]; premaxilla forming short platform on anterior palate [B99]; palatal elements as shown in image [B99]; palatine with plate-like process meeting maxilla [B99] **[4]**; long *interpterygoid vacuity* [B99]; pterygoids with deep recess for *basipterygoid process* [B99]; lower jaw slender, not straight in lateral view [B99]; dentary symphysis short & strong, wedge-shaped in lateral view [B99]; long *retroarticular process* bent medially [B99]; teeth isodont & very small [B99]; premaxilla with ~6 teeth [B99]; maxilla with ~10 teeth (distal 1/3 edentulous), dentary with ~15 [B99]; presacral vertebrae very short [W70]; at least 8 cervicals & perhaps 16-17 dorsals [B99]; cervicals slightly shorter than dorsals [B99]; centra spool-shaped, amphicoelous with deep central depressions & constricted laterally & ventrally [B99]; short cervical ribs present [B99]; neural arches long & low in cervicals, taller & with long transverse processes in dorsals [B99]; gastralia present [B99]; 3-4 sacral vertebrae [B99] [**$p**03]; about 35 caudals [B99]; caudals with posteriorly slanting neural spines [B99]; limb bones hollow [B99]; scapula long & slender, tapering distally [B99]; coracoid not elongate, but short & oval [W70] [B99]; forelimb <55% length of hindlimb [**$p**03]; humerus/femur ratio 0.61 [W70]; humerus long & thin, with short, well-defined *deltopectoral crest*, deeply divided on ventral face distally [B99]; radius & ulna only slightly shorter than humerus [W70] [B99]; carpus & manus short, with 5 metacarpals of similar length (McI may be shorter) [B99]; pelvis small, with low iliac blade & short pubis & ischium [B99]; strong *supraacetabular crest* present [B99] [**$p**03]; iliac blades elongate [B99]; pubis longer than ischium [B99] [**$p**03]; pubis with heavy acetabular margin and possible ventromedial process [B99]; ischial foot absent [B99]; acetabulum closed [B99]; femur slender & without trochanters, except a possible low 4th trochanter [B99]; proximal femur expanded longitudinally & distal femur expanded laterally [B99]; tibia longer than femur [W70] **[1]**; tibia distally (and proximally) expanded, with rectangular



end [B99] [**$p**03]; astragalus not fused to tibia & without ascending process [B99]; **[5]**; tarsus *crocodile-normal* [W70] (*contra* [B99]: astragalus & calcaneum of similar size, and not clear which is which, thus ankle structure is uncertain); metatarsals I-IV roughly equal in length [W70] and closely appressed [B99]; metatarsals II-IV longer than 50% of tibia length [B99] [**$p**03]; MtV short & probably without phalanges [B99]; cranial bones without ornament [B99]; very thin scutes or keratinous scales probably present [B99].

Notes: [1] Walker [W70: 361] states that the limb segment ratios "indicate a definite tendency towards bipedal hopping." Benton [B99] generally agrees, pointing to the elongation of the distal hindlimb, elongate tail, short anterior trunk, small pelvic girdle [B99]. However he notes that the se features are not present to quite the extent one would expect based on living mammal saltators. **[2]** "[**p**03]" refers to our own analysis of published data. **[3]** Interestingly, almost all of the 7 specimens were found in ?dorsal *roadkill* posture [B99], a fact with implications for its mode of life. **[4]** This is not clear in the images provided of the specimens themselves. **[5]** Benton [B99] states both that the fibula is "circular in cross-section" and that it is "flattened." [B99: 1432]. Apparently it is flattened against the tibia only for a small distance in part of the proximal half.

Image: adapted from a drawing by **John Sibbick** in [B99].

Links: Scleromochlus -- The Dinosauricon (some nice images); **恐竜データ集 -ス-** (Japanese); **川崎悟司イラスト集·スクレロモクルス** (Japanese).

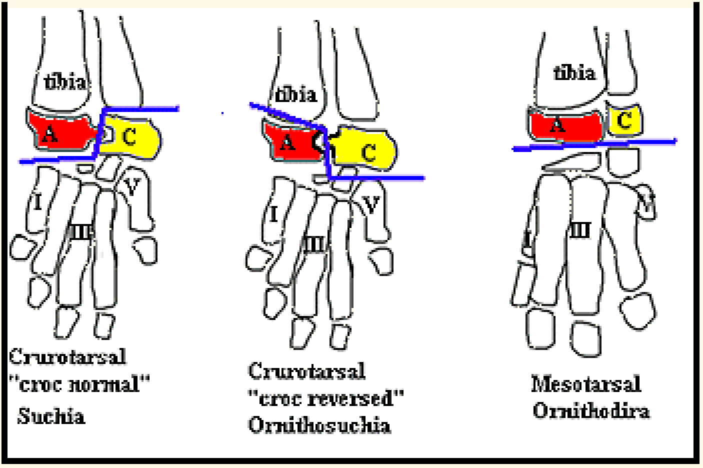
References: Benton (1999) [B99]; Sereno (1991) [S91], Walker (1970) [W70].

Crurotarsi: Crocs > Rocs

Range: from the Early Triassic

Phylogeny: Archosauria **:** Ornithodira + * **:** Phytosauridae + Rauisuchiformes.

Characters: Cervical ribs short & stout [**$p**03]; scapulocoracoid with anterior notch between scapula & coracoid [**$p**03]; humerus with relatively distinct *internal tuberosity*, just distal to which the shaft is strongly curved [$S91]; fibula with *anterior*



trochanter robust & knob-like [$S91]; fibula with distal end wider than proximal end [$S91]; crocodylomorph tarsus in which astragalus acts as extension of the *crus* & calcaneum associated with pes, with joint along articulation between astragalus & calcaneum [$P93]; ventral astragalocalcaneal facet small [$S91] [$**p**03]; astragalus with tibial facet flexed or convex [$S91] [$**p**03]; extended wheel-like ("hemicylindrical") process on calcaneum rotates fibula [$S91] [P93] [$**p**03]; articulated by peg in astragalus fitting into socket in calcaneum (croc normal) or the reverse (croc-reverse); calcaneal tuber broader than long [$S91] [$**p**03]; calcaneal tuber with rounded ("flared" [S91]) end [$S91] [$**p**03]; fifth metatarsal remains large primitively and may have shared tarsal role; pes 5 with 4 phalanges [$**p**03]; single paramedian osteoderm pair per presacral vertebra [$S91].

Notes: "[**p**03]" refers to our own analysis of published data.

Links: Crurotarsi; Lecture 10 - Triassic: Newark, Chinle; Archosauria: More on Morphology; Pseudosuchia; Biology 356.

References: Parrish (1993) [P93], Sereno (1991) [S91]. ATW040103.

Page Back | Unit Home | Page Top | Page Next

checked ATW050702

Archosauria: Archosauria: Phytosauridae

Parasuchus & *Paleorhinus*

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               |  |--Parasuchus
               |  |--Paleorhinus
               |  `--Euphytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
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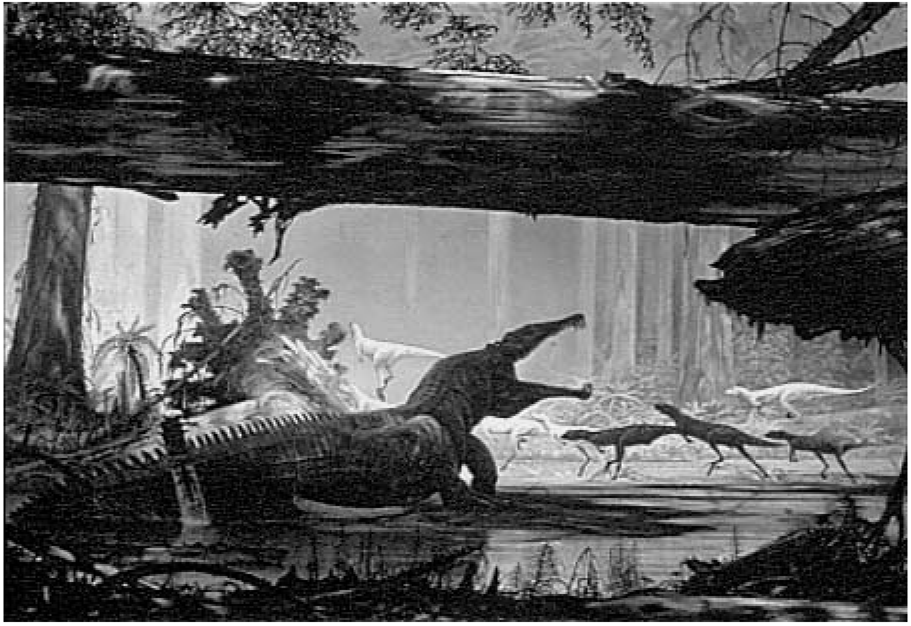
Contents

Taxa on This Page

1. *Paleorhinus* X
2. *Parasuchus* X
3. Phytosauridae X

The Phytosaurs

Introduction



A giant *Pseudopalatus*-grade phytosaur, *"Rutiodon" lithodendrorum*, length to 12 meters, startles a group of small fabrosaurs of the genus *Revueltosaurus*, on one of the wet floodplains of west equatorial Pangea (now, Petrified Forest National Park in Arizona), early Norian age. Illustration © Doug Henderson.

The phytosaurs (this unfortunate name means "plant lizards", because it was mistakenly believed that petrified mud fillings in the jaw of the first specimen found were herbivore teeth) were crocodile-like semi-aquatic thecodonts that suddenly appeared and became very abundant during the latter part of the Triassic period.

They are more appropriately known by the later (but less widely used) name Parasuchia ("alongside the crocodiles"), as they resembled crocodiles to a remarkable degree in size, appearance, and life-style. This is an amazing illustration of convergent or parallel evolution. Phytosaurs were in a sense "crocodile uncles", since phytosaurs and proto-crocodiles shared a common ancestor among the early Crurotarsi. But true crocodiles evolved only long after phytosaurs became extinct at the end of the Triassic.

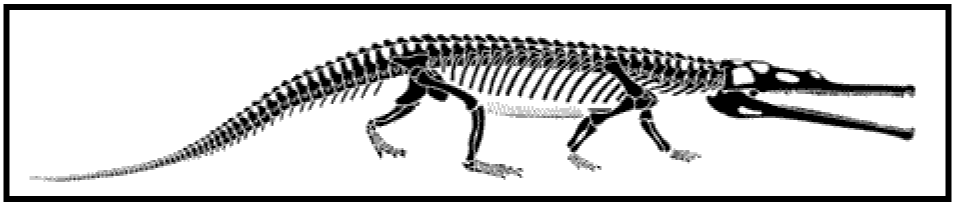
In some ways, the differences between phytosaurs and crocodiles are minor. The most obvious difference between phytosaurs and crocodiles is in the position of the nostrils. Phytosaurs had nostrils placed near or above the level of the eyes. Crocodiles have nostrils placed far forward at the tip of the snout. Another difference is in the palate (roof of the mouth). True crocodiles have a secondary palate that enables them to breathe when partially submerged, even though the mouth is full of water. Phytosaurs lacked this adaptation, and used the nostrils on top of the head in order to swallow air while underwater. Phytosaur limbs were also somewhat more primitive in structure than those of crocodiles. Fossil footprints indicate however that phytosaurs could move in a semi-erect stance on land and did not drag their tails as modern crocodiles do.

Phytosaurs were if anything even better armoured than crocs, with the throat and back of the animal being are protected by heavy armoured scutes, and the belly reinforced with a dense arrangement of abdominal ribs. The armoured scutes are often found as fossils

Phytosaur dorsal scutes.

Phytosaur Morphotypes and Life-style

In fact, phytosaurs are characterized by three distinctive cranial morphotypes, and this seems to be independent of phylogenetic relations. Modern crocodilians exhibit a similar morphological diversity. These skull patterns are linked to characteristics of the dentition; specifically the differentiation or similarity of the teeth along the jaws.



Skeleton of *Parasuchus hislopi*, showing the abdominal ribs and the long slender dolichorostral skull. Length overall 2.5 meters. Late Carnian age of India, very similar forms in Europe, Morocco, and North America. Source: Great Triassic Assemblages Pt 1 - The Chinle and Newark - Professor Paul Eric Olsen.

Dolichorostral ("long snouted") types have a long, narrow snout; and teeth that are homodont, or similar in form. Good examples include *Paleorhinus*, *Rutiodon carolinensis*, and *Mystriosuchus*, the latter representing the highest development. They were most likely piscivorous, like the Gavialidae. The long, narrow snout is suited for capturing fast prey, while the weak teeth could hold and position the fish for swallowing, but could not produced the shear needed to cut up chunks of flesh.

Altirostral ("high snouted") animals have an intermediate condition and primarily heterodont (different lengths or size) dentition. Typical forms might be *Angistorhinus* and *Pseudopalatus*. They were probably generalist feeders like the Alligatoridae.

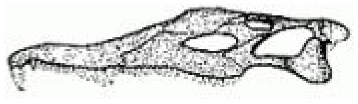
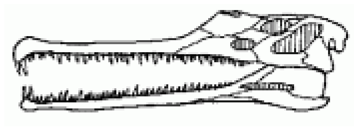
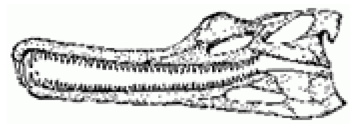
Brachyrostral ("short snouted") forms have a massive, relatively broad snout, skull and jaws; and tends to extreme heterodont dentition. These animals most likely fed on large tetrapods. The mediolaterally flattened posterior teeth would slice the carcass into chunks suitable for swallowing. In addition, they probably used their jaws in intraspecific combat. *Nicrosaurus* and *Smilosuchus* are good examples of this morphotype; the latter representing the most extreme adaptation along these lines.

Phytosaur Biozonation.

Chatterjee, Lucas and others have shown that phytosaur genera can be used to identify the age of a particular formation. Phytosaurs are particularly useful for biozonation because these large river and swamp-dwelling animals were frequently fossilized. Thus *Paleorhinus* and the Angistorhinines dominated the middle (or early part of the late) Carnian. *Rutiodon*-like forms such as *Leptosuchus* and *Smilosuchus* (some of these names perhaps do not deserve distinct generic status - this is a classic instance of "splitters vs lumpers") become a key index fossil for the Adamanian interval (the later part of the late Carnian).

In a number of papers (e.g. Lucas 1998), Dr Spencer Lucas and co-workers have proposed a series of biozones characterized by distinctive genera for the Triassic. In each of the four biozones that make up the late Triassic, different phytosaur types are found. Possibly these intervals were separated by periods of extensive climate change, which greatly stressed these large semi-aquatic reptiles, leading to rapid speciation.

The following table shows each of the four Late Triassic biozones and representative phytosaur genera and subgenera for each:

Geological Age	Land Vertebrate Age	Representative phytosaur genera and subgenera	
Rhaetian (also late Norian?)	Apachean	*Redondasaurus*	
Middle Norian Early Norian	Revueltian	*Pseudopalatus*, *Nicrosaurus*, *Mystriosuchus*.	
latest Carnian (= late Tuvalian)	Adamanian	*Rutiodon*, *Leptosuchus*, and *Smilosuchus*	
earlier late Carnian (= early Tuvalian)	Otischalkian	*Paleorhinus*, *Angistorhinus*	

Classification

The classification of phytosaurs has been somewhat debated. Gregory 1969 (cited in Westphal, 1976 p.117) has three separate lineages, the slender-snouted *Paleorhinus-Mystriosuchus*, the more heavily built *Angistorhinus-Rutiodon/Belodon*, and the most extreme (crested snouted) *Nicrosaurus*.

Chatterjee has only two families, the Parasuchinae, which includes not only primitive types such as *Parasuchus* and

Paleorhinus, but also the typical forms like *Rutiodon* and *Nicrosaurus* and the Mystriosuchinae for *Francosuchus* and *Mystriosuchus*

The traditional view since then has the phytosaurs divided into two subfamilies (recently considered distinct families): the slender-snouted gavial-like ***Mystriosuchinae*** (including *Paleorhinus*) and the heavy crocodile or alligator-snouted ***Angistorhininae*** (= Rutiodontidae). The former would seem to have fed largely on fish and perhaps other small animals, the latter on larger prey as well as fish. Both appear suddenly in the Middle Carnian and continue through to the very end of the Triassic period.

Advocates of this approach to phytosaur classification (e.g. Long & Murry 1995) tend to divide the group into two distinct (but related) families, as follows:

- **Parasuchia** Huxley 1875
  - Mystriosuchidae Huene, 1915
    - Palaeorhininae Long & Murry, 1995
    - Mystriosuchinae Nopcsa, 1928
  - Angistorhinidae Huene, 1936 (= Rutiodontidae Long & Murry, 1995)
    - Angistorhininae Camp, 1930
    - Rutiodontinae Long & Murry, 1995
    - Pseudopalatinae Long & Murry, 1995

Of the above taxa, the Palaeorhininae and the Angistorhininae are the two oldest groups; these are replaced in the Later Carnian by the Rutiodontinae. The Norian then saw these in turn replaced by the Pseudopalatinae and the Mystriosuchinae. The Pseudopalatinae survived till the end of the Rhaetian.

In an alternative classification [Doyle & Sues, 1995, cited in Mikko's Phylogeny - Phytosauria (Parasuchia)], the palaeorhinines (as represented by the genus *Paleorhinus*) are considered the primitive sister group of all other phytosaurs. The similarity between *Paleorhinus* and *Mystriosuchus* are thus the result of parallel evolution, not direct ancestry and descent. This is quite likely, considering that no intermediate forms between *Paleorhinus* and *Mystriosuchus* are known in the latest Carnian or the early Norian; such a long gap in animals so well represented in the fossil record is unusual.

A third approach, indicated by biozonation in association with plesiomorphic or highly derived traits, has the early, unspecialized, forms like *Parasuchus* giving rise to the Angistorhinidae, with the paraphyletic/grade-level Angistorhininae in turn being replaced by their descendents the rutiodontine-grade phytosaurs in the Later Carnian, and these in turn giving rise to the most advanced clade, the Pseudopalatinae, which unlike the earlier taxa is a proper monophyletic grouping, in the Early Norian. This succession of early primitive types with later more advanced forms, and those with their still more advanced descendents, is not unlike the evolution of equids, titanotheres, and other fast-evolving taxa. Of course real-world evolution is more an unruly bush than a tidy ladder, but the generic pattern could still hold to some extent.

In view of no agreed-upon model of phytosaur evolution, the following phylogeny is proposed, based on a synthesis of a number of approaches, along with the author's rampant speculation, and thus should not be considered definitive. (MAK 030727)

Descriptions

Phytosauridae: (= Parasuchia): *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, *Paleorhinus*, *Rutiodon*

Range: Late Triassic of Europe, India, North America, North Africa (Morocco), Madagascar(?), China(?).

Phylogeny: Crurotarsi : Rauisuchiformes + * : *Parasuchus* + *Paleorhinus* + Euphytosauridae.

Characters: 3-12 m; generally similar to crocs in form & niche; skull length >50% of length of presacral vertebral column [$**p**03]; skull dorsoventrally compressed [S91]; premaxilla extended [$S91]; piscivorous snout [$S91];

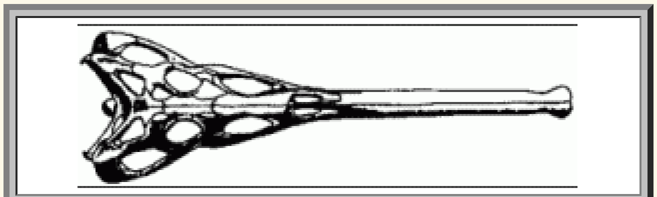
"septomaxilla" (neomorph?) with broad dorsal exposure, sutured to *antimere* at midline [$S91]; nasal with ventrolateral process extending anterior to nares [$S91]; narial openings far back on snout & elevated above orbits; prefrontal, descending process absent [**p**03]; nares & orbits dorsally placed [$S91]; quadratojugal generally triangular [$S91]; occiput twice as wide as tall [$S91]; no bony secondary palate; palatine forms entire lateral margin of choana & extends anteriorly to contact premaxilla [$S91]; palatine with longitudinal ridge (margin of soft secondary palate) [$S91]; postpalatine fenestra reduced to a slit [$S91]; foramina for cebreral branch of internal carotids on posterolateral corner of basisphenoid [$G02] [$**p**03]; lateral wall of braincase formed by large laterosphenoid (also aetosaurs & crocs); some with fang-like teeth in expanded symphysial area of both jaws; gastralia present; interclavicle enlarged [$S91]; coracoid crecentic [$S91]; forelimbs slightly shorter than the hind; grasping manus?; large, spreading feet & hands; manus V with <4 phalanges [$**p**03]; pubis & ischium plate-like, primitive; fifth metatarsal hooked & calcaneal tuber lateral (primitive leverage); throat & back with scutes; paired paramedian osteoderms, with small lateral osteoderms intercalated between lateral tips of main plates [S92]; osteoderms sculptured [$**p**03]; semi-erect trackway evidence; lived near fresh water (no known marine species).

Notes: "[**p**03]" refers to our own analysis of published data.

Links: Phytosaur; dinopics; A PRELIMINARY BIOMECHANICAL; Phytosauria Translation and Pronunciation Guide Introduction; Walking with Dinosaurs - Fact Files; Phytosaur - Rutiodon; Lecture 10 - Triassic: Newark, Chinle; Dino Land Travels Database Dinosaur State Park: Rutidon Model; Rutiodon; Phytosauria [Parasuchia]; Habay-la-Vielle 2 (French).

References: Chatterjee (1986); Gower (2002) [G02]; Long & Murry (1995), Sereno (1991) [S91], Sues (1992) [S92]. MAK030812, ATW031226.

Parasuchus: *Parasuchus hislopi*



Skull of *Parasuchus hislopi*; length about 60 cm. Source: Westphal, 1976, p.115.

Range: Late Triassic (earlier Late Carnian) of India.

Phylogeny: Phytosauridae **:** *Paleorhinus* + Euphytosauridae + *.

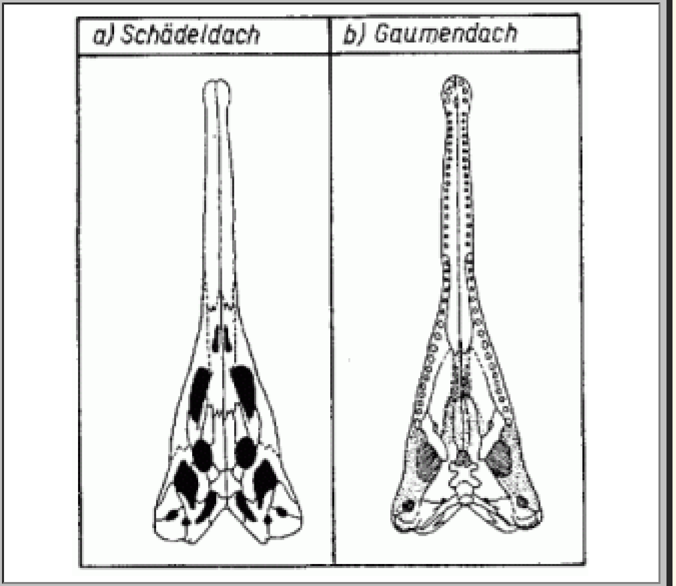
Characters: Small, skull-length about 60 cm; moderately deep skull, orbit directed outwards and upwards; rostrum slender and without crest; nostrils forward along the snout, i.e. external nares well in front of the antorbital fenestrae, squamosals without any posterior process; supratemporal fenestrae at the level of the skull roof, large interpterygoid vacuity, (like *Paleorhinus*); posttemporal fenestrae moderately sized; teeth short and slender, weakly heterodont; overlapping scutes; mildly dolichorostral.

Comments: This animal is more usually included under *Paleorhinus*. As would be expected, there is a story behind the nomenclatural ambiguity. The original description was by Thomas Huxley (who made a name for himself as "Darwin's Bulldog") based on rather fragmentary materials, which another early paleontologist, Lydekker, further confused by including rhynchosaur material. Because not much was known about this animal, similar animals discovered elsewhere were given new generic names. In 1978 Chatterjee assigned two nearly complete specimens from the Maleri Formation to *Parasuchus hislopi*. Since the Indian *Parasuchus* and North American *Paleorhinus* differ in only the most minor details, the latter becomes a junior synonym of the former. Later researchers have preferred to identify the new Indian specimens as a distinct species of the well-known *Paleorhinus*, and have restricted the genus *Parasuchus* to Huxley's type material as a *nomen dubium* (not enough material to give a definitive definition as a type species), although Chatterjee (1974) took the position that the type species was diagnosable based on a portion of a jaw from Huxley's material. [Creisler 1996). Although it is not impossible they represent a separate species, it is much less likely that Chatterjee's specimens represent a distinct genus to Huxley's, especially since all palaeorhinines are currently included under a single genus.

Considered by Chatterjee a subgenus, although other sources simply sink it into *Paleorhinus*. *P. hislopi* possesses some characteristics such as the weakly heterodont teeth, that indicate it may be more plesiomorphic (closer to the common ancestor) than *Paleorhinus* proper. In all likelihood, *Paleorhinus* may turn out to be a paraphyletic assemblage of early phytosaurs.

References: Chatterjee (1978); Creisler 1996. MAK030812.

Paleorhinus: *Paleorhinus bransomi*, *Paleorhinus fraasi* (formerly *Francosuchus*), *Paleorhinus ehlersi* (formerly *Promystriosuchus*)



Skull of *Paleorhinus bransomi*; length about 80 cm.
Source: A. H. Müller, *Lehrbuch der Paläozoologie*.

Range: Late Triassic (Middle and earlier Late Carnian) of Europe, North America, North Africa (Morocco).

Phylogeny: Phytosauridae **:** *Parasuchus* + Euphytosauridae + *.

Characters: low skull, orbit directed more upwards than outwards; Small to medium-sized, skull-length 60-90 cm; rostrum slender to very slender; as in *Parasuchus* the external nares well in front of the antorbital fenestrae, squamosals without any posterior process, and supratemporal fenestrae at the level of the skull roof; posttemporal fenestrae small; teeth homodont; non-overlapping scutes; large interpterygoid vacuity; teeth short and slender, homodont; dolichorostral morphotype.

Comments: Considered by Chatterjee a subgenus of *Parasuchus*. He also considers *Francosuchus* a distinct genus, although in his short genus-level review of the family it is almost identical to *Paleorhinus* (but not to *Parasuchus*, hence I have retained a distinction between the two latter). The subfamily **Palaeorhininae** is probably a plesiomorphic grade, united by shared primitive characteristics, with more advanced phytosaurs separating at an early stage,

Links: Late Triassic graveyard of large Triassic tetrapods in the Opole Silesia (in Polish);

References: Chatterjee (1978). MAK030812.

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

checked ATW050702, last modified MAK050119

Archosauria: Phytosauridae: Euphytosauridae

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               |  |--Parasuchus
               |  |--Paleorhinus
               |  `--Euphytosauridae
               |     |--Angistorhinus
               |     |--Brachysuchus
               |     `--Rutiodontinae
               |        |--Rutiodon
               |        |--Smilosuchus
               |        `--Pseudopalatinae
               |           |--Pseudopalatus
               |           |--Nicrosaurus
               |           `--o Mystriosuchus
               |              |--  Mystriosuchus
planirostris
               |              `--  Mystriosuchus
westphali
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

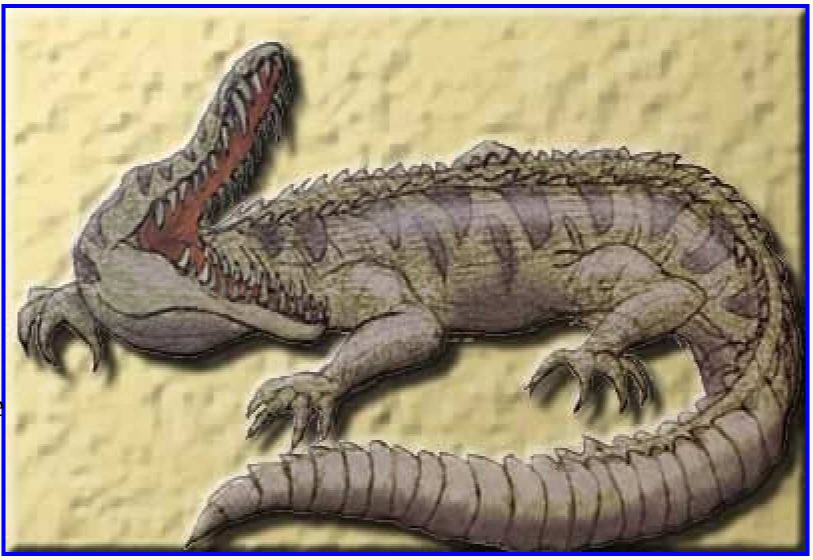
Contents

Taxa on This Page

1. *Angistorhinus* X
2. *Brachysuchus* X
3. Euphytosauridae X
4. *Mystriosuchus* X
5. *Mystriosuchus planirostris* X

6. *Mystriosuchus westphali* X
7. *Nicrosaurus* X
8. Pseudopalatinae X
9. *Pseudopalatus* X
10. *Rutiodon* X
11. Rutiodontinae X
12. *Smilosuchus* X

Descriptions



Euphytosauridae: "Crown Group" Phytosaurs

Range: Late Triassic (Late Carnian to Rhaetian) of Europe, India, North America, North Africa (Morocco).

Phylogeny: Phytosauridae **:** *Parasuchus* + *Paleorhinus* + * **:** *Angistorhinus* + *Brachysuchus* + "Rutiodontinae".

Characters: nostrils well back, i.e. external nares posterior, between the antorbital fenestrae; squamosals primitively with short rounded posterior process; supratemporal fenestrae primitively at the level of the skull roof; small interpterygoid vacuity; primitively dentition weakly heterodont; primitively non-overlapping scutes; primitively altirostral morphotype.

Comments: This clade could also be called "Euphytosauria", because it includes all phytosaurs more advanced than the basal palaeorhinine condition.

The subfamily **Angistorhininae** is almost certainly paraphyletic, as it is in some ways transitional between the Palaeorhininae and higher phytosaurs. The angistorhinines were all large animals, often double and more the linear dimensions of the palaeorhinines. The two groups co-existed, filling distinct ecological niches, the palaeorhinines being fish-eaters, and the angistorhinines feeding also on larger animals.

Image: *Smilosuchus* image donated to Palaeos by Jason Haymond.

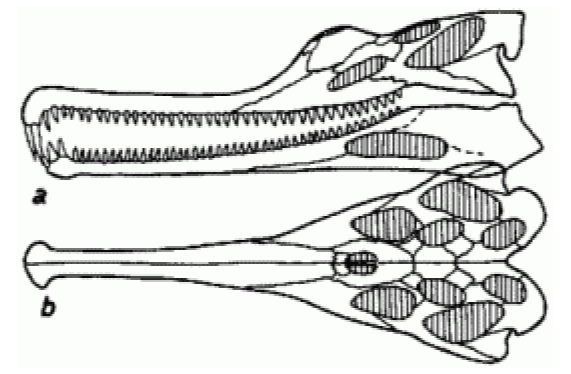
References: Chatterjee (1978). MAK030812.

Angistorhinus: *Angistorhinus grandis*, *Angistorhinus alticephalus*

Range: Late Triassic (Early part of Late Carnian) of North America, North Africa (Morocco).

Phylogeny: Euphytosauridae **:** *Brachysuchus* + "Rutiodontinae" + *.

Characters: large, skull-length 90 to 122 cm; altirostral morphotype; rostrum long and strong with prominent down-turned tip; moderately deep skull, orbit directed outwards and upwards; infratemporal and posttemporal fenestrae both large; posterior squamosal process short and rounded; teeth weakly heterodont with compressed and enlarged posterior teeth; non-overlapping scutes.



Skull of *Angistorhinus grandis*; length 90 to 120 cm. Source: Westphal, 1976, p.110.

References: Chatterjee (1978). MAK030812.

Brachysuchus: Case 1929. *B. megalodon*

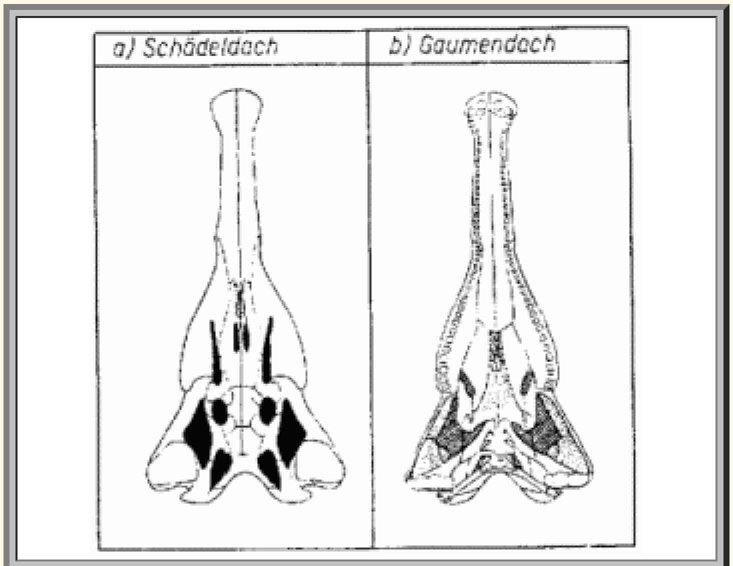
Range: Late Triassic (Early part of Late Carnian) of North America.

Phylogeny: Euphytosauridae **:** *Angistorhinus* + "Rutiodontinae" + *.

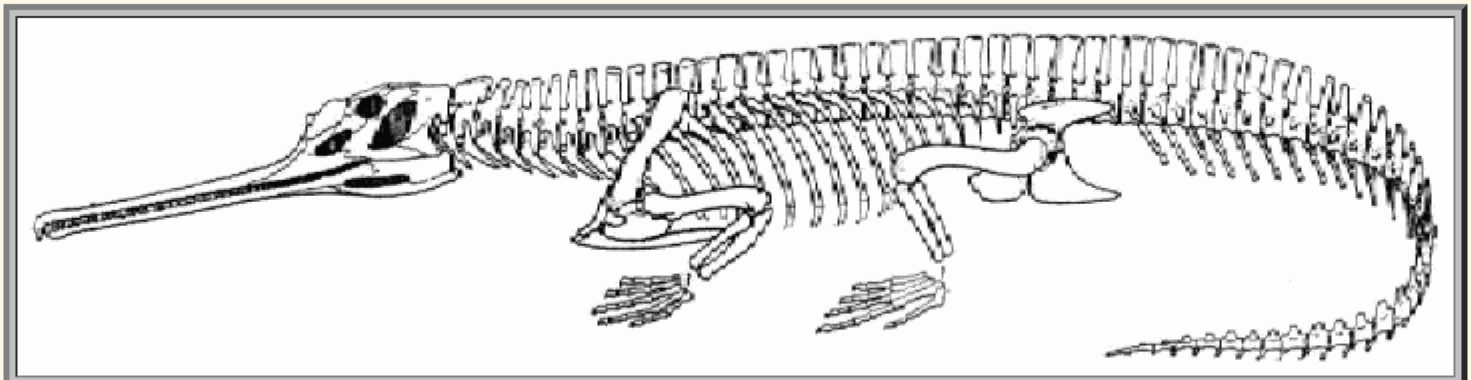
Characters: very large, skull length around 125 cm, rostrum quite short and very heavy; no rostral crest

Links: Phytosauria Translation and Pronunciation Guide.

References: Creisler 1996. MAK030812, ATW031129.



Skull of *Brachysuchus megalodon*; length 90 to 120 cm.
Source: A. H. Müller, *Lehrbuch der Paläozoologie*.



Skeleton of *Rutiodon carolinensis*; overall length 2 to 2.5 meters.
Source: Sullivan and Lucas, 1999 (original page).

"Rutiodontinae": Advanced phytosaurs

Range: Late Triassic (Latest Carnian to Rhaetian) of North America and Europe.

Phylogeny: Euphytosauridae **:** *Angistorhinus* + *Brachysuchus* + * **:** *Rutiodon* + *Smilosuchus* + Pseudopalatinae.

Characters: medium to very large; moderately deep skull; orbits directed obliquely more outwards than upwards; interpterygoid vacuity small and narrow; supratemporal fenestrae depressed; posterior squamosal process primitively rounded and elongate.

Comments: The subfamily **Rutiodontinae** is almost certainly paraphyletic, as it is in some ways transitional between the Angistorhininae and Pseudopalatinae. The rutiodontines replaced both the palaeorhinines and Angistorhinines, both earlier groups apparently dying out before the end of the Carnian.

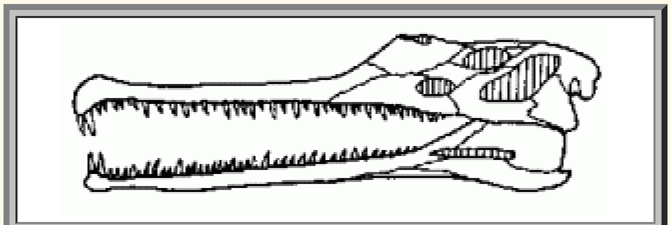
References: Chatterjee (1978). MAK030812.

Rutiodon: *Rutiodon carolinensis*, *Leptosuchus crosbiensis*

Range: Late Triassic (Latest Carnian) of North America.

Phylogeny: Rutiodontinae **:** *Smilosuchus* + Pseudopalatinae + *.

Characters: medium sized, long slender rostrum; dolichorostral morphotype; posterior squamosal process slender; teeth with strong



Skull of *Rutiodon carolinensis*; length 75 cm.
Source: Westphal, 1976, p.110, after Colbert 1947

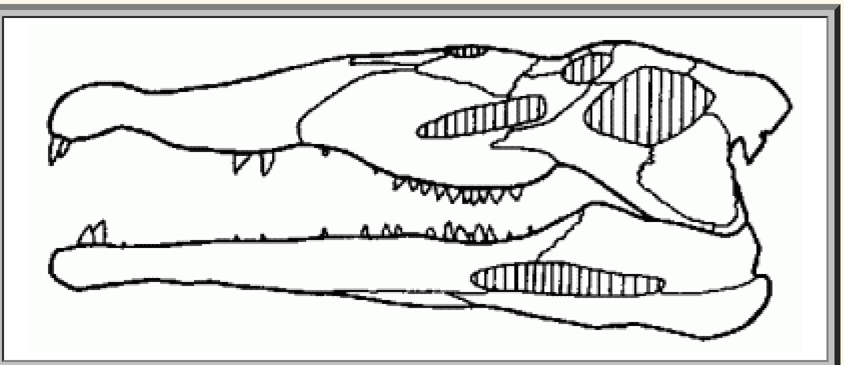
vertical striations; weakly homodont dentition; non-overlapping scutes.

Comments: Phytosaurs attributed to *Rutiodon* are also recorded from the Norian and Rhaetian of Europe, but there is no guarantee that these species belong to this genus. If they do, these phytosaurs survived there much longer than in North America (western Pangea). Long & Murry (1995) restrict the name to forms known from the East Coast of North America, but the western form *Leptosuchus* probably is a junior synonym (although a distinct species).

Links: Dinosaur State Park: Rutidon Model (*R. carolinensis*); We Had Dinosaurs in York County? (skeleton and skull of *R. carolinensis*); PHYTOSAUR RUTIODON (some nice images and basic information); Rutiodon - Phytosaure de l'Ere Seconadaire (image of tooth); [루티오돈(Rutiodon)] (Korean); Paleontology and Geology Glossary- R (interesting paragraph); Dino Land Travels Database Dinosaur State Park- Rutidon Model; Vertebrate (detailed image of scutes); Natural Canvas Fossils - Reptiles 2 (teeth & a nice jaw fragment); Yahooligans! Science-Dinosaurs; A PRELIMINARY BIOMECHANICAL; HUBER. ATW030921.

References: Chatterjee (1978); Creisler 1996; Long & Murry (1995); Lucas 1998. MAK030812.

Smilosuchus: *Smilosuchus gregorii*



Skull of *Smilosuchus gregorii*; length one to one and a half meters. Source: Westphal, 1976

Range: Late Triassic (Latest Carnian) of North America.

Phylogeny: Rutiodontinae : *Rutiodon* + Pseudopalatinae + *.

Characters: extremely large, skull length 100-155 cm and more; moderately deep skull; rostrum with marked dorsal crest, (hence the older term *Machaeroprosopus* "knife face," alluding to the sharp crest); squamosal process short and deep; brachyrostral morphotype, short broad massive jaws and strongly heterodont teeth.

Comments: A gigantic phytosaur, *Smilosuchus* attained up to 12 meters in length, and was the largest land animal of the Triassic.

References: Chatterjee (1978); Creisler 1996. MAK030812.

Pseudopalatinae: *Pseudopalatus*, *Nicrosaurus*, *Redondasaurus*, *Mystriosuchus* (usually placed in separate subfamily)

Range: Late Triassic (Early Norian to Rhaetian) of North America and Europe.

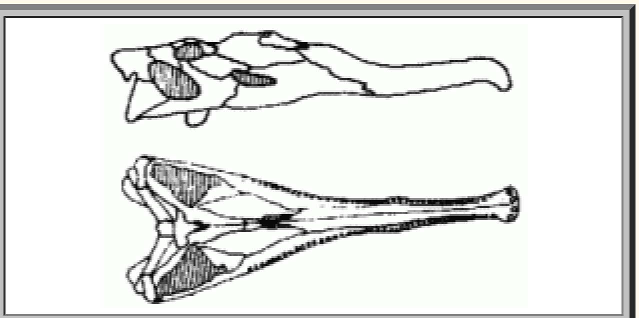
Phylogeny: Rutiodontinae **:** *Rutiodon* + *Smilosuchus* + * **:** *Pseudopalatus* + *Nicrosaurus* + *Mystriosuchus*.

Characters: large, skull length 80-120 cm; moderately robust rostrum with irregular, vertical longitudinal dorsal crest, posterior squamosal process slender; orbits directed obliquely outwards and upwards;

Comments: The most advanced phytosaurs.

Links: Triassic Page 4 - scroll down for image of *"Rutiodon" buceros*. MAK030813.

Pseudopalatus: *P. andersoni*, *P. pristinus*, *Redondasaurus* is closely related.



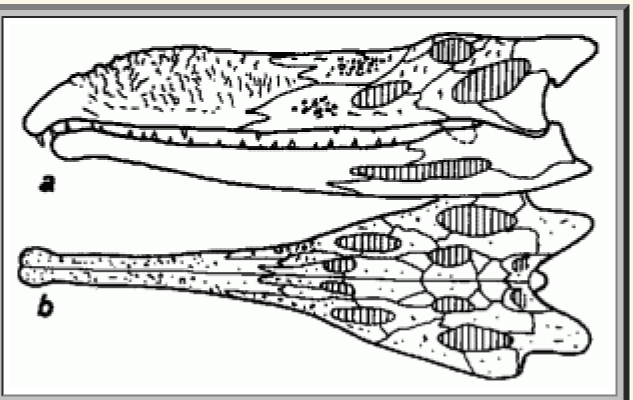
Range: Late Triassic (Early Norian to Rhaetian) of North America

Phylogeny: Pseudopalatinae **:** *Nicrosaurus* + *Mystriosuchus* + *.

Characters: medium to large, skull length 80-120 cm; moderately robust rostrum with dorsal crest, posterior squamosal process slender;

orbits directed obliquely outwards and upwards. MAK030813.

Skull of *Pseudopalatus andersoni*; length 85 cm.
Source: Murray 1986 p.128



Skull of *Nicrosaurus kapffi*; length 65 to 75 cm.
Source: Westphal, 1976

Nicrosaurus: Fraas, 1866. *N. kapffi* von Meyer. This taxon has numerous junior synonyms.

Range: Late Triassic (Early to Middle Norian) of Europe.

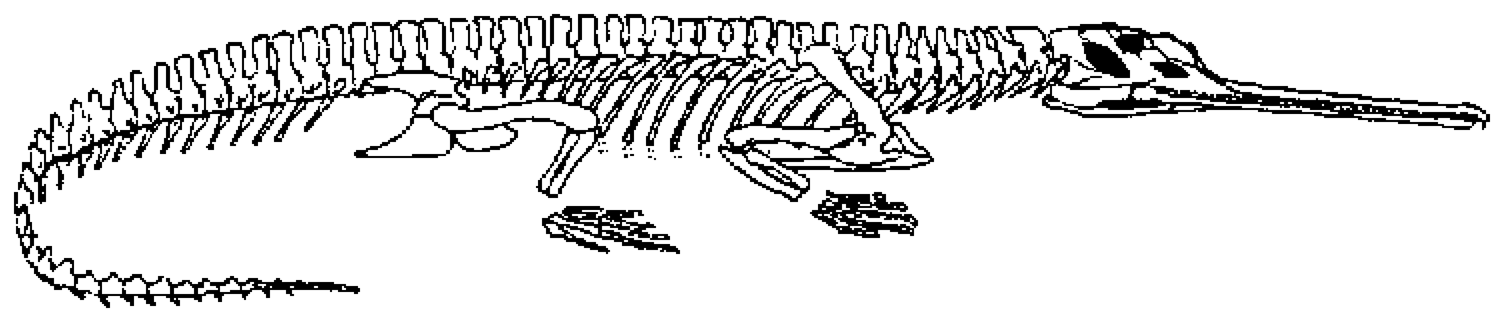
Phylogeny: Pseudopalatinae **:** *Pseudopalatus* + *Mystriosuchus* + *.

Characters: medium-sized, skull length 75 cm; skull at least as deep as wide; very pronounced dorsal crest; very strong, croc-like rostrum; dentition strongly heterodont; overlapping scutes.

Comments: A very common European species. Also known as *Belodon*, this was probably the original "*Phytosaurus*". Represents a specialized pseudopalatine condition.

Links: NICROSAURUS; IT> ... (abstract on heterodonty in *Nicrosaurus*); Phytosauria Translation and Pronunciation Guide Introduction.

References: Zittel, 1932; Chatterjee (1978). MAK030813.



Skeleton of *Mystriosuchus planirostris*; length 2.9 meters.
Source: A. H. Müller, *Lehrbuch der Paläozoologie*.

Mystriosuchus

Range: Late Triassic (Middle Norian) of Europe.

Phylogeny: Pseudopalatinae **:** *Pseudopalatus* + *Nicrosaurus* + *. **:** *Mystriosuchus planirostris* + *Mystriosuchus westphali*

Characters: **$** slit-like interpremaxillary fossa; **$** triangular cross-section of the postorbito-squamosal bar; **$** strongly reduced posttemporal fenestra; distinct cranial sculpture [Hungerbühler 2002]; small to medium-sized, skull length 75-105 cm (specimen cited by Zittel 80 cm, with snout 60 cm), fairly deep; rostrum long and slender; cranium high, sharply separated from the subcylindrical snout; pronounced tusked spoon shaped extension at tip of snout; specialized posterior nares with raised rim, close to orbit; dorsal crest lost; posterior squamosal process extremely reduced; supratemporal fenestrae greatly depressed; orbits directed upwards and backwards; fully homodont dentition of uniform conical teeth, teeth delicately fluted; four series of dorsal plates of nearly equal size, ventral shield of smaller plates protect the throat; skeleton more lightly built than *Nicrosaurus*; strongly dolichorostral morphotype

Comments: This highly derived and specialized fish-eating genus represented the most extreme dolichorostral adaptation of any phytosaur. It is usually placed in its own subfamily, the **Mystriosuchinae**, and in appearance and most certainly habits would have paralleled the modern gavial to a great degree. Recent research however shows that *Mystriosuchus* is nested within the Pseudopalatinae [e.g. Hungerbühler 2002]. And though *Mystriosuchus* is certainly very different in appaearance to other pseudopalatine phytosaurs, much of this modification is clearly due to specific piscivorous adaptations.

References: Zittel, 1932; Chatterjee (1978); Hungerbühler 2002.

Links: Taxonomic history of *Mystriosuchus* E. Fraas, 1896

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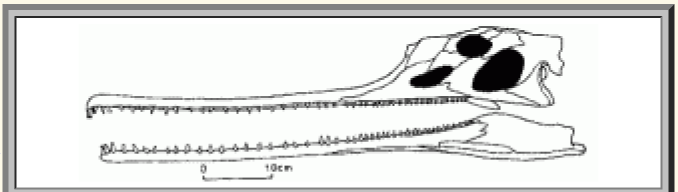
Mystriosuchus planirostris



Skull of *Mystriosuchus planirostris*; length 80 cm. Source: A. H. Müller, *Lehrbuch der Paläozoologie*.

Range: Late Triassic (Middle Norian) of Europe.

Phylogeny: Pseudopalatinae ::: *Mystriosuchus* : *Mystriosuchus westphali* + *

Characters: naris facing forward anteriorly and upward posteriorly, and the longest rostrum and the highest degree of depression of the supratemporal opening in any phytosaur. [Hungerbühler 2002]

Comments: The type species of the genus. Although traditioanlly considered freshwater, like other phytosaurs, a recently discovered specimen from the *Calcari di Zorzino* of Northern Italy, which seems to belong to this species, apparently took to a completely marine existence, thus foreshadowing the Jurassic Teleosauridae.

Links: Nuova pagina 1; Norian Fauna and Flora (mentions the apparently fully marine (or lagoonal and marine) mystriosuchine found in the Calcari di Zorzino of Northern Italy); Mystriosuchus - Dr Silvio Renesto

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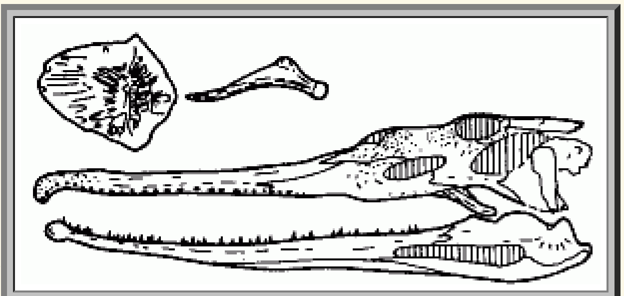
Mystriosuchus westphali



Skull of *Mystriosuchus westphali*; Source: xxxx.

Range: Late Triassic (Middle Norian) of Europe.

Phylogeny: Pseudopalatinae ::: *Mystriosuchus* : *Mystriosuchus planirostris* + *

Characters: distinct premaxillary crest; **$**squamosal-prootic contact; **$** absence of a posterior process of the squamosal; **$**, and a slit-like posttemporal fenestra. [Hungerbühler 2002]

Comments: *Mystriosuchus westphali* is based on a large, well-preserved cranium and a snout fragment from the Stubensandstein (Norian) of south-west Germany [Hungerbühler 2002]. This animal has also been known as *Belodon plieningeri* and *Mystriosuchus plieningeri*

MAK050119

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

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Archosauria: Rauisuchiformes

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  |  |--Ornithosuchus
                  |  |  |--Venaticosuchus
                  |  |  `--Riojasuchus
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

Contents

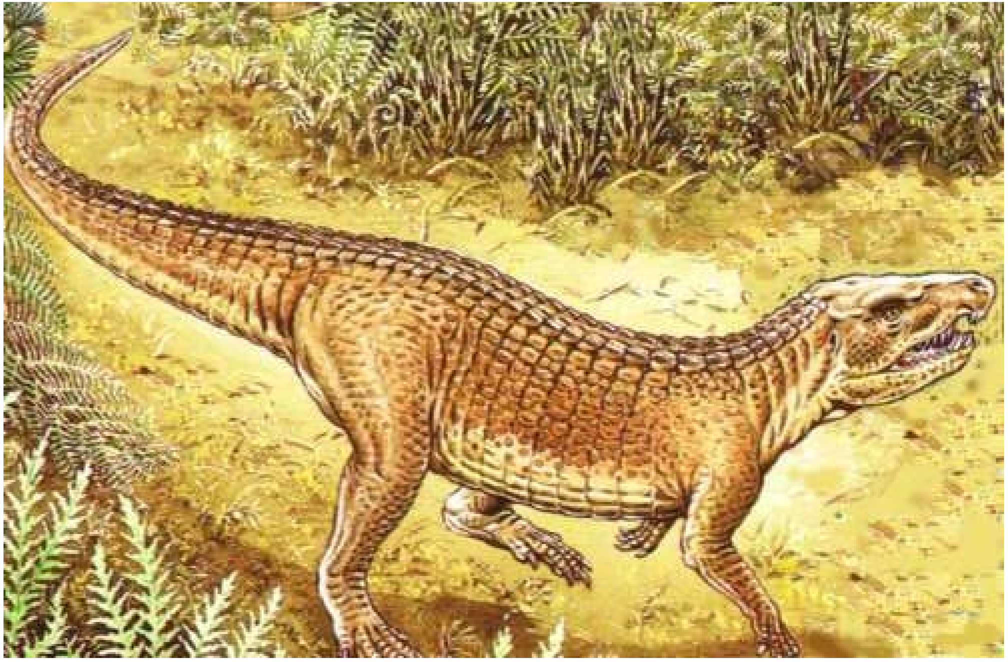
Taxa on This Page

1. Ornithosuchidae X
2. Rauisuchia X
3. Rauisuchiformes

The Ornithosuchids

Introduction

The ornithosuchids are yet another of the many archosaur lineages that constituting the confusing Triassic family tree of these animals. They have been variously considered dinosaur ancestors, crocodile relatives, and an separate branch of Crurotarsi. Much of this confusion is due to the fact that Triassic archosaur relationships rest to a large degree on ankle structure, with some, like dinosaurs, having bird-like ankles, and others, like "pseudosuchians", having croc-like ankles.



***Venaticosuchus* rusconii*, a typical ornithosuchid. This animal filled the role of intermediate- sized predator. Length 2 meters, late Carnian of south-west Pangea (Gondwana). Drawing from *The Cambridge Encyclopedia of Life Sciences*, ed. Adrian Friday & David S. Ingram, © Cambridge University Press 1985. Some parts of the original retouched.**

The ornithosuchids were also one of a number of groups of Triassic archosaurs which evolved a fully-erect (bird- and mammal-like) limb posture, as opposed to the sprawling and semi-erect postures of more primitive archosauromorphs, and even of crocodiles today. *Ornithosuchus* itself was originally considered a "pseudosuchian thecodont," then reclassified as an early theropod dinosaur, then later as a dinosaur-uncle, and is now considered to be a side-branch on the line to crocodiles. Thus far, ornithosuchid fossil remains are known only from Scotland and South America, although it can be assumed their distribution was much broader.

In the past, the ornithosuchids and close relatives were distinguished from most other advanced archosauriforms by a different sort of ankle structure: the so-called "Crocodile-Reversed" (CR) joint. Both the crocodylomorph "Crocodile-Normal" (CN) and the ornithosuchid "Crocodile-Reversed" (CR) ankle joints were ways of increasing the mobility of the animal; both had a definite advantage over the older protosuchian/erythosuchian ankle, which was a multi-part hinge. The trouble with this scheme is that ornithosuchid ankle structure is ambiguous, and it is unclear exactly how the ankle joint worked. So determining the phylogenetic position of these interesting and clearly highly specialized animals is not so simply accomplished.

Early books illustrate *Ornithosuchus* as a theropod-like biped, with long strong legs and diminutive fore-arms. And whilst these creatures could indeed move on their hind legs (and probably did for bursts of speed) they may have been equally comfortable on all fours, as indicated in the illustration of *Venaticosuchus*, right.

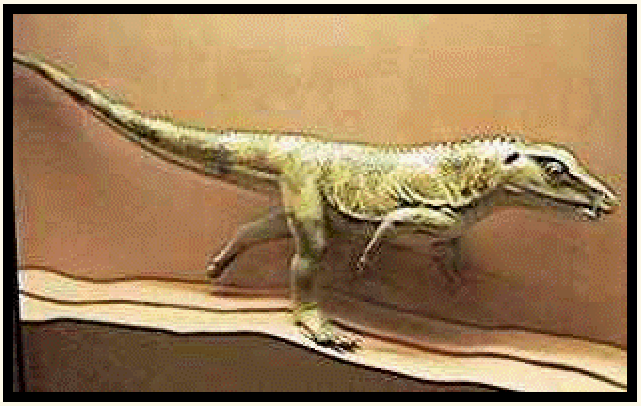
Ecology

The ornithosuchids were medium-sized or large (2 to 3.3 metres long) armoured carnivores, with mouths full of over-sized teeth. They were clearly active hunters, and the hindlimbs were much larger than the forelimbs. It used to be thought that this meant the creature was an obligate biped (like the large carnivorous dinosaurs for example), but they were more probably only facultative bipeds; that is although they were able to run on their back legs when they wanted to, they probably preferred quadrupedal locomotion.

Like those other characteristic late Triassic archosaurs, the phytosaurs, aetosaurs, and poposaurs, the ornithosuchids appear seemingly out of nowhere during the Carnian. These were active, fast-moving animals, with fully erect and upright posture, just like dinosaurs and mammals. It is possible that they evolved this posture from sprawling ancestors independently of other erect groups. Alternatively, if they can be derived from a prestosuchid (or rauisuchid?) ancestor (and that is not certain) they may have retained the stance that way. In any case, superior locomotive ability obviously conferred great adaptive advantages, and hence developed among a number of only distantly related archosaurs. (this posture developed in at least three or four distinct clades)

Although not very common, as would be expected from a predator near or at the top of the food chain, the ornithosuchids are widely distributed , being known from both Scotland (Laurasia) and Argentina (Gondwana). The name "bird crocodile" seems to nicely describe all the great archosaurs of Mesozoic, combining as they did features of both crocs and birds.

Phylogenetic Relationships



The ornithosuchids have had a rather uncertain phylogenetic history. Originally they were classified among the "Pseudosuchia," as one of a number of small bipedal running thecodonts, along the lines of *Hesperosuchus*, *Saltoposuchus*, and so on. It is now known that most of these latter forms are either basal crocodylomorphs (Sphenosuchia) or very close to the crocodylomorph stem.

In the early 1960s *Ornithosuchus* was re-classified as an early and very primitive member of the theropod dinosaurs (Walker, 1964). However, *Ornithosuchus*, like other members of its family, have a number of primitive (plesiomorphic) features, such as a double row of bony plates down its back a short broad pelvis attached to the backbone by only 3 vertebrae, and five toes on each hind foot (as opposed to three in the case of theropod dinosaurs). These characteristics are shared by most basal archosaurs, and show that *Ornithosuchus* is only distantly related to the dinosaurs.

During the 1980s an influential paper by Gauthier (Gauthier, 1986) followed by Benton & Clark, 1988, placed the ornithosuchids as the most basal group of the Dinosaur-Pterosaur line (Ornithodira). This was termed the "Ornithosuchia" in contrast to the Crurotarsan (or Crocodylotarsan) clade. The 1990s saw the pendulum swing again, with first Sereno (Sereno, 1991), and then Parrish and others publishing archosaur phylogenies that reject Gauthier's thesis and place the Ornithosuchidae on the Crurotarsan position. This has been the standard position since. So despite having a dino-bird-like ankle, ornithosuchids are still on the crocodylian side of the tree. Unless the phylogeny changes again of course!

Still not agreed on is the position of ornithosuchids within the Crurotarsi. Parrish (1993) placed Ornithosuchidae basal to all other crurotarsans (the Crocodylotarsi), Juul (1994) has them as the sister taxon to the "Paracrodylomorpha" (= Crocodylomorpha + *Gracilisuchus* + *Postosuchus*), and Benton (1999) and Benton and Walker 2002 tentatively find that Ornithosuchidae were sister group to the "Rauisuchia" (except for *Fasolasuchus* all Prestosuchidae) + *Postosuchus*. Since the Prestosuchidae and the Poposauridae / Rauisuchidae (*Postosuchus*' exact position there is uncertain) together may form only a paraphyletic, if not polyphyletic, assemblage, this is not as helpful as it may seem.

Our own analysis finds the Ornithosuchidae as the most basal group of the Rauisuchia, a large clade of vaguely theropod-like Crurotarsi which includes both the Prestosuchidae and the Rauisuchidae. Then again, it may also include *Doswellia*, which not really like much of anything else at all. At the present time, none of the possible arrangements of Triassic Crurotarsi can really be excluded, but it is relatively certain that the Ornithosuchidae will occupy a comparatively basal position in whatever phylogeny ultimately prevails.

MAK 000123 & 030730. ATW040124.

Image: Left: *Ornithosuchus* courtesy of the Elgin Museum.

Descriptions

Rauisuchiformes: *Rauisuchus* + *Aetosaurus*

Range: from the Early Triassic

Phylogeny: Crurotarsi **:** Phytosauridae + * **:** Rauisuchia + Suchia.

Characters: skull <50% length of presacral vertebral column (reversal) [**$p**03]; foramina for entrance of cerebral branch of internal carotid on anterolateral surface of basisphenoid [**$p**03]; medial wall of vestibule almost completely ossified [**$p**03]; lagenar recess present, elongate & tubular [**$p**03]; external foramina for abduscens nerve not entirely within prootic [**$p**03]; auricular recess extends onto internal surface of supraoccipital and/or epiotic [**$p**03]; antitrochanters on ischium & ilium [**$p**03]; pubis acetabular margin recessed [$S91] **[2]** [**$p**03]; pubis longer than ischium & > 3x width of acetabulum [$S91] **[2]**; .

Notes: **[1]** "[p03]" refers to our own analysis of published data. **[2]** Sereno has a very different phylogenetic framework. However, his clade Suchia + Ornithosuchidae is generally equivalent to Rauisuchiformes as used here. ATW031226

References: Sereno (1991) [S91].

Rauisuchia: *Rauisuchus* > *Aetosaurus*.

Range: from the Early Triassic

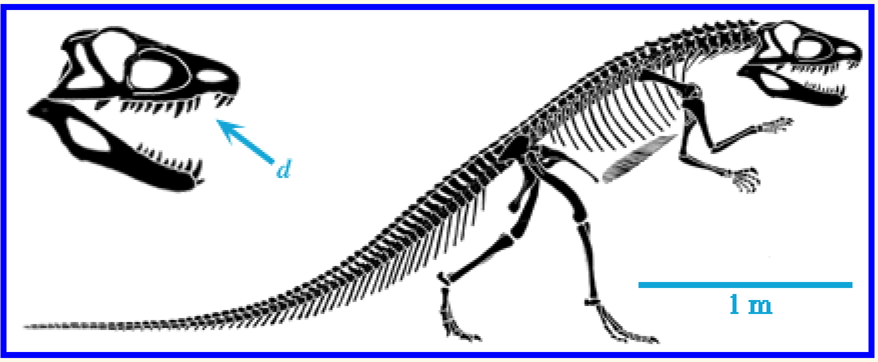
Phylogeny: Rauisuchiformes **:** Suchia + * **:** Ornithosuchidae + (*Tarjadia* + (Prestosuchidae + (*Doswellia* + (Poposauridae + Rauisuchidae)))).

Characters: subnarial fenestra formed as part of joint between premaxilla & maxilla [B84] [$P93] **[1]**; maxilla anterior to antorbital fenestra shorter than exposure posterior to anterior margin of fenestra [**$p**03]; antorbital fenestra tends to be keyhole-shaped [B84]; basisphenoid with elongate open trough on ventral surface formed by elongated *basipterygoid processes* [$P93]; ribs with anterolaterally projecting flange on proximal portion [$P93]; ilium low [B84]; acetabulum faces ventrally [B84] **[2]**; supraacetabular crest present [**$p**03]; digits V with 2 Phalanges [$P93] [**$p**03]; osteoderms not sculptured (reversal) [**$p**03].

Notes: **[1]** see diagram at *Batrachotomus*. In the current phylogeny, this is probably not a valid synapomorphy. The character is present outside Rauisuchia in prestosuchids, and absent inside Rauisuchia in *Gracilisuchus*, most rauisuchids and crocodylomorphs). **[2]** Benton's influential note [B84] proposed that rauisuchians developed an erect stance convergently and differently from the dinosaurs, by angling the acetabulum ventrally rather than putting an angled neck on the femur. **[3]** "[**p**03]" refers to our own analysis of published data.

References: Benton (1984) [B84], Parrish (1993) [P93]. ATW031226

Ornithosuchidae: *Ornithosuchus*; *Riojasuchus*.



Range: Late Triassic (Carnian to Norian) of Europe (Scotland) & South America.

Phylogeny: Rauisuchia **:** (*Tarjadia* + (Prestosuchidae + (*Doswellia* + (Poposauridae + Rauisuchidae)))) + * **:** *Ornithosuchus* + *Venaticosuchus* + *Riojasuchus*.

Discussion: Ornithosuchids are so dinosaur-like that the were originally believed to be carnosaurs. In fact when the major divergence of the archosaurs into the crocodile and dinosaur lineages was originally recognized, the dinosaur line was named after its earliest known representatives: "Ornithosuchia." It now appears that the Ornithosuchidae are in fact on the other side of the archosaur split. That is, the Ornithosuchids are not ornithosuchians. As a result, the dinosaur line is now referred to as the Ornithodira, although many sources retain the older name. The other branch has also suffered its own nomenclature problems, since this lineage was known as the Pseudosuchia or "false crocodiles." Unfortunately, as an unintended result of applying cladistic principles to Nineteenth Century nomenclature, the "false crocodiles" now include the *true* crocodiles (the less confusing term "Crurotarsi" is used at this site). Just to compound the difficulties, there are still those who believe that the Ornithosuchidae are more directly related to dinosaurs than crocodiles.

Characters: Large, gracile, large head; nasal - prefrontal contact reduced or absent [$S91]; descending process of prefrontal present [**$p**03]; large diastema between premaxilla and maxilla, with constriction accommodating two large dentary teeth [$S91]; teeth laterally compressed; large antorbital fenestra with fossa; frontal and nasals form long, flat dorsal surface to skull; additional palatal fenestra between pterygoid & palatine [$S91]; dentary & splenial symphyses extend for at least 30% jaw length [$S91]; neck robust and short; cervical ribs slender (reversal) [**$p**03]; 3 pairs of sacral ribs [**$p**03]; long ventrally directed caudal ribs; furcula present; forelimbs perhaps 2/3 length of hindlimbs; scapulocoracoid notch absent (reversal) [**$p**03]; pubes extend far ventrally (>3x width of acetabulum) [**$?p**03]; acetabulum semi-perforate [**$p**03]; femoral head only slightly turned; fourth trochanter forms sharp aliform ridge [**$p**03]; lesser (anterior) trochanter forms spike or crest [**$p**03]; prominent cnemial crest [**$p**03]; distal end of tibia transversely expanded & rectangular [**$p**03]; calcaneal tuber without dorsoventrally aligned median depression [**p**03]; ventral astragalocalcaneal articulation with astragalus concave & calcaneum convex [$S91]; pedal unguals laterally compressed [$S91]; perhaps facultatively bipedal; one pair of paramedian scutes, with lateral potion of cervical plates bent almost 90° down from medial portion [S92]; osteoderms with posterolateral dorsal keel [S92].

Notes: "[**p**03]" refers to our own analysis of published data.

Image: Left: *Riojasuchus* skull courtesy of Steve Harvey (Wiccart). *Ornithosuchus* image courtesy of Prof. Paul E. Olsen.

Links: Lecture 10 - Triassic: Newark, Chinle; ornithosuchus.jpg.

References: Sereno (1991) [S91], Sues (1992) [S92]. MAK030730, ATW040118.

Page Back | Unit Home | Page Top | Page Next

checked ATW050704

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

Archosauria: Rauisuchiformes: Other Ornithosuchidae

Vanaticosuchus, *Riojasuchus*, and *Tarjadia*

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  |  |--Ornithosuchus
                  |  |  |--Venaticosuchus
                  |  |  `--Riojasuchus
                  |  `--+--Tarjadia
                  |     `--+--Prestosuchidae
                  |        `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

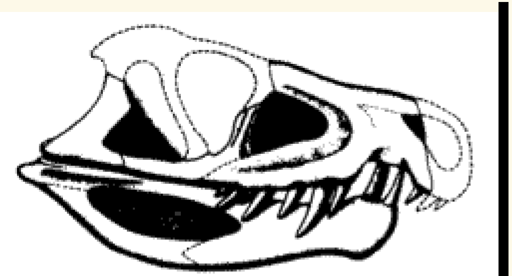
Contents

Taxa on This Page

1. *Riojasuchus* X
2. *Tarjadia* X
3. *Venaticosuchus* X

Descriptions

Venaticosuchus: *V. rusconii* Bonaparte 1971



Venaticosuchus
Skull from Bonaparte (1971).

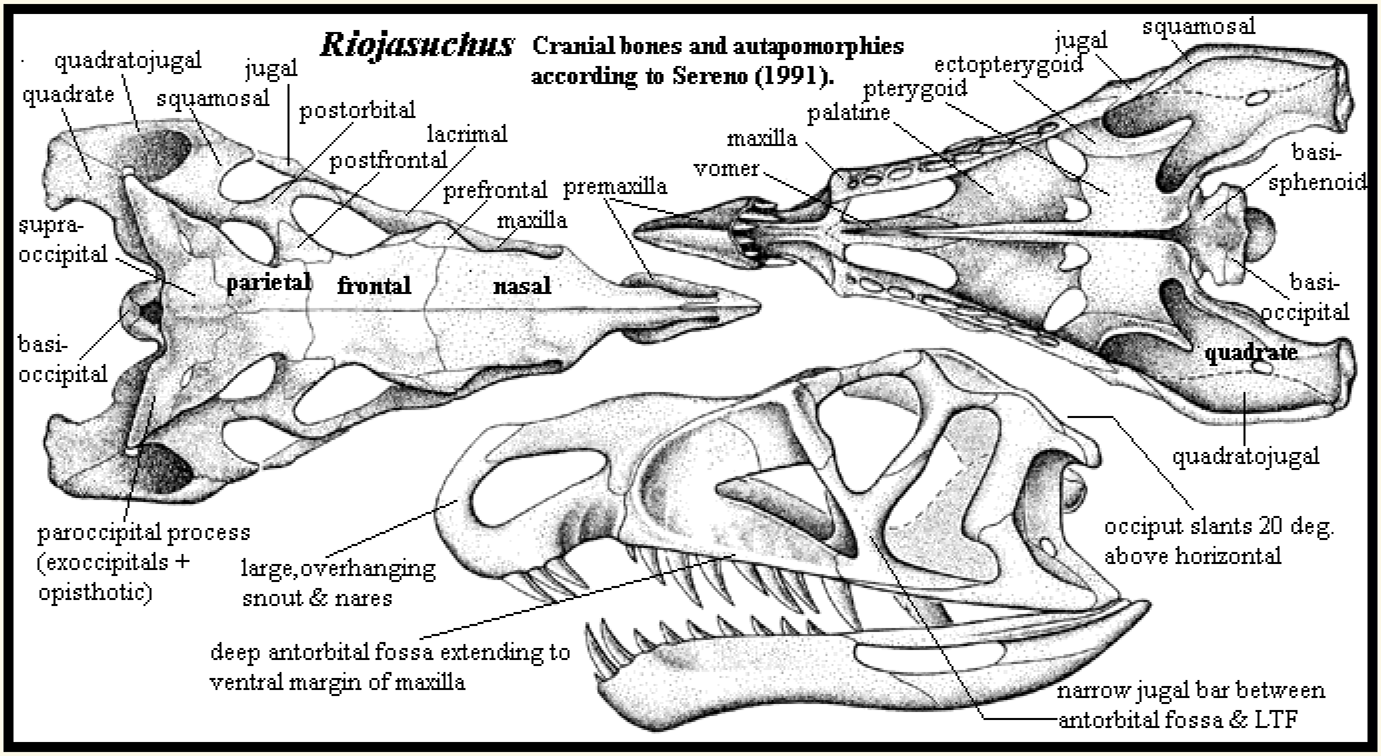
Range: Late Triassic (Late Carnian - Ischigualastan) of South America (Argentina)

Phylogeny: Ornithosuchidae **:** *Ornithosuchus* + *Riojasuchus* + *.

Comments: A typical ornithosuchid thecodont; very similar to *Ornithosuchus* (Late Carnian) and *Riojasuchus* (Rhaetian), from which it differed largely in minor details of the jaw and skull. The teeth are serrated, making them more efficient cutting tools, and each jaw carries two large canine-like teeth. Known from an incomplete skull and forelimb, some osteoderms, from the Middle Ischigualasto Formation. The lower jaw is 26 cm; total length was about 2 metres.

References: Bonaparte (1971) MAK030730.

Riojasuchus: *Riojasuchus tenuisceps* Bonaparte, 1967



Riojasuchus **Cranial bones and autapomorphies according to Sereno (1991).**

Range: Latest Triassic (Coloradean) of South America (Argentina)

Phylogeny: Ornithosuchidae **:** *Venaticosuchus* + *Ornithosuchus* + *.

Characters: large, overhanging snout & nares [$S91]; deep antorbital fossa extending to ventral margin of maxilla [$S91]; rugose postorbital crest (as in *Ornithosuchus*) absent [S91]; only narrow jugal bar separates antorbital fossa & *LTF* [$S91]; occiput slants at 20° above horizontal [$S91]; *atlantal* neural arch bases contact at midline [$S91]; vertebral intercentra present [P93]; ulnar & radial shafts slender [$S91]; proximal carpals elongate, with shaft-like midsection [S91]; metacarpal 1 robust, with asymmetrical condyles [S91]; calcaneal tuber with lateral side concave & medial side convex [P93]; rotary, crurotarsal ankle joint present [P93]; distal tarsal 3 transversely compressed [$S91].

Comment: Closely related to *Ornithosuchus*, but differs in the extreme dorsal position of the supraoccipital region and disappearance of the occipital crests (which are well defined in *Ornithosuchus*). Found in association with *Hemiproterosuchus*, *Pseudohesperosuchus*, and a tritylodontid.

References: Bonaparte (1971), Parrish (1993) [P93], Sereno (1991) [S91]. MAK030730, ATW040117.

Tarjadia: *T. ruthae* Arcucci & Marsicano, 1998. Known only from a few fragments -- probably an immature specimen. [AM98].

Range: Middle Triassic (Anisian or Ladinian) of South America (Argentina).

Phylogeny: Rauisuchia **::** (Prestosuchidae + (*Doswellia* + (Poposauridae + Rauisuchidae))) + *.

Comment: If we had to guess, we'd make this a peculiar basal prestosuchid or close relative. [AM98] give *Tarjadia* no specific phylogenetic placement, but seem inclined to give it a more basal position. Accordingly, we have moved it slightly upstream in the cladogram. However, the placement is somewhat arbitrary.

Characters: skull roof bones with perforations for blood vessels, particularly near orbit [AM98]; skull sutures serrated and clearly visible [AM98]; frontals with strong ridges for laterosphenoid attachment [AM98]; internal surface of frontals suggests undivided nasal bulb with long olfactory channel [AM98]; parietals not fused & with strong sagittal crest between upper temporal fenestrae [AM98]; sagittal crest splits anteriorly to form anterodorsal margins of upper temporal fenestra [AM98]; postfrontal present & participates in orbital margin [AM98]; supraoccipital smooth, slightly concave & triangular, with point directed posteriorly [AM98]; ventrally, supraoccipital overlaps paroccipital processes & forms dorsal margin of foramen magnum [AM98]; exoccipitals fused to opisthotics to form anterolaterally projecting paroccipital processes [AM98]; paroccipital processes with deep otic notch close to suture with basioccipital [AM98]; notch with depression for vestibule and groove to tympanic recess [AM98]; vertebral centra laterally excavated & ventrally concave [AM98]; parapophyses anteroventrally directed & joined to (unfinished) diapophyses by horizontal ridge [AM98]; prezygapophyses & postzygapophyses flat, facing dorsally & ventrally, respectively [AM98]; neural spines tall, straight & expand distally to dorsoventrally flattened table with a small longitudinal groove [AM98]; osteoderms without strong processes or projections [AM98]; double row of thick, quadrangular osteoderms with one paramedian pair per vertebral segment [AM98]; rounded lateral osteoderms [AM98]; osteoderms & skull table bones with coarse, pitted ornament [AM98] osteoderms thickest centrally & medially, with spongy bone between two thin layers of compact bone [AM98].

Links: For some reason, *no one* has mentioned this genus on a web site except our esteemed Mikko Haaramo.

References: Arcucci & Marsicano (1998) [AM98]. ATW031226

Page Back | Unit Home | Page Top | Page Next

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Archosauria: Rauisuchiformes: *Ornithosuchus*

Abbreviated Dendrogram

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ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  |  |--Ornithosuchus
                  |  |  |--Venaticosuchus
                  |  |  `--Riojasuchus
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
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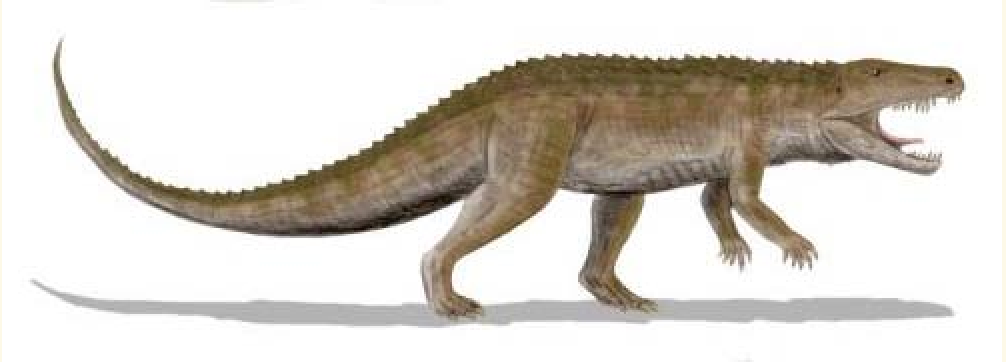
Contents

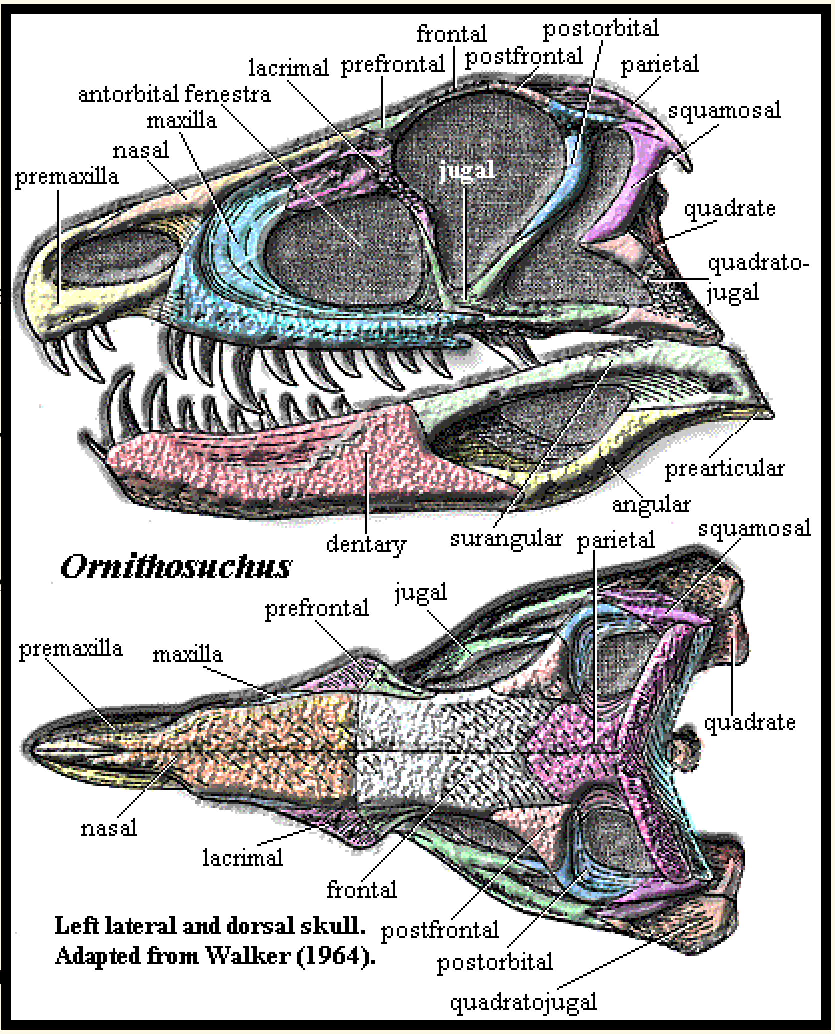
Taxa on This Page

1. *Ornithosuchus* X



Life reconstruction of *Ornithosuchus longidens*
Artwork by Nobu Tamura , via Wikipedia, GNU Free Documentation/Creative Commons Attribution

The Carnian Carnosaurs of Moray Firth



Left lateral and dorsal skull. Adapted from Walker (1964).

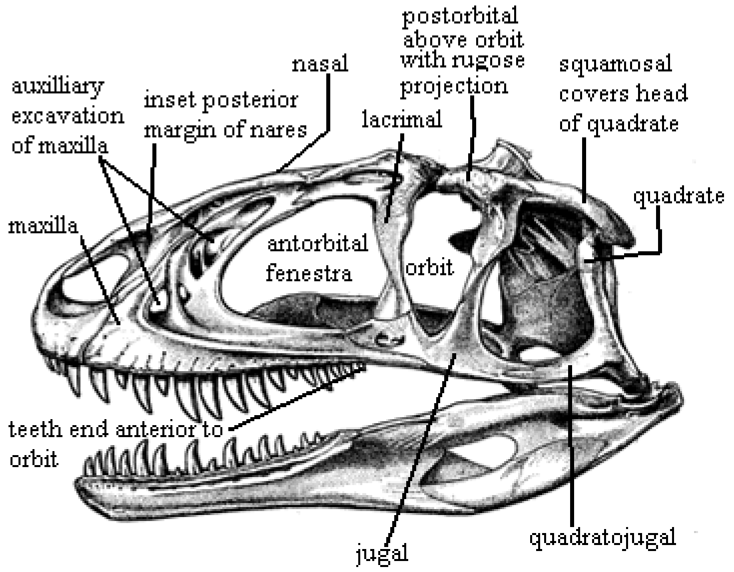
In these latter days of dinosaur paleontology, most of the main lines of descent in that part of phylospace have been sketched out. We tend to dismiss papers like Walker (1964) as hopelessly obsolete. Walker argued that *Ornithosuchus* was ancestral to the "megalosaurs" and carnosaurs of the Jurassic. Now, it is fair to say that he was quite wrong, and that he was misled by similar characteristics which Carnosauria and ornithosuchians evolved independently. However, it would be a mistake to suppose that Walker was foolish or unobservant. The similarities, as we will see, are rather startling. But, more to the point, it would be an even more serious mistake to disregard Walker's wrong ideas about phylogeny as useless antiques.

Synapomorphies -- unique characteristics -- are the keys to phylogeny. Synapomorphies tell who is related to whom. But homoplasies -- "convergent" characteristics -- are the keys to evolution. Homoplasies might tell us *why* animals evolved as they did. If two closely related animals are alike, we learn nothing except that they are related. If two unrelated animals are alike, we can legitimately suspect that they were subject to similar selective pressures. By sorting out the characters they do share from the characters they don't share, we may be able to determine what selective pressures were most important in shaping the forms we observe in the fossil record.

The *wrong* ideas about phylogeny in prior decades are thus potentially much more useful than *right* ideas. No one today needs to know why Walker thought *Hallopus* was a crocodylomorph. Walker (1970). He was entirely correct; but we have better fossils now, as well as some improved analytical tools; and these can usually be counted on to give us better reasons than Walker had. On the other hand, *erroneous* phylogenies by experienced and competent observers like Alick Walker are pre-compiled collections of homoplasies ripe for analysis of selective pressures. This data is much harder to collect today, since compiling this kind of information requires that we put aside what we have learned so laboriously in working out the correct phylogeny.

Some of the homoplasies involved are really extraordinary. By way of example, we show the skull of the ornithosuchid ***Ornithosuchus*** on the right from the Carnian (Late Triassic) of Scotland **[1]**, adapted from Walker (1964). On the left is the allosauroid *Sinraptor*, from the Late Jurassic of China, as reconstructed by Currie & Zhao (1993). Their last common ancestor was probably something like *Euparkeria* from the Middle Triassic of South Africa.

Thus, eighty million years and tens of thousands of miles separate *Sinraptor* from its last common ancestor with *Ornithosuchus*. Yet the two share numerous details of skull structure. The nares are enlarged and bordered almost entirely by the premaxilla. The nares are extended by a well-developed posterodorsal fossa. The anterior margin of the antorbital fenestra is strongly developed as an elaborate, rimmed fossa comprised of an ascending



Skull of Sinraptor dongi in left lateral view, showing some apomorphies of Sinraptoridae.

maxillary process. The maxilla and lacrimal meet on the dorsal rim of this fenestra in a tight, complex suture. The skull table is long and narrow. It contains a probable transverse hinge (albeit very differently placed and formed). A transverse ridge marks the posterior end of the skull table, and the upper temporal fenestrae are deeply inset and sharply marked off. The lacrimal and jugal form the antorbital bar. The bar is twisted, with part of the upper surface rugose. The orbit is triangular with markedly roughened surfaces dorsal to the midline of the orbit. The postorbital has a rugose lateral projection above the orbit. The maxilla meets the jugal below the orbit. In *Ornithosuchus*, the maxilla forks and grasps the jugal with multiple tines. In *Sinraptor* the junction is simple, but the jugal - quadratojugal suture is split. The lower temporal fenestra is large, and the squamosal and quadratojugal meet behind it at an angle. The dentary is more massive anteriorly in *Ornithosuchus*, in almost every other respect the jaws virtually identical, with the same bones covering essentially the same areas around an enlarged mandibular fenestra, bearing the same large posterior fossa. Both have a short, fairly strong retroarticular process. The tooth row is rather short and ends about level with the preorbital bar.

These are, obviously, not small matters. In particular, the similarity of the structures surrounding the antorbital fenestra is downright odd. In some imaginative dinosaur reconstructions, this is often an area with a colorful, inflated area of skin used as a mating display, as it is in some lizards today. In other reconstructions, the region is simply patched over since the structure has no obvious purpose. Yet, this extraordinary similarity suggests that it may have been *strictly* functional, an organ or structure so highly constrained by its purpose that it appears in almost precisely the same form in two lineages with no direct relationship. The similarities in the orbital region, immediately posterior, are not quite so uncanny at first sight. However, in some ways they are even weirder, since the skull tables of *Ornithosuchus* and *Sinraptor* are put together quite differently. What possible use is the little pocket and lacrimal awning above the antorbital fenestra? Why is the preorbital bar twisted and dorsally rugose? Did they have eyestalks like snails? It hardly seems likely. What does seem likely is that these peculiar similarities are likely the only remaining evidence of important selective factors that shaped large terrestrial carnivores consistently over an enormous period of time in the early Mesozoic and beyond.

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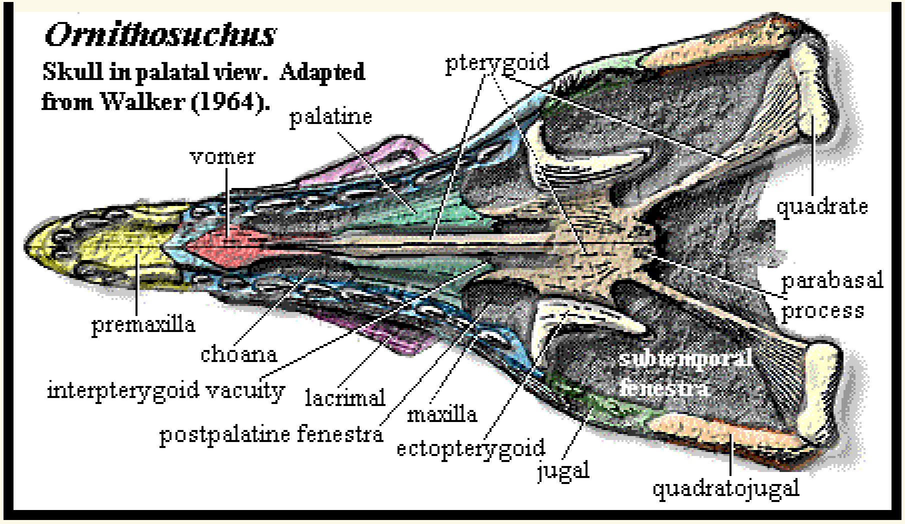
[1] In fact, on the south shore of Moray Firth -- hence the name of our essay.

ATW040130.

Descriptions

Ornithosuchus: Newton 1894. *O. longidens* (Huxley 1877)

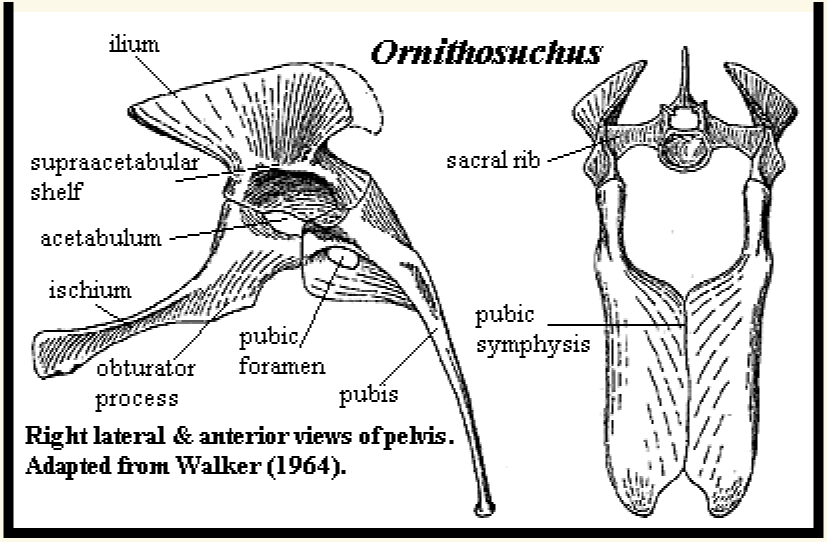
Range: Late Triassic (Latest Carnian) of Scotland


Ornithosuchus

Skull in palatal view. Adapted from Walker (1964).

Phylogeny: Ornithosuchidae **:** *Venaticosuchus* + *Riojasuchus* + *.

Characters: length to 4 m, skull to 45 cm [W64]; premaxilla recessed posteriorly for passage of enlarged dentary teeth [W64] **[3]**; skull table slopes smoothly up to frontals [W64]; nasal with strong medial flange posterior to nares, supported by ascending process of maxilla [W64]; continuous suture between nasal + frontal and lacrimal + prefrontal + postfrontal [W64]**[1]**; postfrontal confined to skull table [W64]; skull table posterior to frontals slightly raised [W64]; postorbitals & parietals form most of UTF [W64]; parietals with occipital flanges [W64] **[2]**; maxilla excluded from naris by premaxilla - nasal suture [S91]; maxilla overlies lacrimal with a thin*squamous suture* and also bears thin process inserting between lacrimal & nasal [W64]; maxilla forks posteriorly, where it meets the jugal [W64] [$S91]; lacrimal with strongly *rugose*, posteriorly - directed flange on descending process [W64]; jugal, lacrimal process tapers to a point, fitting into a groove in the descending process of the lacrimal [W64]; opposite articulation with postorbital (i.e., groove on the jugal) [W64]; maxilla and jugal with strong lateral ridge [W64] **[4]**; postorbital dorsally rugose, with strong crest overhanging its own descending process [W64] [$S91]; squamosal - quadratojugal bar with strong anterior projection [W64]; external surface of quadratojugal strongly rugose [W64]; quadrate with small, thin, triangular process extending onto surface of pterygoid [W64]; large quadrate foramen [W64]; occipital area poorly known [W64]; probably a large, rectangular supraoccipital [W64]; laterosphenoid present [S91]; anterior palate **[5]** not well known & median contact of maxillae is not certain [W64]; palatines arch strongly upwards, forming a vault with the anterior processes of the pterygoids [W64]; pterygoids with long, straight, rod-like anterior bars, meeting *antimere* along a flat medial surface [W64]; small anterodorsal pterygoid processes may have defined notch for cartilaginous epipterygoid [W64]; pterygoids with short, blunt, ventrally directed *transverse flange* [W64]; *basipterygoid process* small, located between *parabasal process* and *quadrate ramus* [W64]; dentary symphysis long [W64]; anterior dentary curves medially to form symphysis & accommodate anterior maxillary teeth [W64]; splenials medially flat & meet in short splenial symphysis [W64]; angular with long anterior process passing into jaw and between dentary & splenial, forming floor of *Meckelian cana*l [W64]; angular forming concave lower margin of posterior jaw [$S91] **[7]**; surangular large, forming much of mandibular fenestra, with marked rugosity posterodorsally [W64]; surangular with foramen near ventral margin, under jaw articulation [$S91]; small coronoid present [W64]; prearticular small, probably with some lateral exposure and short *retroarticular process* [W64]; articular blocky and complex, with articular surface facing ?medially [W64]; interdental plates alternate with teeth [W64]; teeth laterally compressed, more rounded anteriorly than posteriorly, recurved and finely serrated on posterior & distal anterior edges [W64]; premaxilla with 3 teeth, with 1st or 2nd largest [W64]; <10 maxillary teeth & ~10 dentary teeth [W64]; dentary with small, anterior, procumbent tooth [S91]; neural canal large & "sag" down into centra [W64]; 24 presacral vertebrae, with no clear cervical - dorsal distinction & all of about the same length [W64]; 3 sacrals (plus one partially incorporated) & 45-50 caudals [W64]; cervical centra strongly compressed between articular ends, especially ventrally **[5]** [W64]; dorsals constricted, but without ventral keel [W64]; *parapophyses* start low on centrum & move up onto arch, *diapophyses* begin low on arch, directed ventrally and move dorsally, oriented more laterally, along the dorsal series [W64]; both parapophyses & diapophyses with various supporting ridges, particularly to *zygapophyses* [W64]; cervicals with narrow neural spines, with transversely expanded apices (compare *Euscolosuchus*) [W64]; ribs short, slender & poorly known [W64]; caudal centra become round & spool-like, ventrally grooved from 3rd caudal & with broadly expanded transverse processes [W64]; proximal caudal neural spines much taller than any others [W64]; caudal centra with anterior vertical median lamina [W64]; clavicle present , interclavicle long & very thin [W64]; scapula slender, with gradual distal expansion [W64] **[6]**; small, oval muscle attachment area above glenoid [W64]; *scapulocoracoid notch* minor or absent [W64]; coracoid thin and crescent-shaped, pointed posteriorly, forming most of large, shallow *glenoid* [W64]; forelimb <2/3 length of hindlimb [W64]; major limb bones probably hollow [W64]; humerus very thin with large *deltopectoral crest*, small *internal tuberosity* & deep anterior trochlear recess [W64]; radius very slender with lateral recess distally overlapped by an ulnar shelf [W64]; ulna somewhat stouter, with poorly developed olecranon [W64]; distal ulna curves postaxially (very unusual) [W64]; probably 5 digits on manus, I largest and rest progressively smaller [W64]; manus I may have been opposable (!?) [W64]; ilium tall, peaking above anterior part of acetabulum, curving ventrally &



Right lateral & anterior views of pelvis. Adapted from Walker (1964).

laterally posterior to acetabulum [W64]; ilium with marked medial shelf for sacral ribs [W64]; acetabulum deep, perforate in part, with strong *supraacetabular shelf* [W64]; pubis with large pubic foramen and long, continuous *pubic symphysis*, with a sort of bifid pubic boot [W64]; ischium with *obturator process* interrupting symphysis (medial edges bent anteroventrally to form obturator process) [W64]; femoral head with distinct medial bend, but without well-defined neck [W64]; *greater trochanter* small, probably finished in cartilage, but *lesser trochanter* well developed [W64]; *4th trochanter* present as elongate ridge on medial face of femur [W64]; femoral shaft with slight anteriorly - directed bow [W64]; tibia with triangular proximal face & well-developed laterally-curving *cnemial crest* [W64]; crus shorter than femur [W64]; calcaneum with prominent tuber & calcaneal form suggests croc-reversed tarsus, but region is not well-preserved in any specimen [W64]; pes digits symmetrical about III, with none greatly reduced [W64]; skull with irregular ornament of small pits [W64]; paired paramedian scutes sutured across the midline arranged so as to cap neural spines [W64]; caudal scutes fuse across midline after 10th caudal [W64].

Notes: **[1]** Walker does not mention it, but note that the naso-frontal suture is also continued by the lacrimal - prefrontal suture. It is difficult to explain this unless the skull were highly kinetic in this region. **[2]** Walker speculates that these supported the most anterior set of armor plates [W64]. **[3]** Is it also for a sliding joint with the maxilla? **[4]** Note the similarity to *Erpetosuchus* and probably also poposaurs. **[5]** *c.f.* *Saurosuchus*. **[6]** The general form of the post-cranial skeleton is illustrated at Ornithosuchidae. **[7]** however this is also perhaps true of *Postosuchus*.

Comments: Known from skull and postcrania, *Ornithosuchus* was the first member of this family to be described, from the late Carnian Lossiemouth Beds of Elgin, Scotland. At 3.3 metres or more in length, this was a large animal, without doubt the top predator of its environment. Originally reconstructed as a biped, and certainly capable of bipedal locomotion, it probably spent most of its time on all fours. The skull is strikingly similar to that of large theropod dinosaurs like *Tyrannosaurus*, leading to the suggestion at one time that tyrannosaurs originally evolved directly from ornithosuchids (this is now not believed to be the case). Although at one time believed to be a primitive member of the Dinosauria, *Ornithosuchus*, like other members of its family, have a number of primitive (plesiomorphic) features, such as a double row of bony plates down its back, a short broad pelvis attached to the backbone by only 3 vertebrae, and five toes on each hind foot (as opposed to three in the case of theropod dinosaurs). These characteristics are shared by most basal archosauromorphs, and show that *Ornithosuchus* is only distantly related to the dinosaurs. MAK.

References: Sereno (1991) [S91], Walker (1964) [W64]. MAK030730, ATW031130.

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

checked ATW040109

Archosauria: Rauisuchiformes: Prestosuchidae

Saurosuchus

Abbreviated Dendrogram

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ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     |  |--Saurosuchus
                  |     |  `--+--Ticinosuchus
                  |     |     `--Batrachotomus
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

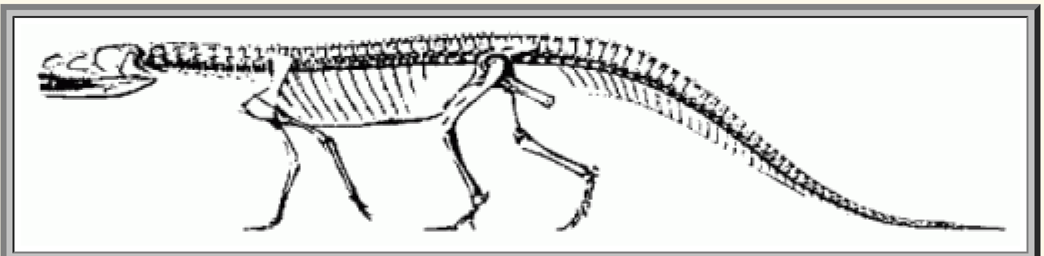
Contents

Taxa on This Page

1. Prestosuchidae X
2. *Saurosuchus* X

Prestosuchidae

Included here is the beginning of an assemblage of rather poorly known but phylogenetically important crurotarsan archosaurs. The **Prestosuchidae** probably fall somewhere in the middle range of basal Archosauria. In most cladograms they more derived than phytosaurs and ornithosuchids, but usually less derived than the rauisuchids and aetosaurs of the Late Triassic. The prestosuchids were active terrestrial predators, and were highly successful during the Triassic. These were all large animals, even the smaller representatives being around 2.5 meters in length. ***Saurosuchus*** reached 6 metres and more.



***Ticinosuchus* ferox, from the Grensbitumenhorizonts (Anisian/Ladinian boundary, middle of the Middle Triassic) of Monte San Giorgio, Tessin Alps, Switzerland. Reconstructed skeleton, length about 2.5 meters. AH Müller, *Lehrbuch der Paläozoologie*, p. 296, after Huene (1956).**

The Prestosuchidae have sometimes been included in the Rauisuchidae, which are variously considered the sister group of the Crocodylomorpha (Gauthier, 1986), the Ornithosuchidae (Benton & Walker, 2002), or the sister group of the aetosaurs, the two constituting a monophyletic Pseudosuchia (Benton & Clark, 1988). Alternatively, separate from the more advanced Rauisuchia, they are variously referred to as an independent lineage that falls outside a crocodylomorph - poposaurid - rauisuchid - aetosaur clade (Parrish, 1993), or the sister group of the aetosaurs in a monophyletic Pseudosuchia (Juul, 1994). However, most investigators find that the synapomorphies (unique features) that characterize the prestosuchids are not enough to place them securely in a separate clade. So, it is entirely likely that they represent a paraphyletic assemblage or gradation (like, say, "Pelycosauria" or "Therapsida") that are intermediate between primitive forms (in this case basal Crurotarsi) and more advanced types (such as the Aetosauridae and Rauisuchidae), with the Prestosuchidae proper being a much smaller assemblage (Gower 2002). In our hands, they fall in a fairly neat morphocline between the ornithosuchids and rauisuchids.

The success of these animals during the Triassic may have been due in part to their reptilian (sauropsid) metabolism which gave them an edge over our synapsid relatives in the arid Pangean climate, and in part to their efficient stance. Unlike earlier archosaurs, which had a typically reptilian sprawling or only semi-erect limb-posture, the "prestosuchid" archosaurs, and the rauisuchids and poposaurids (postosuchids) had a fully erect gait and posture. They had mobility like dinosaurs and mammals, rather than like reptiles. Benton (1984). Increasingly efficient limb-posture and mobility may also indicate that these creatures had a different, perhaps more energetic, metabolism than their predecessors. Their main centre of evolution seems to have been West Gondwana, although a relatively small form (*Ticinosuchus*) flourished in Europe during the mid-Triassic.

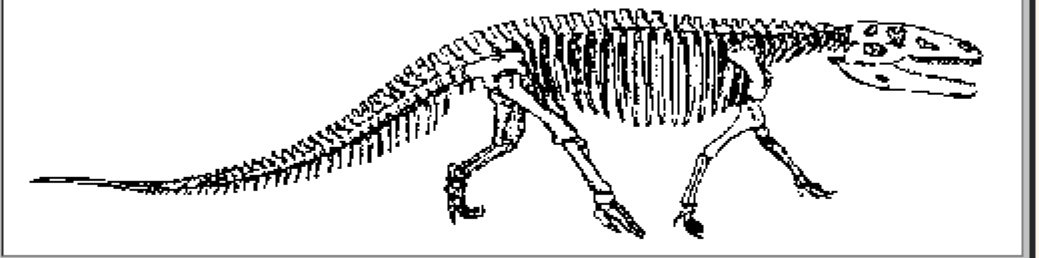
Anatomically, the prestosuchids are a more massive, solid version of the ornithosuchids. The cranial peculiarities of *Ornithosuchus* discussed previously are still present, but sometimes masked by the greater thickness of bone. The protruding premaxilla, still partly separated from the maxilla has become even more blocky and rectangular, particularly in *Saurosuchus*. The basic structure of the antorbital fenestra is the same, although the twisted antorbital bar has been replaced by a straight, girder-like extension of lacrimal which locks on to a jugal process oriented at a right angle to the lacrimal process. The prefrontal "awning" is smaller, but still present, and is elongated by a similar lateral process of the frontal which extends laterally over the orbit. The region around the upper temporal fenestra looks even more like *Sinraptor* than does the corresponding region in *Ornithosuchus*. In fact, when due allowance is made for a heavier covering of bone, there is little to distinguish the dermal skulls of *Ornithosuchus* and *Saurosuchus*. The palate is more distinctive, but the prestosuchid skull is much wider, and the anterior palate of *Ornithosuchus* is not well known, so that one cannot make to much of the comparison. The postcranial skeleton is likewise quite similar, again with due allowance for the difference in mass. The pelvis, in particular, is built along very much the same lines.

MAK 991019 and 030808. ATW040130.

Descriptions

Prestosuchidae: *Prestosuchus chiniquensis* Huene, 1942, *Prestosuchus* *loricatus* Huene, 1942, *Tikisaurus romeri* Chatterjee & Majumdar, 1987.

Range: Late Middle and Early Late Triassic of Gondwana (Ladinian & Carnian of South America; Late Carnian of India).

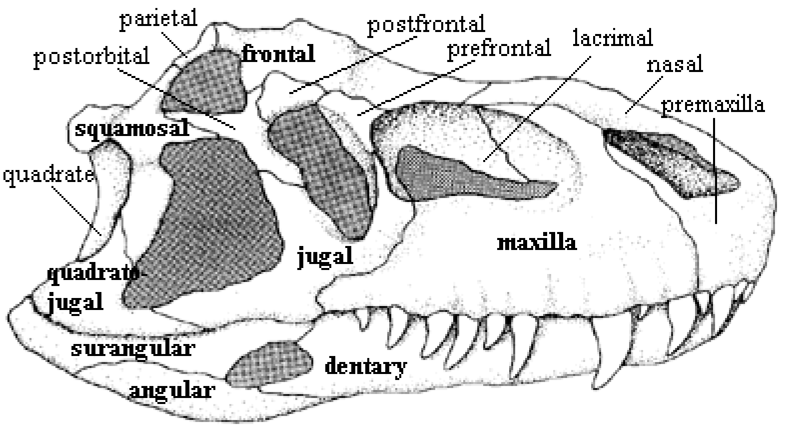


Prestosuchus sp., from the Carnian of Brazil (Santa Maria Fm); reconstructed skeleton, length about 5 meters. A. H. Müller, *Lehrbuch der Paläozoologie*, p.296. after Huene 1956

Phylogeny: Rauisuchia ::: (*Doswellia* + (Rauisuchidae + Poposauridae) + * : *Saurosuchus* + (*Ticinosuchus* + *Batrachotomus*).

The Prestosuchidae have previously been included under the Rauisuchidae, or as a large Middle and Late Triassic grouping, but are here defined as a much smaller clade outside the Suchia

Characters: medium to large size [S74]; skull large, narrow & deep [S74]; some genera with small crescentic accessory antorbital fenestra (probably homologous with max-premax diastema of ornithosuchids, thus a rauisuchian synapomorphy) [S74] [p$03]; antorbital fenestra large & elongate [S74]; upper temporal fenestra small [S74]; descending process of prefrontal present [p$03]; orbit keyhole-shaped [S74]; postorbital-jugal bar with distinct "step" [p$$03]; exoccipital with lateral crest lying anterior to *hypoglossal foramen* [$G02] [p$$03]; ventral ramus of opisthotic extends laterally further than exoccipital [p03]; foramina for cerebral branch of carotid on lateral face of basisphenoid [G02] [1]; maxillae meet at midline anterior to choana to form secondary palate [p$03]; teeth recurved, flattened & serrated [S74]; neural arches high, not inclined, rectangular, with deep *interspinous notch* [S74]; accessory neural spine on midcaudal vertebrae [p$03] [3]; manus V with 4 phalanges [p$$03]; pelvis triradiate [S74]; ilium with strong posterior process & *brevis shelf* [S74]; ischium elongate & rod-like, fused at midline along most of its length [S74]; pubic plate reduced and pubis with little participation in acetabulum [S74]; pubis shorter than ischium (reversal) [p$03]; acetabulum closed [S74]; acetabulum ventrally deflected [p$03] [4]; femur long & slightly sigmoid [S74]; femur *4th trochanter* poorly defined or absent [S74]; shallow socket on the calcaneum articulating with astragalar ball ("*crocodile-normal*" tarsus) medial to the fibular facet [S74] [$P93]; posteriorly directed calcaneal tuber [J Conrad, iNet]; calcaneal tuber, distal end with dorsoventrally aligned median depression [p$$03]; metatarsal V hooked [S74]; pes V with 1 phalanx [p$$03]; erect limb posture; quadrupedal [S74]; paramedian plates with anterior articular processes [$?P93] and posterior dorsal keel [S92]; carnivorous.



Prestosuchus **skull in right lateral view. From Parrish (1993).**

Notes: [1] synapomorphy of clade uniting Prestosuchidae with Suchia [G02]. [2] "[p03]" refers to our own analysis of published data. The prefix "$$" indicates a synapomorphy of the larger clade including Prestosuchidae + Rauisuchidae. [3] Might be related to supposed angled mid-caudal vertebral centrum of *Doswellia*. [4] homologous to, but less extreme, than condition in *Postosuchus*.

Links: Rauisuchia Translation and Pronunciation Guide Introduction.

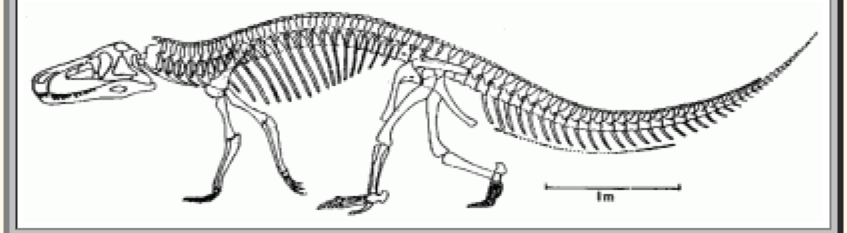
Reference: Gower 2002 [G02], Parrish (1993) [P93], Sill (1974) [S74], Sues (1992) [S92]. ATW031213.

***Saurosuchus*: *Saurosuchus galilei* Reig 1959**

Range: Late Triassic (Carnian) of South America (Argentina).

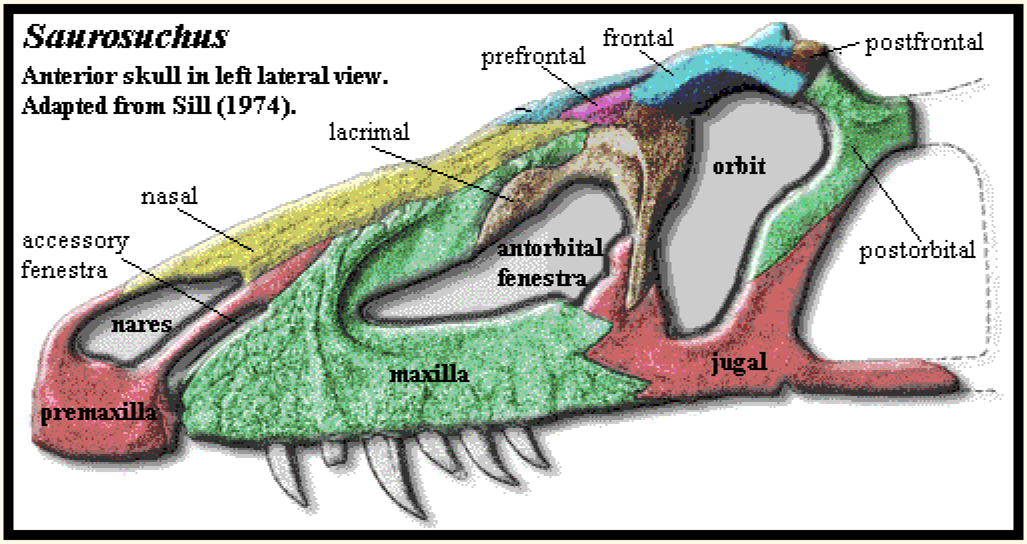
Phylogeny: Prestosuchidae : (*Ticinosuchus* +

Batrachotomus) + *.



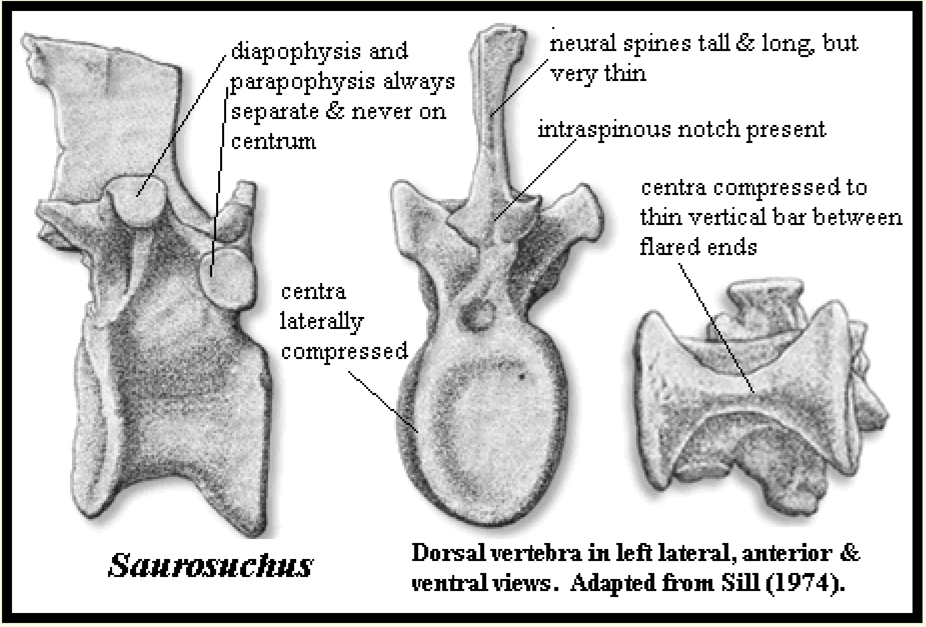
S. galilei, from the Carnian of Argentina (Ischigualasto Formation); reconstructed skeleton (scale bar 1 meter). From Benton (1984).

Comments: *Saurosuchus*, known from a skull and several postcranial remains, from both the lower and the upper sections of the Ischigualasto Formation, San Juan Province, Argentina, was an enormous predator. With a length of 6 or 7 metres and a skull alone of up to a meter in length, it was as large as a decent-sized Jurassic or Cretaceous theropod (say a medium-sized *Allosaurus* or tyrannosaur). Although in some features primitive [P93] [G02] it was more advanced than *Prestosuchus* and *Rauisuchus*, with a more elongate ischium and femur, and strong pneumatisation (air-spaces) of the vertebrae [B71], all of which would seem to indicate a more active and metabolically advanced animal. Without doubt the "top predator" of the day, this huge carnivore would have fed upon the large kannemeyeriid dicynodonts whose remains occur in the same formation.



Saurosuchus
Anterior skull in left lateral view.
Adapted from Sill (1974).

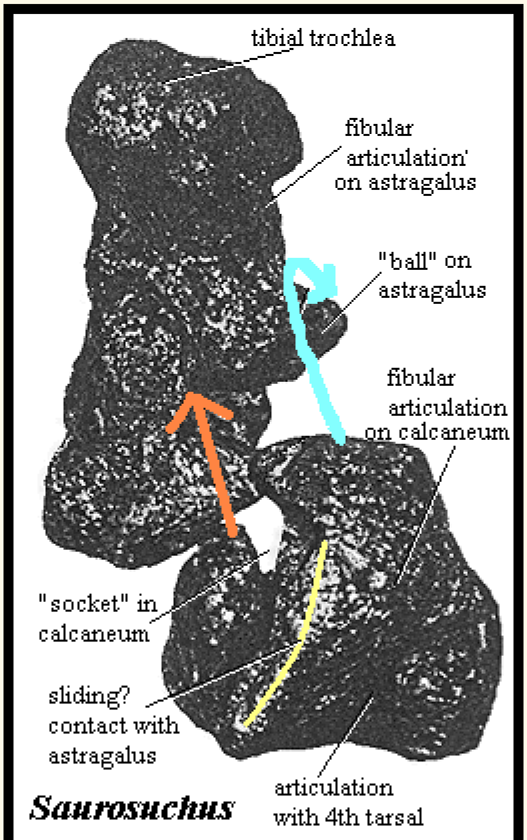
Characters: large (to 6m) [S74]; skull deep, transversely narrow, elongate & strongly constructed [S74]; skull roof finely sculptured [S74] [A00]; body of premaxilla is massive rectangular block with 2 narrow processes on either side of naris [S74] [A00]; premaxilla with thickened oral rim bearing 4 tooth positions [S74] [A00]; premaxillae with long, thick symphysis [S74]; premaxillae not strongly sutured to maxilla [S74]; very large nares bordered only by nasals & premaxillae [S74]; accessory subnarial fenestra between maxilla and premaxilla [S74] [$P93]; maxilla U-shaped, large & plate-like, forming entire ventral margin of antorbital fenestra & half of dorsal margin (overlapping part of lacrimal) [S74] [A00]; maxilla forms prominent crista parallel to ventral border of fenestra [A00]; maxilla with large foramen on medial surface, just anterior to jugal suture [S74]; maxilla sculptured [A00]; antorbital fenestra large (slightly smaller than orbit) & elongate, with well-defined smooth border [S74]; nasal anteriorly thin, very elongate, overlapping medial process of premaxilla [S74] [A00]; nasal thickens & becomes somewhat broader posteriorly [S74] (*contra* [A00]); nasal with ornament of irregular anteroposterior grooves [S74]; prefrontal small, oriented dorsally & not contacting orbit [S74] (*contra* [A00], participates in orbit); prefrontal with distinct posterior process underlying frontal dorsal to orbit, joining with parietal to form ventral depression having possible kinetic contact with laterosphenoid [A00] [p$03] [3]; frontal dominated by massive supraorbital arch [S74] [A$00]; frontal with pit & groove ornament [S74]; frontal with median longitudinal ridged (nasal tract?) [S74]; frontal with pocket posteriorly for laterosphenoid anterior process [S74]; frontal with lateral process forming



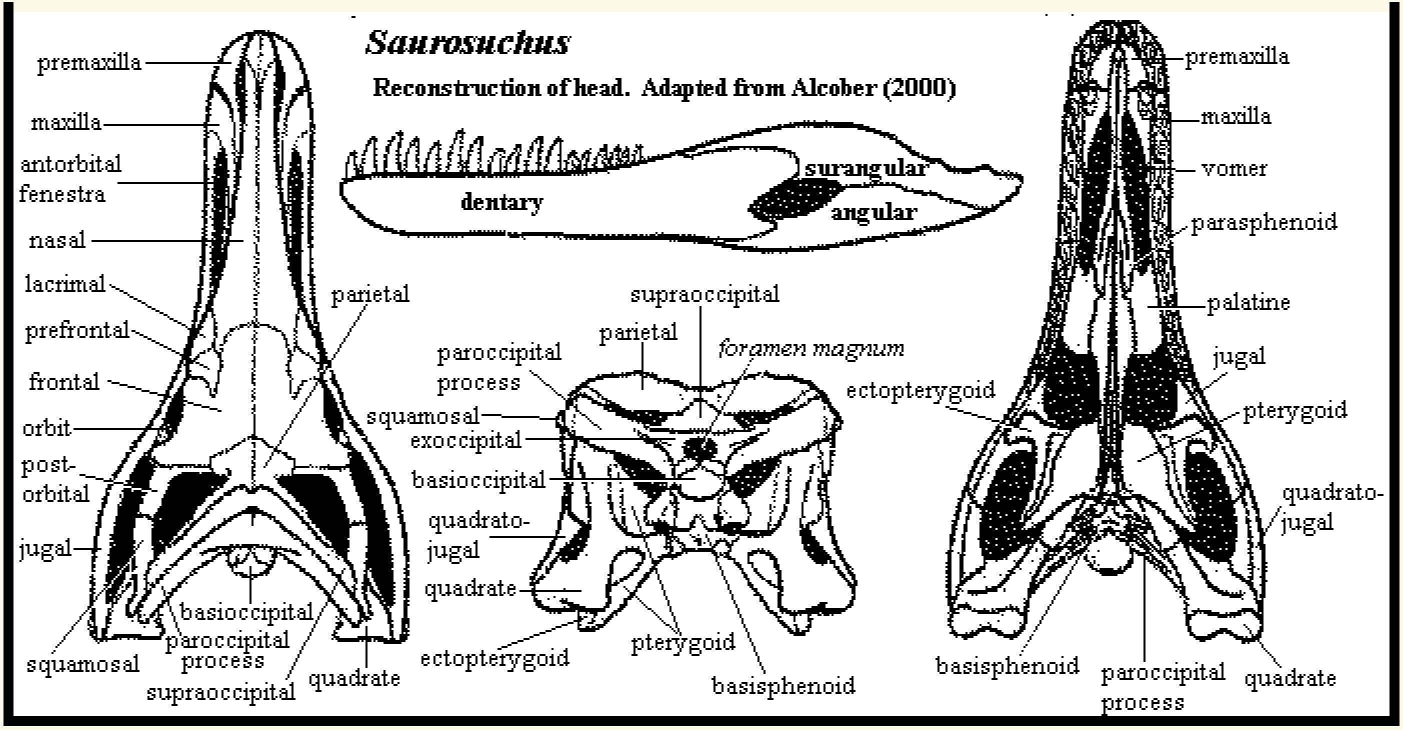
Saurosuchus

Dorsal vertebra in left lateral, anterior & ventral views. Adapted from Sill (1974).

posterolateral margin (i.e. the supraorbital arch projects laterally) [A$00]; upper temporal fenestra small & on dorsal face of skull [S74]; postfrontal reduced, not participating in orbit & hidden in dorsal view by frontal [A$00]; parietal forms dorsal border of upper fenestra [A00]; parietal overlaps supraoccipital and contacts laterosphenoid [A00]; parietal crest which runs along posteromedial border of upper fenestra, participates in posttemporal foramen, & broadly overlaps squamosal [A00]; orbit keyhole-shaped [S74]; lacrimal lies mostly in antorbital fenestra as smooth-surfaced thin plate [S74]; lacrimal forms cylindrical process and prong posteriorly, overlying antorbital process of jugal in a probably mobile articulation [S74] [A$00]; possible lacrimal foramen near border with frontal [S74] (*contra* [A00] no foramen); lacrimal strongly sutured to prefrontal [A00]; lacrimal without transverse component [S74]; strong orbital arch formed by frontal [S74]; jugal having zig-jag suture with maxilla [S74] (*contra* [A00] jugal with moveable, overlapping contact with maxilla); jugal with pit & groove sculpturing [S74]; jugal with strong diagonal abutment with postorbital [S74]; jugal with thin, tapering bar below lower fenestra [S74] [A00]; jugal with medial bulge just ventral to orbit marking internal, kinetic ectopterygoid contact [S74] [A00]; postorbital triradiate, fairly large, with prominent tuberosity just posterior to orbital arch [S74] [A00]; postorbital forming lateral and anterior border of upper temporal fenestra [S74] [A00]; postorbital with short posterior process fitting under anterior process of squamosal [A00]; lower temporal fenestra approximately same size as orbit [S74]; squamosal with ventral process overlapping quadratojugal [A00]; squamosal with short, blunt posterior process [A00]; quadrate vertical with thick vertical column bearing anterior flange which overlaps quadratojugal [A00]; quadrate column curved posteriorly for to form border for tympanum [A00]; quadrate with convex articular condyle [A00]; supraoccipital contributes to *foramen magnum* [p$03]; supraoccipital triangular, fused to exoccipitals & opisthotics [A00]; exoccipitals fused to opisthotics and paroccipital process [A00]; paroccipital process not fully ossified distally [A00]; *metotic foramen* communicates nerves IX-XI, with separate *hypoglossal foramen* posterior to metotic foramen [A00]; paroccipital process forms base of *posttemporal foramen* [A00]; basioccipital forms most of occipital condyle [A00]; condyle bearing notochordal pit [A00]; basioccipital broadly overlaps basisphenoid [A00]; basioccipital with well-developed basal tubers [A00]; basioccipital with blind *basioccipital recess* [A00]; semilunar depression absent from braincase [G02]; basisphenoid dorsoventrally short [G02]; presphenoid may [A00] or may not [G02] be present above *trigeminal notch*; olfactory bulb at end of long peduncle [A00]; maxilla with palatal process massive, meeting on midline and vaulted, meeting vomer (also contact with palatine & ectopterygoid) [S74] [A00]; long triangular *interpterygoid vacuity* present [S74]; vomers not contacting premaxilla (but see figure) [A00]; palatines thin, with overlapping contacts [A00]; palatines, and palate generally, arches upward sharply [A00]; pterygoid large, contacting, vomer, ectopterygoid, palatine, quadrate & basisphenoid, bearing the usual palatal, transverse and quadrate rami [A00]; anterior ramus strongly convex ventrally & near vertical at midline [A00]; ectopterygoid with expanded lateral foot contacting jugal [A00]; dentary robust, not dorsoventrally expanded, & external surface is almost flat [A00]; dentary medial surface almost covered by splenial & coronoid [A00]; dentary symphysis with two flanges grasping opposite ramus [A00]; palatal dentition absent [S74] [P93]; teeth *homodont*, large, robust, laterally compressed, recurved, sharply pointed & serrated [S74]; tooth roots twice as long as crowns [S74]; teeth with thin, striated enamel [S74]; 4 teeth on premaxilla, 10 on maxilla [S74] (*contra* [A00] 12 on maxilla); interdental plates present [S74] [A00]; vertebrae amphicoelous [S74]; vertebrae with neural spines anteroposteriorly elongate & flat [S74]; vertebrae with prominent *interspinous notch* on anterior face [S74]; vertebrae with grossly constricted centra, leaving thin, vertical plate between flared rims [S74]; 23-25 presacral vertebrae [S74]; dorsal vertebrae compressed laterally & reduced to thin vertical plate between flared ends [S74]; rib facets well separated & on different levels throughout column, but never on centra [S74]; transverse processes short [S74]; prezygapophyses short, not overhanging centrum [S74]; neural spines flat, tall, thin, not inclined [S74]; ribs massive, with prominent ridge on proximal anterior surface [S74]; 2 sacral vertebrae, not fused & generally similar to dorsals [S74]; 2nd sacral & 1st caudal with anterior centrum flare enclosing and immobilizing end of preceding centrum [S74]; sacral transverse processes massive [S74]; caudal vertebrae shorter & with large rounded rims, less strongly constricted than dorsals (& becoming even less constricted



Astragalus in anterolateral & calcaneum in anteromedial views. Adapted from Sill (1974)


Saurosuchus

Reconstruction of head. Adapted from Alcober (2000)

distally) [S74]; caudal prezygapophyses elongate distally, overhanging centra [S74]; shoulder girdle & forelimbs unknown [S74]; ilium with broad *brevis shelf* [S74]; ilium posterior blade long & heavy [S74]; ilium anterior blade short and emarginated ventrally [S74]; ischium long, rodlike, somewhat expanded distally & fused at midline over most of its length [S74]; ischium participates little in acetabulum [S74]; ischial blade *dacriform* in cross-section, with thin part forming symphysis [S74]; pubis almost excluded from acetabulum [S74]; pubis broad proximally, thinning rapidly to rod-like proportions [S74]; acetabulum high up on ilium, large, deep, & closed [S74]; femur with dacriform head [S74] femur slightly S-shaped [S74]; greater & lesser trochanters absent [S74]; *4th trochanter* present as small rugose bulge [S74]; femur with long posterior flange over proximal 1/2 of length [S74]; tibia length 80% of femur, with *cnemial crest* extending 1/3 shaft length, separated by broad flat region from *lateral condyle* [S74]; tibia flares distally to broad articulating surface (as broad as distal femur) for astragalus & calcaneum [S74]; fibula with prominent *iliofibularis tubercle* [S74]; *croc-normal tarsus* [S74]; astragalus (anteroposteriorly?) shallow, with tibial *trochlea* & fibular articulations separated by a steep step, & bulbous anterior surface for metatarsal I [S74]; in articulation, astragalus & calcaneum line up so that fibular articulations of both are adjacent & form a sort of double ball & socket joint [S74]; calcaneum with posterior upturned "heel" [S74]; calcaneal tuber with lateral side concave & medial side convex [P93];*fourth tarsal* large, tetrahedral [1], with prominent rounded facet for metatarsal V [S74]; only distal tarsals III & IV present [S74]; pes with 5 digits [S74]; metatarsal II largest [S74]; metatarsals II-IV of similar length, with III somewhat slender and IV concave laterally and closely appressed to III [2] [S74]; metatarsal V widely separated, hooked, & with broad medial expansion [S74]; pes 1&2 robust [S74]; pes 3 longest [S74]; pes5 broad, flat & pointed laterally [S74]; phalangeal formula 2345(1-3) [S74]; dermal armor present as two paramedian rows of small, leaf-shaped, *imbricating* scutes, drawn to a point anteriorly, with these stems being overlapped by the next anterior scute [S74].

Notes: [1] Sill [S74] states at one point that distal tarsal IV is "subtriangular" [S74: 322]and elsewhere that it is "tetrahedral" [S74: 346]. His photograph suggests that the latter is correct. [2] That is, the metatarsals approach the *arctometatarsalian* condition of certain theropods. [3] "[p03]" refers to our own analysis of published data.

Links: UTDMG--Saurosuchus galilei.

References: Alcober (2000) [A00], Benton (1984) [B84], Bonaparte (1971) [B71], Gower (2002) [G02], Parrish (1993) [P93], Sill (1974) [S74]. MAK991019, ATW031128.

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

checked ATW060119

Archosauria: Rauisuchiformes: Prestosuchidae (2)

Ticinosuchus & *Batrachotomus*

Abbreviated Dendrogram

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ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     |  |--Saurosuchus
                  |     |  `--+--Ticinosuchus
                  |     |     `--Batrachotomus
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
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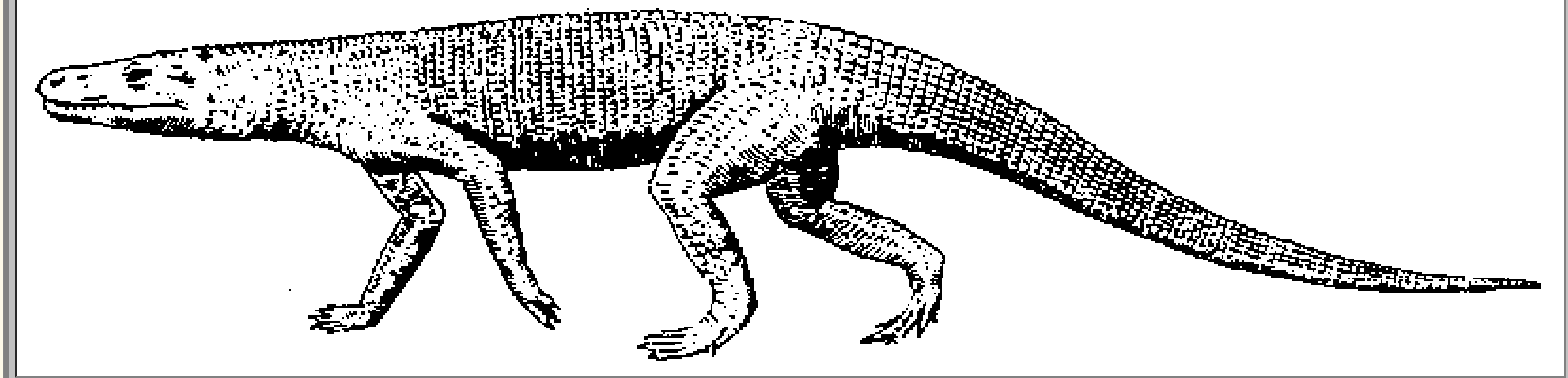
Contents

Taxa on This Page

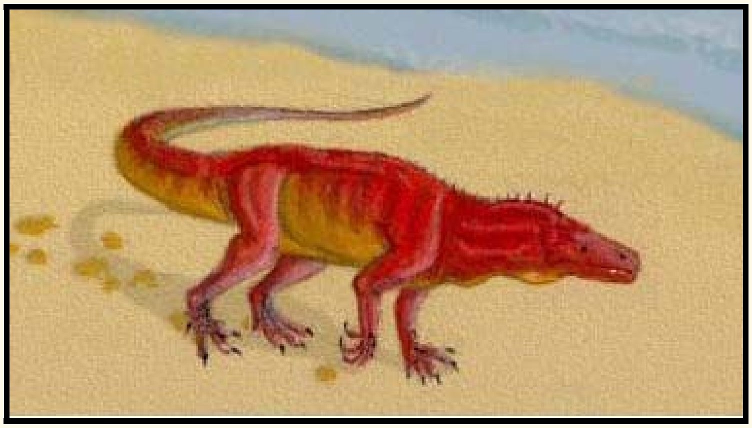
1. *Batrachotomus* X
2. *Ticinosuchus* X

Descriptions



Ticinosuchus *ferox* as it may have appeared in life, length about 2.5 meters. Anisian/Ladinian of the north Tethys shoreline. These animals, collectively called Rauisuchia or Prestosuchidae, seem to represent the central line of archosaur evolution during the Middle Triassic. They were active, terrestrial, carnivorous animals with an efficient fully erect gait; not unlike a sort of terrestrial crocodile which erect rather than sprawling (semi-erect) stance. Whilst some like *Ticinosuchus* were modest-sized animals, others attained as much as 6 meters or more in length. Because of their terrestrial lifestyle, and because big predators tend to be less common than herbivores and smaller animals, the "Prestosuchia" are poorly represented in the fossil record, and the precise phylogenetic relationships of the group remain disputed. Image in A. H. Müller, *Lehrbuch der Paläozoologie*, p.296, after Krebs 1965.

***Ticinosuchus*:** *T. ferox* Krebs, 1965; "*Mandasuchus*"



Range: Middle Triassic (Anisian and Ladinian) of Europe and Africa

Phylogeny: Prestosuchidae **::** *Batrachotomus* + *.

Comments: A partial skeleton of *Ticinosuchus ferox* is known from the Grenzbitumenzone (Anisian-Ladinian boundary), Tessin River, near Monte San Giorgio, Canton Tessin, Switzerland. However, this animal is also known from the Ladinian of northern Italy. At 2.5 metres it filled the medium terrestrial predator niche. Fossilized footprints called *Chirotherium* "hand beast" have also been found. They were probably left by an animal very like this one.

Characters: vertebral intercentra absent [P93]; cervical vertebrae elongate [S74]; calcaneal tuber with lateral side concave & medial side convex [P93]; rotary, crurotarsal ankle joint present [P93]; one pair of paramedian armor plates per vertebral segment [$P93].

Image: *Ticinosuchus*, courtesy (not to mention considerable tact and patience) of Daniel Bensen.

Links: Ticinosuchus (German)

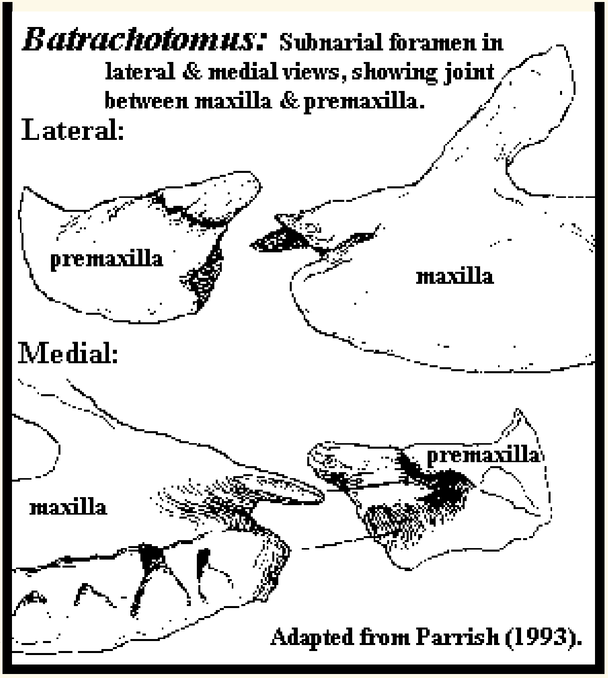
References: Parrish (1993) [P93], Sill (1974) [S74]. MAK991019 and 030808, ATW031129.

***Batrachotomus*:** *Batrachotomus kupferzellensis* Gower

Range: Late Ladinian (Lettenkeuper) of Germany

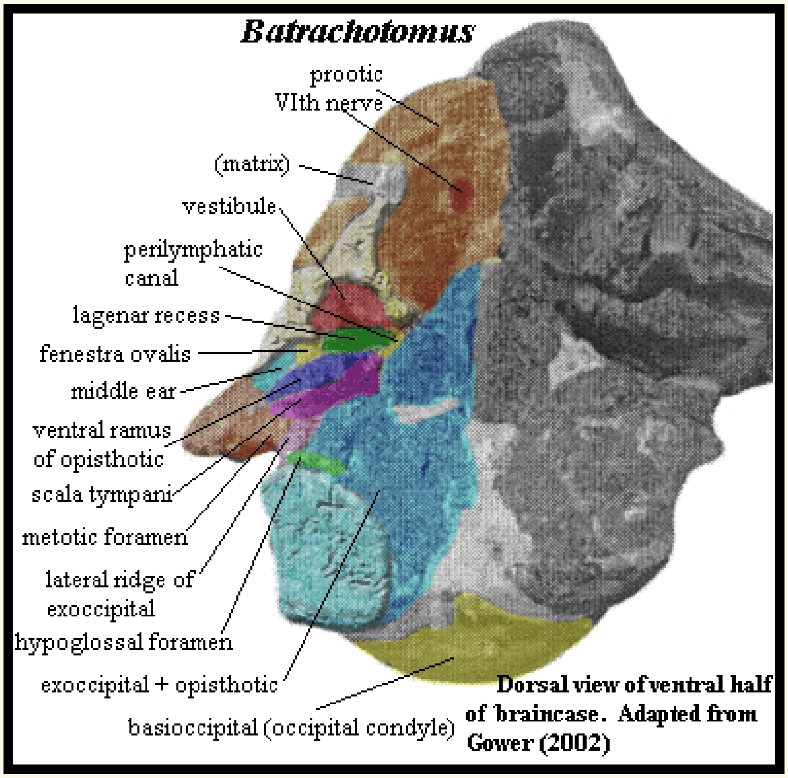
Phylogeny: Prestosuchidae **::** *Ticinosuchus* + *.

Comments: The dominant predator of the Lower Keuper environment, *Batrachotomus* was an enormous animal, up to 6 meters long (the size of *Saurosuchus*) It is well-known by teeth, partial skeletons and cranial material, and resembled other large archosaurs like *Ticinosuchus*, *Saurosuchus*, and *Postosuchus*. Cladistic analysis by Benton & Walker (2002) gives a very close relationship between *Batrachotomus* and *Prestosuchus*, with *Saurosuchus* as the sister taxon of these two. This species may therefore be included within a monophyletic Prestosuchidae, or as a very close sister group.



Adapted from Parrish (1993).

Characters: subnarial foramen with joint between maxilla & premaxilla [P93] **[1]**; jugal excluded from antorbital fenestra [**p**$03]; basioccipital forming almost all of occipital condyle [G02]; two pairs of basal tubera on basioccipital [G02]; basioccipital almost or entirely excluded from *foramen magnum* [G02]; supraoccipital triangular & much wider than long, forming dorsal border of foramen magnum [G02]; supraoccipital, dorsal surface with median ridge and depressed lateral facets for parietals [G02]; supraoccipital with posterolateral processes overlapping paroccipital processes [G02]; exoccipitals & opisthotics fully fused [G02]; exoccipital with large vertical *crista* forming posterior margin of *metotic foramen* [G02]; *hypoglossal foramen* anterior to crista [G02] **[2]**; paroccipital processes short & strongly expanded distally [G02]; metotic foramen not subdivided **[3]** [G02]; *epiotic* present as thin, irregular strip adjacent to supraoccipital facets for parietals [G02]; inner ear with moderately well-developed *lagenar* recess and ventral opisthotic ramus separating *scalae vestibuli & tympani* (see image **[4]**) [G02]; lagena not partitioned from remainder of scala vestibuli (in contrast to crocodylomorphs) [G02]; additional foramen (posterior cephalic vein?) passing into dorsal end of metotic foramen [**p**$03]; epiotic, prootic & opisthotic meet in Y-shaped suture medial to vestibule [G02]; perilymphatic foramen (into *rec. scala tympani*) small compared to crocs & aetosaurs [G02]; *crista prootica* slight [G02]; basisphenoid bends ventrally anterior to otic capsule [G02] **[5]**; deep, blind, undivided basioccipital recess on ventral surface between tubera, possibly homologous to crocodylian *median eustachian foramen* (which communicates with pharynx) [G02]; basisphenoid strongly waisted between tubera and *basipterygoid processes* [G02]; entrance of *internal carotid artery* on lateral face of basisphenoid in notch between *basal tubera* of basisphenoid & basipterygoid process [G02]; *Vidian canal* absent [G02]; external foramen for exit of abduscens nerve on underside of horizontal surface [**p**$03] **[6]**; *trigeminal foramen* at least partially divided by prootic from foramen for middle cerebral vein [**p**$03]; laterosphenoid probably long and thin [G02]; vertebral intercentra absent [P93]; rotary, *crurotarsal* ankle joint present [P93].



Dorsal view of ventral half of braincase. Adapted from Gower (2002)

Notes: **[1]** Note the surprising reappearance of this character, which one associates with more basal taxa, such as the Proterosuchidae or perhaps the Ornithosuchidae. **[2]** The point is important, since it differentiates *Batrachotomus* from the Suchia. **[3]** For the significance of this, see discussion at the **Inner Ear**. The subdivision in question splits the metotic foramen into a *vagus foramen* (nerve exits) and a separate *fenestra pseudorotunda* of the *recessus scala tympani*. **[4]** it may help to copy the image and magnify it about 4X. **[5]** This effect has been exaggerated by preservational artifact, and its hard to tell how seriously we may take Gower's [G02] description of the fossil (entirely accurate as far as we know) as a description of the living animal's skeleton. He does not provide a reconstruction. **[6]** "[**p**03]" refers to our own analysis of published data.

Reference: Gower 2002 [G02], Parrish (1993) [P93]. ATW031122.

Page Back Unit Home Page Top Page Next

checked ATW060119

Archosauria: Derived Rauisuchia

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     |--Doswellia
                  |     `--+--Rauisuchidae
                  |        `--Poposauridae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

1. *Doswellia* X
2. Poposauridae X
3. Rauisuchidae X

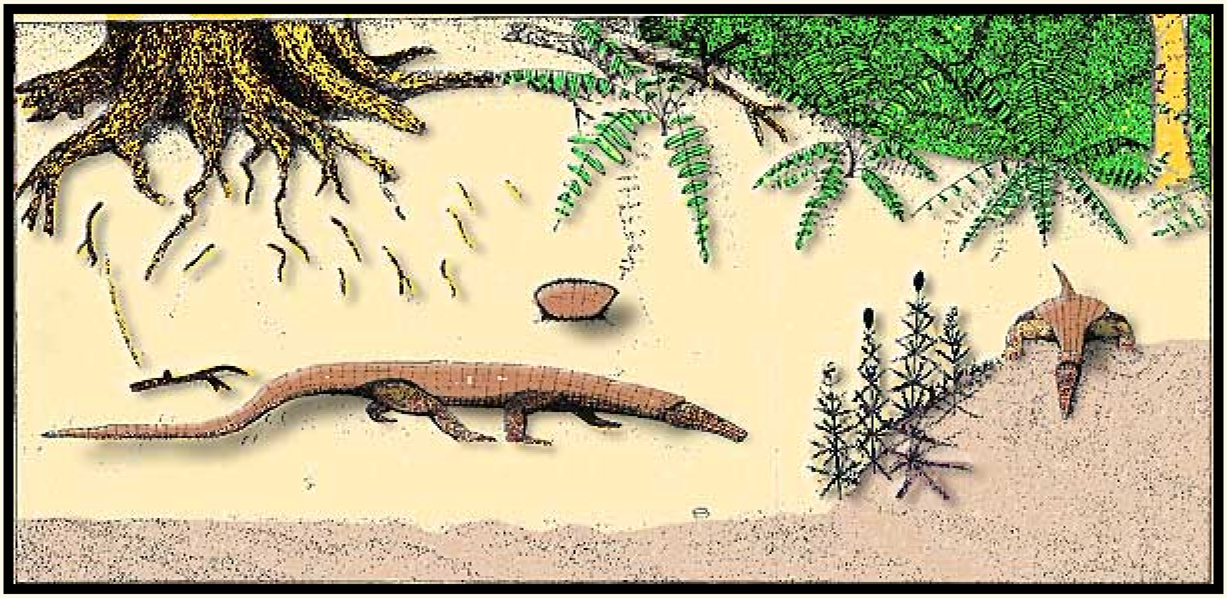
Doswellia

So, what is this silly-looking thing and what is it doing between the theropod-like prestosuchids and the equally ferocious-looking rauisuchids? Perhaps its some kind of anachronistic cross between an aetosaur and an armadillo. Truthfully, neither we nor anyone else has a firm idea. Its not even completely clear that *Doswellia* is an archosaur. It has palatal teeth and not a trace of a lower temporal fenestra. It may or may not have an antorbital fenestra, since that part of the skull is unknown. So are the critical ankles. The pelvis is not much like other archosaurs. The dorsal ribs are not much like any other known tetrapod. Although bits and pieces of *Doswellia*-like material (mostly scutes) are widely known, only one (or one and a half) articulated skeletons have been recovered.

Generally speaking, it has enough archosaur-like characteristics that it is probably an archosaur. But, as we saw with

Ornithosuchus and *Sinraptor*, appearances can be quite deceptive in the absence of firmly established synapomorphies. At least one, and perhaps two, new*Doswellia* papers are said to be in process, so nothing much is gained by speculating. We will simply have to wait and see. ATW040130.

Descriptions

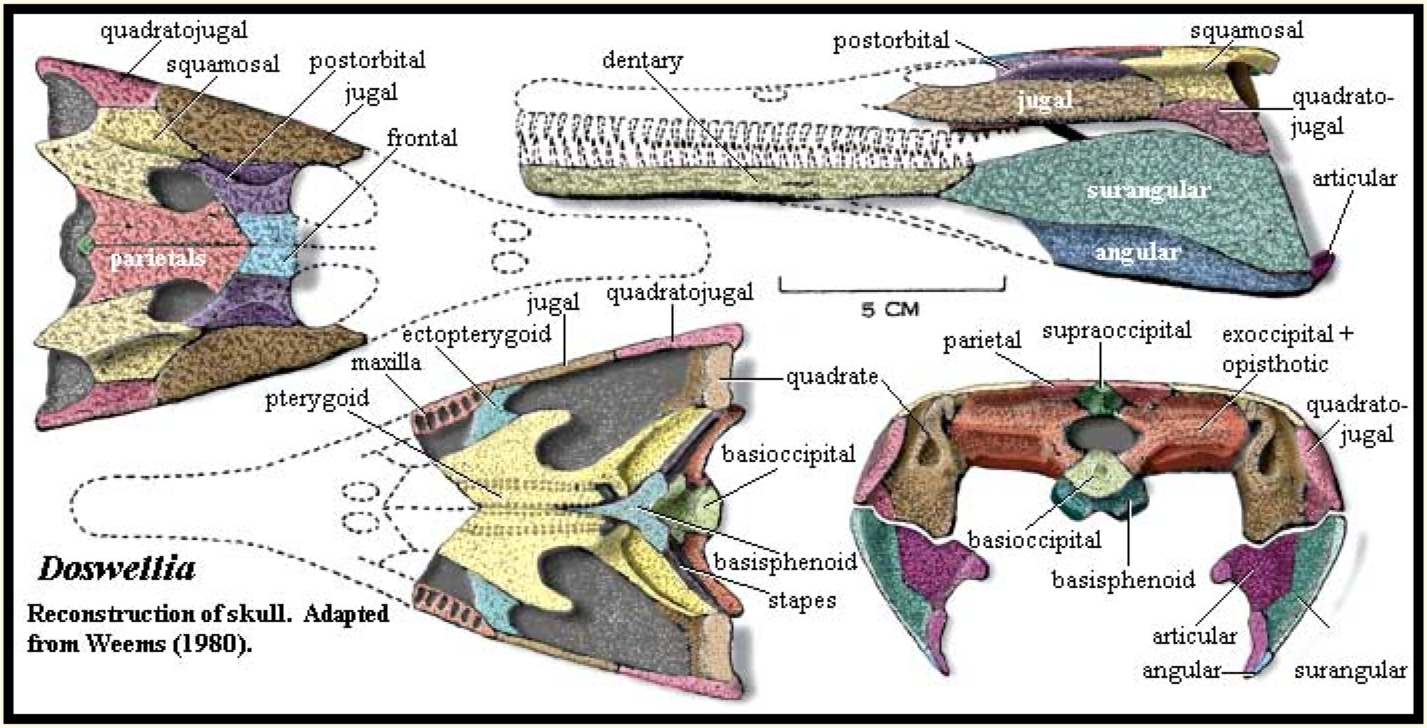


***Doswellia*:** *D. kaltenbachi* Weems, 1980.

Range: Late Triassic (Carnian) of North America (Eastern US)

Phylogeny: Rauisuchia ::: (Rauisuchidae + Poposauridae) + *.

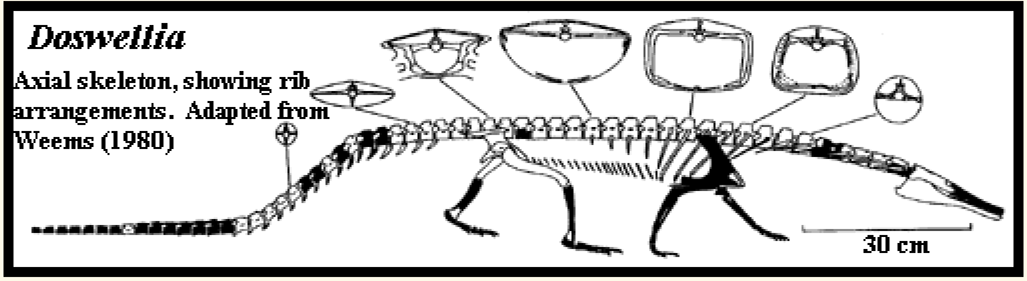
Characters: ~2 m, with head 15 cm [W80]; skull sculptured, akinetic [W80]; narrow, elongate rostrum [W80]; subnarial fenestra absent (reversal) [**p**$03]; orbits dorsal & closely spaced [W80]; frontals & parietals very narrow [W80]; postfrontal absent [**p**$03] [W80]; postparietals absent [W80]; occipital margin of skull indented on either side of midline [W80]; jugals expanded & enlarged; postorbital-jugal bar with distinct "step" [**p**$$$03]; lower temporal fenestra reduced & triangular, or absent entirely [**p**$$03] (completely absent and cheek bones tightly sutured in *Doswellia* [W80]); squamosal overhangs quadrate & quadratojugal but excluded from lower temporal fenestra [**p**$$03]; squamosal, postorbital & parietal surround *UTF* [W80]; squamosals form prominent posteriorly-directed "horns" [W80]; quadratojugal participates in jaw joint [W80]; quadrate with prominent otic notch [W80]; quadrate wide & massive, with anterior process along quadrate ramus of pterygoid **[3]** [W80]; supraoccipital with small, posteriorly projecting exposure on skull table [W80]; exoccipitals close, but not in contact dorsal to *foramen magnum* [**p**$03]; exoccipitals & opisthotics fused in paroccipital process [W80]; paroccipital processes dorsoventrally narrow & without great distal expansion [**p**$03]; posttemporal fenestra reduced to foramen [**p**$$03] (in fact



Doswellia

Reconstruction of skull. Adapted from Weems (1980).

absent [W80]); depression for posterior tympanic recess on anterior face of paroccipital process [**p**$03]; stapes lies in well-developed quadrate notch [W80]; stapes with elliptical foot plate & without arterial foramen [W80]; *dorsum sellae* bears prominent *clinoid processes* which partially encircle the *trigeminal* foramen [W80]; basipterygoid process surrounded by pterygoids [W80]; ventral epipterygoid plate ossified and sutured to pterygoid plate [W80]; laterosphenoid absent & no other ossified braincase elements anterior to basisphenoid [W80]; *interpterygoid vacuities* absent [W80]; pterygoid flanges wide & thin [W80]; articular with dorsomedial process on posterior end [**p**$03]; dentaries fused at symphysis, with bulbous expansion anteriorly [W80]; jaw deep posteriorly [W80]; articular & angular both contribute to jaw articulation [W80]; surangular convexly curved on dorsal margin, matching opposite curvature of jugal and quadratojugal [W80] **[4]**; articular forms wide socket for quadrate, strongly restricting lateral mobility of the jaw [W80]; *retroarticular process* prominent [W80] **[5]**; palatal teeth present (reversal) [**p**$03]; pterygoid with three rows of short, blunt teeth [W80]; marginal teeth *thecodont*, *homodont* & probably recurved [W80]; dentary with 33 tooth positions, becoming progressively smaller posteriorly [W80]; body elongate and flattened [W80]; vertebral count 8?+14+3 [W80]; centra *amphicoelous* [W80]; cervical neural spines low anteriorly, rising rapidly [W80]; neck elongate [W80]; cervicals elongate & without ventral keel or intercentra [W80]; cervical ribs present, very wide, but thin, with short necks [W80]; cervical ribs with sharp posterior bend, posterior arm having rugose area for armor attachment [W80]; presacral & 1st sacral ribs 2-headed, others single-headed [W80]; anterior dorsal ribs with abrupt, almost right angle, ventral bend with dorsal knob at point of flexure [W80]; unique rib articulation in which posterior dorsals have extremely elongate transverse tubercular facets with ventral groove to accommodate rib [W80]; large, massive ventral rib elements, probably articulating with distal ends of dorsal ribs, in addition to gastralia [W80]; 3+ sacral vertebrae [**p**$03]; 1st caudal ribs arcuate, with long contact on posterior border of ilium [W80]; tail broad with a sharp down-flexure in the 8th caudal (Weems speculates an armadillo-style defense mechanism) [W80]; proximal caudals with ribs, distal caudals with fused ribs or transverse processes [W80]; chevrons short [W80]; clavicle sharply angled [W80]; interclavicle cruciate, fairly long, & flat [W80]; forelimbs unknown [W80]; ilea flare broadly anteriorly & posteriorly [W80]; pubis & ischium plate-like, with ventral curve distally but quite short [W80]; small fenestra between pubis & ischium, but obturator foramen separate [W80]; acetabulum large, deep, round & open ventrally [W80]; femur sigmoidal, head probably cartilaginous [W80]; *4th trochanter* present but weakly developed [**p**$03]; armor laterally and dorsally, but not ventral [W80]; at least 10 parallel longitudinal columns of plates posteriorly [W80]; osteoderms sculptured [**p**$03]; osteoderm sculpture of scattered pits, somewhat like aetosaurs [W80]; armor plates sutured medially & laterally [W80]; plates *imbricated* except *nuchal* plate and suturally articulated sacral plates [W80]; nuchal plates "strikingly" similar to turtles [W80]; paramedian osteoderms with longitudinal bend near lateral edge [**p**$03]; osteoderms have elongate dorsolateral eminence as in Euscolosuchus [S92]; overlapped, anterodorsal area separated from remainder of osteoderm by distinct sulcus [S92]; .



Doswellia

Axial skeleton, showing rib arrangements. Adapted from Weems (1980)

Note: **[1]** There are suggestions on the web that a couple of new *Doswellia* papers are in the works. **[2]** "[**p**03]" refers to our own analysis of published data. "[**p**$$03]" indicates a synapomorphy of the clade uniting *Postosuchus* and *Doswellia*. "[**p**$$$03]" indicates a synapomorphy of the clade including Postosuchus, *Doswellia*, and Prestosuchidae. **[3]** This is also found in *Ornithosuchus*. Weems notes that the jaw was locked in position and would have had essentially no lateral mobility. **[4]** This appears to be another variant of the large shelf found in, *e.g.*, *Erpetosuchus*. **[5]** Actually, it isn't prominent at all; but that's what Weems says.

Links: BIOTIC PROVINCIALITY OF THE LATE TRIASSIC EQUATORIAL HUMID ZONE (assemblage); VOL. 27, NO. 4 (found in Pennsylvania); Revista geol ica de Chile - Redescripci del aetosaurio <I> ... (possibly similar form from Chile).

References: Sues (1992) [S92], Weems (1980) [W80]. ATW040104.

Rauisuchidae: *Fasolasuchus*, *Lotosaurus?*, *Rauisuchus*. Early competitors of the dinosaurs, with more erect gait than most in the croc lineage. Quite possibly includes the Early Triassic (Olneckian) [!!] Russian form, *Vytshegdosuchus* and possibly *Dongusuchus* [GS00].

Range: Early Triassic to Late Triassic of South America, Europe, North America, East Africa, India, Russia & China.

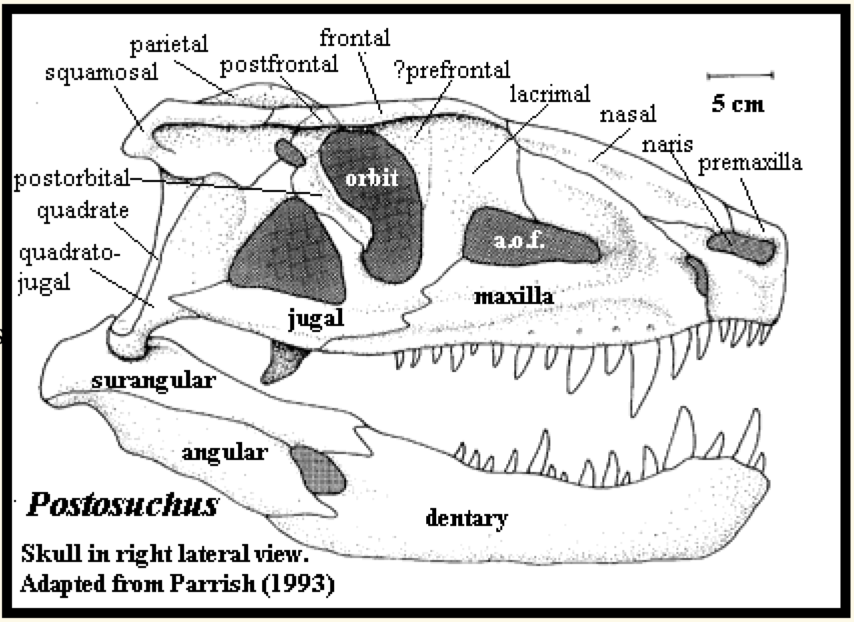
Phylogeny: Rauisuchia **::::** Poposauridae + *.

Introduction: The Rauisuchidae were one of a number of large predatory crurotarsan archosaurs that lived an active terrestrial lifestyle, probably more like theropod dinosaurs than standard reptiles. These were all large animals, and in some cases huge. The last known genus, *Fasolasuchus*, was as large as an allosaur or tyrannosaur, and preyed on contemporary melanorosaurid dinosaurs. So efficient were the rauisuchids in their office of top predator that no large (around 6 metres) dinosaurian predators evolved until the rauisuchids had become extinct. (MAK 981218)

Characters: Large (up to 6 m); skull tall & narrow; slit between maxilla and premaxilla, at least in juveniles [A00]; 3 sacral vertebrae; pubis and ischium more horizontal than vertical; *supraacetabular shelf* present (but rounded and without sharp crest) [$P93]; legs short but vertical; femoral head only slightly in-turned, but acetabulum re-oriented to come down over femoral head; as in Crocodylia, calcaneal tuber oriented posteriorly; laterally compressed foot; pes V reduced & no longer acts as lever (replaced by calcaneum); quadrupedal; dermal armor of 2 rows along trunk, above & below tail; plates linked by anterior processes; quadrupedal, terrestrial carnivores [B84].

Links: Lecture 10 - Triassic: Newark, Chinle; Untitled Document; Rauisuchia Translation and Pronunciation Guide Introduction; Postosuchus Printout- ZoomDinosaurs.com.

References: Alcober (2000) [A00], Benton (1984) [B84], Gower & Sennikov (2000) [GS00], Parrish (1993) [P93]. ATW031214.



Postosuchus
Skull in right lateral view.
Adapted from Parrish (1993)

Poposauridae: *Bomsgroveia*, *Poposaurus*, *Postosuchus*, *Teratosaurus*.

Range: Middle Triassic of North America.

Phylogeny: Rauisuchia **::::** Rauisuchidae + *.

Introduction: The Poposauridae were large carnivores closely related to the Crocodylomorpha (crocodiles and their kin). At least some forms were bipedal or capable of bipedal locomotion, much like the large theropod dinosaurs of the Jurassic and Cretaceous. One paleontologist has even suggested that the poposaurs were directly ancestral to the tyrannosaurs. Chatterjee (1985). Certainly there are a number of extraordinary similarities between the two, as indicated for example by the form of the skull and pelvis (hip-bone). Chatterjee's conclusion has been rejected by his co-workers, who point out that *Postosuchus* had a crocodile-like, rather than a dinosaur-like, wrist/ankle structure. Murry (1986). What seems more likely is that creatures like *Postosuchus* were an example of parallel evolution, the same kind of creature evolving to fill the same ecological role; a morphogenetic preview of the large theropod archetype of the great dinosaurian carnivores of the later Mesozoic. (MAK991017).

Characters: subnarial fenestra present (synapomorphy of Rauisuchia) [**p**03]; descending process of prefrontal absent [**p**$03]; descending process of squamosal anterior to quadrate absent [**p**$03]; exoccipital extends further laterally than ventral ramus of opisthotic [**p**$03]; exoccipital with lateral crest lying anterior to *hypoglossal foramen* [**p**$$$03]; additional foramen (posterior cerebral vein?) passing into dorsal surface of *metotic foramen* [**p**$03]; enlarged basipterygoid process [A00]; parasphenoid rostrum becomes dorsoventrally expanded wedge [**p**$03]; accessory hyposphene-hypantrum vertebral articulations [**p**$03]; clavicle reduced or absent [**p**$03]; interclavicle absent [**p**$03]; acetabulum open ventrally [**p**$03]; acetabulum semi-perforate [**p**$03]; prominent *supraacetabular shelf* [$P93]; pubis length >3x width of acetabulum [**p**$03]; large, posteroventrally projecting pubic boot [$P93] [**p**$03]; femur anteroposteriorly flattened, with wide, flat *4th trochanter* extending over most of width of posterior surface [$P93]; calcaneal tuber, distal end with dorsoventrally aligned median depression [**p**$$$03]; pes V absent [**p**$03] [**p**$$$03]; some members bipedal [B84].

Notes: [1] "[**p**03]" refers to our own analysis of published data. "[**p**$$03]" indicates a synapomorphy of the clade uniting *Postosuchus* and *Doswellia*. "[**p$$$**03]" indicates a synapomorphy of the clade including *Postosuchus*, *Doswellia*, and Prestosuchidae. **[2]** The acetabulum of *Doswellia* is closed ventrally, but only weakly, and the peculiar shape suggests that this may well be secondary.

Links: WWD: Postosuchus.

References: Alcober (2000) [A00], Benton (1984) [B84], Parrish (1993) [P93]. MAK000421.

Page Back | Unit Home | Page Top | Page Next

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Other Suchia

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--+--Euscolosuchus
                        `--+--Gracilisuchus
                           `--+--Erpetosuchus
                              `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

1. *Erpetosuchus* X
2. *Euscolosuchus* X
3. *Gracilisuchus* X

The Road to Crocodylomorphs

Here, at last we come to the close relatives of the crocodylomorphs, where archosaur phylogeny becomes a bit more straightforward. The basal archosaurs, as we have seen, seem to fall into three basic morphotypes: (a) large, heavy predators, (b) small to medium-sized lightly built forms which were probably insectivores or carnivores, and (c) low-slung, heavily armoured tanks, including both herbivores and carnivores, often (but not always) associated with watery environments. The basal type seems to be (b), the relatively small, lightly-built form -- far from what we think of as the basic reptile type. Yet most undoubtedly basal forms, such as *Euparkeria*, *Scleromochlus*, and the Ornithosuchidae, all fall in that range. As Sereno (1991) first noted, there is no consistent trend away from that morphotype. Heavy pacers and croc-like sprawlers diverge from the stem with equal frequency.

The case is no different near the crocodylomorph boundary. ***Euscolosuchus*** and, to a lesser extent, ***Gracilisuchus***, appear to tend to the armored sprawler type. However, the sister of Crocodylomorpha, ***Erpetosuchus***, is a very light, very terrestrial form which looks like a sleek, streamlined ornithosuchid.

Euscolosuchus is known only from osteoderms and a few vertebrae. The osteoderms fit closely, overlap, and have a particularly elegant system of strong, but flexible interlocking grooves and projections. the dorsal osteoderms end in intimidating lateral spikes, rather like desmatosuchid aetosaurs. However, their shape and dimensions suggest an animal a good deal leaner than an aetosaur. The vertebrae have conventional, spool-like centra; but the neural arches are strongly specialized to support the armor plates. The dorsal end of the neural spines are broadened, forming a spinal table, and the transverse processes are broad and tilted to support the osteoderms ventrally.

Gracilisuchus was a tiny, lightly built archosaur. It has been variously interpreted through the years; originally as a primitive ornithosuchid by Romer (1972) and Bonaparte (1975), then as a possible crocodylomorph by Brinkman (1981), as a basal member of the Crocodylotarsi Benton & Clark, 1988 (between Parasuchia and Stagonolepididae), and as the sister to the Poposauridae + Crocodylomorpha by Parrish 1993. By contrast, Juul (1994) found *Gracilisuchus* to be the sister of *Postosuchus* which in turn was a sister taxon to the Crocodylomorpha (as part of the "Paracrocodylomorpha"). Gower & Wilkinson (1996) placed it in an unresolved trichotomy with *Postosuchus* and the Crocodylomorpha; while Benton & Walker (2002) concluded that it was outgroup to the clade consisting of *Postosuchus* + *Erpetosuchus* + Crocodylomorpha. The consensus therefore is to place it within the general Crocodylomorpha-and-friends lineage. As such, it is the earliest known member of the clade. Interestingly, if Romer's original suspicion was correct and *Gracilisuchus* is a basal ornithosuchid, that would indicate the validity of Juul 1994's Dromaeosuchia, with *Gracilisuchus* as a transitional form between (and near the common ancestor of) the Ornithosuchidae and Paracrocodylomorpha.

The best known of this group, and perhaps closest to the Crocodylomorpha, is *Erpetosuchus*. It shares a number of rather specific characters with the Crocodylomorpha. These include parietals which are completely fused along the midline, loss of the postfrontal, and formation of a fairly complete secondary palate. It also possesses some peculiar apomorphies including a deep "otic notch" and a maxilla and jugal that bend back under the skull. Many Crurotarsal have a ridge at the ventral margin of the skull, but *Erpetosuchus* is unique in the degree to which the marginal bones are bent back in towards the middle. It is hard to imagine *Erpetosuchus* with cheeks or jowls -- and it was certainly not an herbivore -- but the general arrangement does remind one of a hadrosaur. In addition, its orbits faced rather anterodorsally, an unusual arrangement for this part of phylospace. Unfortunately, the postcranial skeleton is not well known. It was a lightly built form with unusual, small, and nearly featureless circular coracoids. Thehind limbs are completely unknown.

It seems likely that the diversity of these smaller, lightly constructed Crurotarsi is undersampled. Since they seem to be the stem lineage from which more specialized forms developed, the remaining uncertainties of archosaur phylogeny are probably due to our broad ignorance of animals of this type. Unfortunately, Triassic Crurotarsi are not dug out with the frequency of Cretaceous dinosaurs. We may have to wait some time before the path of the tree is much clearer. ATW040131.

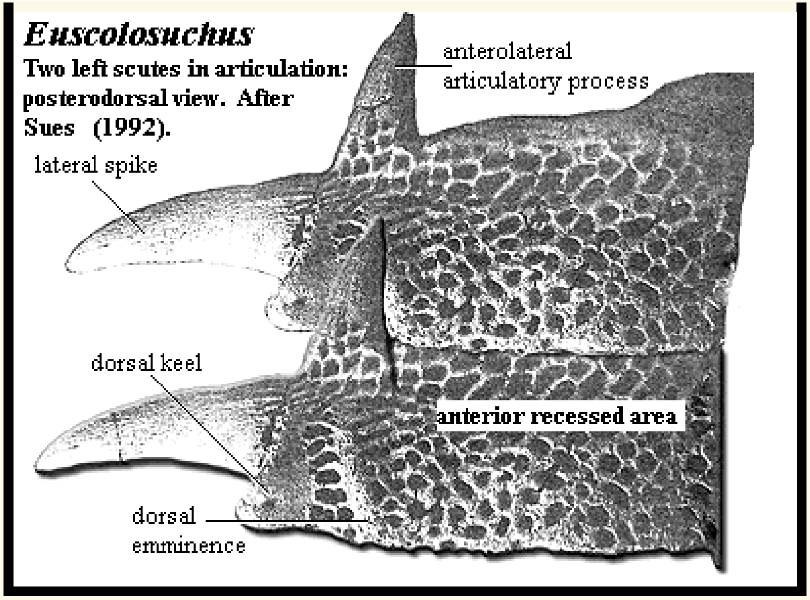
Descriptions

Euscolosuchus: *E. olseni* Sues 1992. **[2]**

Range: Late Triassic (middle Carnian) of North America (Eastern US)

Phylogeny: Suchia **::** (*Gracilisuchus* + (*Erpetosuchus* + Crocodylomorpha)) + *.

Characters: vertebral centra spool-shaped (slightly wider than tall) and small by comparison to neural arches [S92]; neural arches low & very wide [S92]; *postzygapophyses* widely spaced & overhang posterior surface of centrum & connected to transverse processes by thin lamina of bone extending out along the ventral


Euscolosuchus

Two left scutes in articulation: posterodorsal view. After Sues (1992).

side of the transverse process [S92]; transverse processes blade-like and axially expanded, with blade rotated ~20° so that dorsal surface faces anterodorsally [S92]; dorsal end of neural spine broadly expanded into a "spinal table" (presumably to support the osteoderms) [S92]; narrow dorsal carapace composed of *imbricating* pairs of *paramedian* osteoderms [S92] **[1]**; posterior cervical & dorsal osteoderms with lateral spikes [S92]; anterior1/3of each plate is set off by a step [S92]; each plate overlaps the plate posterior to it [S92]; each plate probably with anterolateral articulatory process [S92]; plates bear posterolateral dorsal eminence plus (lateral to the eminence) a much larger dorsal keel [S92]; ornamentation on osteoderms of deep pits [S92];

Notes: [1] this phrase, directly quoted from [S92], appears to be slightly inaccurate. The osteoderms do not overlap their *antimeres* across the midline. Rather, each plate overlaps the plate posterior to it on the same side of the backbone. **[2]** The genus is known only from scutes and a few fragmentary vertebrae [S92].

Image: This image has been significantly manipulated by us to illustrate how the osteoderms may have articulated.

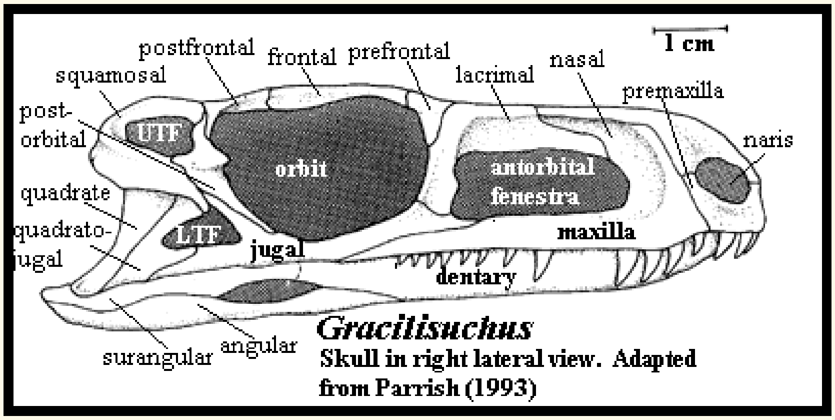
Links: BIOTIC PROVINCIALITY OF THE LATE TRIASSIC EQUATORIAL HUMID ZONE (crocodylomorph?); HUBER.

References: Sues (1992) [S92]. ATW040103.

Gracilisuchus: *G. stipanicicorum* Romer, 1972

Range: Middle Triassic (Ladinian) of Argentina

Phylogeny: Suchia ::: (*Erpetosuchus* + Crocodylomorpha) + *.



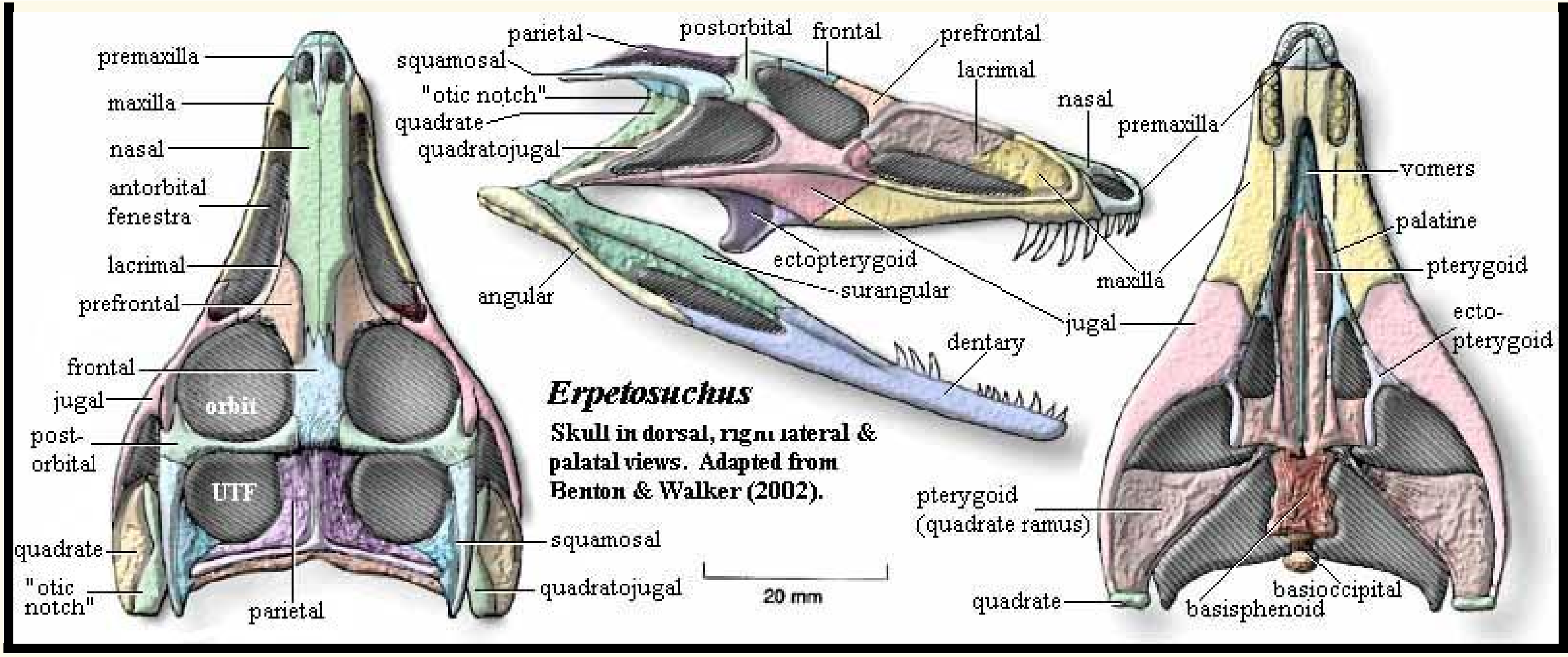
Gracilisuchus

Skull in right lateral view. Adapted from Parrish (1993)

Characters: subnarial foramen absent [P93]; facial exposure of maxilla longer posterior to antorbital fenestra [O+00] **[1]**; postfrontal present [O+00]; parietals partially fused [O+00]; sagittal crest absent [O+00]; occipital margin of parietals V-shaped in dorsal view [O+00]; midline ossification at rear of skull table (interparietal?) [P93]; jugal participates in posterior margin of antorbital fenestra [O+00] **[1]**; quadratojugal does not contact postorbital [O+00] **[1]**; squamosal does not overhang posttemporal region [O+00]; quadrate does not contact prootic [O+00]; paroccipital process dorsoventrally wide and broadly expanded distally [O+00]; articular lacks posterior dorsomedial projection [O+00]; vertebral intercentra absent [P93]; coracoid circular in lateral view [O+00]; femoral head confluent with shaft (no neck) [O+00]; tibia shorter than femur [O+00]; calcaneal tuber with lateral side concave & medial side convex [P93]; rotary, crurotarsal ankle joint present [P93].

Notes: [1] these are derived conditions per [O+00].

References: Olsen *et al*. (2000) [O+00], Parrish (1993) [P93]. ATW031214.



Erpetosuchus

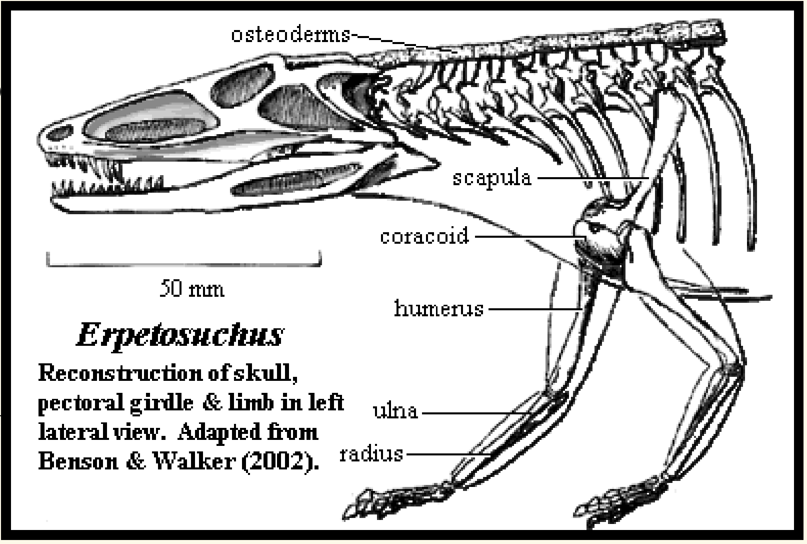
Skull in dorsal, right lateral & palatal views. Adapted from Benton & Walker (2002).

Erpetosuchus: *E. granti* Newton, 1894.

Range: Late Triassic (Carnian) of Europe (Scotland) & North America (Connecticut).

Phylogeny: Suchia :::: Crocodylomorpha + *.

Characters: skull ~7 cm [O+00]; skull low & wide [O+00] [BW02]; rostrum narrow [O+00] [BW02]; premaxilla short & facial exposure restricted to area around nares [BW02]; premaxilla, palatal exposure separated from maxilla by small notch and "step" [BW02] **[5]**; maxilla forming vertical suture with premaxilla [O+00]; premaxilla with straight sutures with antimere & maxilla [BW02]; exposure of maxilla anterior to front edge of antorbital fossa shorter than portion posterior to margin [**p**$03]; maxilla forms deep ventral border of antorbital fossa [BW02]; antorbital fenestra very large [W70]; deep antorbital fenestra, perimeter with distinct, angled bony ridge [$O+00] [$BW02]; maxilla facial exposure separated from palatal by distinct ridge [BW02]; lacrimal large, forming much of antorbital fossa & with thin sheet extending to orbit, nasals & prefrontal [BW02]; nasals smooth externally, with having interdigitating suture only with frontal [BW02]; prefrontal does not reach jugal [BW02]; postfrontals absent [O+00] (*compare* [BW02], treating postorbital/postfrontal as a fusion) **[2]**; postorbital as lateral bar between orbit & UTF [BW02]; parietals fused without trace of suture [O+00] **[2]**; sagittal crest present [O+00]; parietal with sagittal crest between supratemporal fenestrae [**p**$03]; parietals completely fused and without *parietal foramen* [BW02]; parietals sweep deeply into UTF [BW02]; occipital margin of parietals straight in dorsal view [O+00]; *UTF* circular & oriented dorsally [BW02]; orbit very large [O+00] [BW02]; orbits directed somewhat dorsally [BW02]; maxilla & lower jugal with strong longitudinal ridge such that ventral skull margin split into dorsally & ventrally facing surfaces [$O+00] [$BW02]; jugal triradiate **[1]** & deep below orbit [O+00]; jugal, infratemporal process tapers to a point posteriorly [O+00]; *LTF* triangular and large [BW02] [O+00]; squamosal with small descending process meeting quadratojugal [W70]; squamosal with ridge bordering supratemporal fenestra dorsally [**p**$03]; squamosal with deep & superficial portions, with deep portion meeting quadratojugal and parietal [BW02]; quadratojugal lying behind quadrate, with minor lateral exposure [W70]; quadratojugal with long dorsal process along posterior margin of lower temporal fenestra [O+00]; quadratojugal contacts postorbital [O+00]; quadrate & quadratojugal steeply inclined anterodorsally [O+00]; quadrate & quadratojugal fully visible in dorsal view [BW02]; quadrate visible in lateral view [**p**$03]; distinct otic notch between squamosal and quadrate + quadratojugal [O+00] [$BW02]; paroccipital processes terminate on a ledge on posterior squamosal below parietal [BW02]; posttemporal fenestra probably fairly large between parietal and paroccipital process [BW02]; occipital condyle small [BW02]; basioccipital short [BW02]; braincase long & slender [BW02]; basisphenoid with long *basipterygoid processes* diverging from midline [BW02]; maxillae, palatal processes meet medially to form full secondary palate [O+00] **[2]**; dentary covers more than half lateral surface of lower jaw [BW02]; dentary with small grooves & pits anteriorly for blood vessels etc. [BW02]; dentary with trough on ventral part of medial surface to receive splenial [BW02]; lower jaw with long mandibular fenestra [O+00]; mandibular fenestra, dorsal margin continued as ridge posterior to fenestra [$O+00] [$BW02]; articular lacks posterior dorsomedial projection [O+00]; splenial large & thin, covering entire medial face anteriorly [BW02]; coronoid small or absent [BW02]; prearticular in far posterior of medial side (extent unknown) [BW02]; articular only visible on medial surface [BW02]; teeth conical, not laterally compressed [O+00]; teeth oval in cross-section, lacking carinae, or marginal serrations [$BW02]; reduced maxillary tooth row (4-5 teeth) restricted to area anterior to antorbital fenestra [$BW02]; maxillary tooth row deeply inset from margin [O+00]; dentary teeth in two clusters, 8 small teeth interlocking with premaxillary teeth & 3 large recurved fang-like teeth after long *diastema* [BW02]; cervicals strongly compressed laterally, with sharp ventral keel [BW02]; cervical zygapophyses and neural spines axially short [BW02]; cervical ribs slender (reversal) [**p**$03]; cervical rib articulations continuous [BW02]; dorsal ribs similar to cervicals [BW02]; interclavicle long, thin & slightly concave dorsally, coming to a point posteriorly [BW70]; scapula slender & strap-like, extending posteriorly as broad plate at proximal end [BW02]; substantial contact between scapula & coracoid but anterior scapulocoracoid notch is present [BW02]; coracoid circular in lateral view [O+00]; coracoid without medial constriction [W70]; coracoid without coracoid foramen or posterior process [BW02]; humerus generally straight, with slight lateral bow at mid-shaft [BW02]; humerus 38 mm, with narrow, curved, sheet-like *deltopectoral crest* ending just proximal to mid-shaft [BW02]; radius & ulna ~30 mm, somewhat flattened and straight, with little terminal expansion [BW02]; manus I most robust [BW02]; manus IV with <5 phalanges [**p**$03]; more than one pair paramedian scutes per vertebra [BW02] [**p**$03]; paramedian osteoderms with distinct longitudinal bend near lateral edge [**p**$03]; scutes with radiating sculpture of fine lines or small tubercles [BW02]; .



Erpetosuchus

Reconstruction of skull, pectoral girdle & limb in left lateral view. Adapted from Benson & Walker (2002).

Notes: [1] really pentaradiate, as stated in [BW02], since the anterior prong is split into antorbital and maxillary rami by the antorbital fenestra, and the palatal exposure is a large and entirely separate area. **[2]** According to [O+00], these characters are synapomorphies of the clade *Erpetosuchus* + Crocodylomorpha. **[3]** "[**p**03]" refers to our own analysis of published data. **[4]** According to our analysis, the synapomorphies of *Erpetosuchus* + Crocodylomorpha are: (a) postfrontal absent, (b) squamosal overhanging quadratojugal & quadrate but excluded from lower temporal fenestra, (c) maxillae meet on palate midline to form secondary palate, and (d) parietals completely fused. This is in general agreement with [O+00]. **[5]** This appears to be an intermediate condition between the usual smooth curve of the upper jaw and the jointed, fenestrated border between maxilla and premaxilla found in, *e.g.*, ornithosuchids and at least some prestosuchids. *See* detailed image of *Batrachotomus*. *Erpetosuchus* should perhaps be scored differently for this character than crocodylomorphs.

Links: RAPID COMMUNICATION FIRST RECORD OF ERPETOSUCHUS (REPTILIA- ...; Lecture 11 - Triassic-Newark, Chinle; OLSEN1; Fossil of crocodile with erect stance found; CROCODILE SPECIALIST GROUP NEWSLETTER 154E; November 10, 1996 Reconstructing a Galloping Crocodile After a ...; **中国公众科技网** (Chinese version of same story); ALBE R IANA T.

References: Benton & Walker (2002) [BW02], Olsen *et al*. (2000) [O+00]; Walker (1970) [W70]. ATW031229.

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

ATW031118

Archosauria: Suchia (Aetosauridae)

Aetosaurus, Coahomasuchus & *Stagnolepis*

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     |  |--Aetosaurus
                     |  `--"Stagonolepia"
                     |     |--"Stagonolepidinae"
                     |     |  |--Coahomasuchus
                     |     |  `--Stagonolepis
                     |     `--"Desmatosuchia"
                     `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

(names of taxa in "inverted commas" are suggested here and have not been formally recognized)

1. Aetosauridae X
2. *Aetosaurus* X
3. *Coahomasuchus* X
4. "Stagonolepia" X
5. "Stagonolepidinae" X
6. *Stagonolepis* X
7. Suchia

Introduction to the Aetosauria

***Stagonolepis scagliai*, a primitive aetosaur. Aetosaurs were an important component of the Late Triassic terrestrial biota. This species, which reached a length of 2.5 meters, was, like all its tribe, an herbivore that relied on its armour plating for protection against predators. Late Carnian of south-west Pangea (Gondwana). Drawing from *The Cambridge Encyclopedia of Life Sciences*, ed. Adrian Friday & David S. Ingram, © Cambridge University Press 1985.**

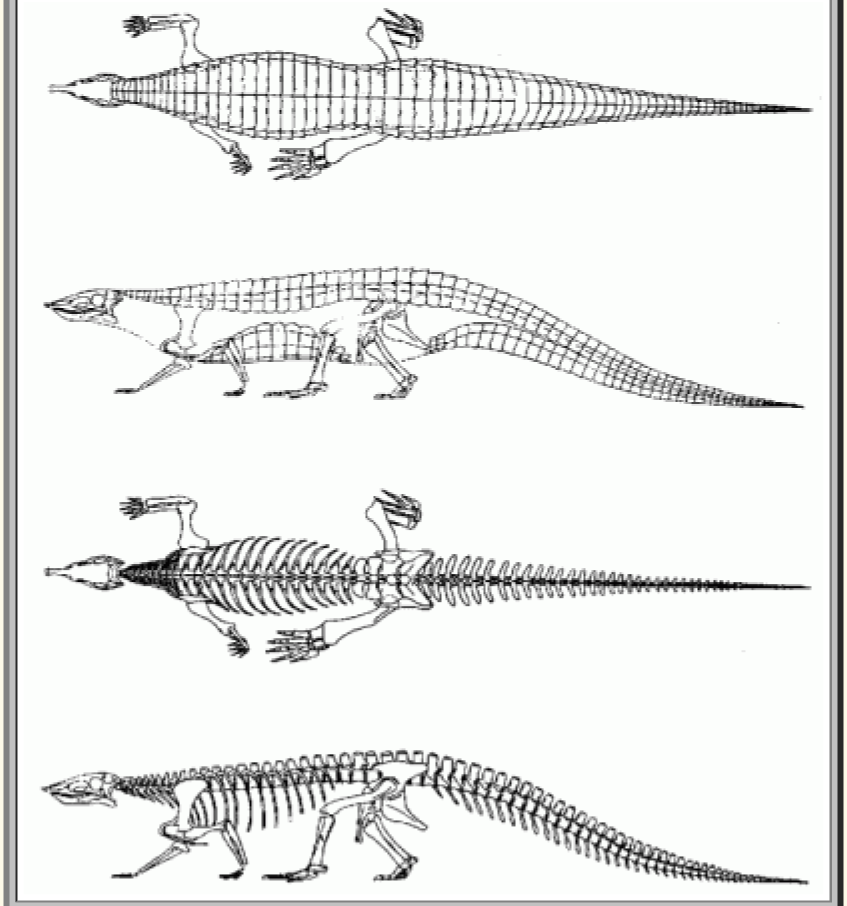
The aetosaurs, or Stagonolepididae, were large herbivorous armoured archosaurs, and an important characteristic part of Late Triassic faunas. Aëtosaurs ranged in size from less than 1 to 4 or 5 meters, the average size being between 2.5 and 3 meters. They flourished for almost entire extent of the Late Triassic. A number of types are known, the best known genera being ***Aetosaurus***, ***Stagonolepis*****,** and ***Desmatosuchus***. Their fossil remains have been found late Triassic rocks of Scotland, Germany, Argentina, and the United States, but these creatures most certainly had a world-wide distribution.

Like the phytosaurs and ornithosuchids, the aetosaurs appeared in the Late Carnian. They are clearly of Suchian stock, but their immediate ancestors have not yet been determined. They are not known from the purported early Carnian fauna of Madagascar (basal Isalo II [Burmeister *et al* 2000], but are prominent in the early late-Carnian faunas of North and South America. In all likelihood the aetosaurs evolved from prestosuchids, with which they share many common features of the skeleton. However, study of the braincase indicates -- at least in this respect -- they are more similar to crocodylomorphs than to other major suchian groups [Gower & Walker. 2002). Although the body and tail was typically crurotarsan (prestosuchian-crocodilian) in appearance, the head however is very different, having become quite small, the teeth chisel shaped, and the front of the snout flat and blunt, giving a sort of pig-like appearance.

These reptiles were exceedingly well armoured, even by archosaur standards. Their bodies protected by bony plates, including large, interlocking plates over the back, and sometimes spikes as well. All were quadrupedal, walking on four legs and probably relying on armour and (often) large size rather than speed to protect them from their enemies.

The small heads and weak, leaf-shaped chisel-like teeth indicate a herbivorous lifestyle. The teeth are leaf-shaped and chisel-like, very much of the sort that other plant eating reptiles have, indicating that they probably nipped off leaves and digesting them in their gut with the aid of symbiotic bacteria. Advanced forms (***Typothorax*** etc) especially had bulky bodies, indicating fermentation of plant material. However, it has recently been suggested [Small 2002] that an edentate-like lifestyle of feeding on insects may also be possible

Unlike the phytosaurs and basal archosauriformes, but as with other advanced archosaurs, for example dinosaurs and sphenosuchid crocodylomorphs, aetosaurs had a fully erect posture, with the hind limb held beneath the body. Aetosaurs are united with prestosuchids and rauisuchians in the horizontal orientation of their acetabulum. This seems to have been an adaptation for an erect posture, but it is not agreed whether or not it is a



***Stagonolepis robertsoni,* a typical aetosaur, top and side views, showing arrangement of armor plates (scutes) (above) and skeleton without armor (below). In life, this species looked very like the illustration at the right. Length 2.7 meters. Lossiemouth Beds, Elgin, Scotland, Late Carnian of north-central Pangea (Laurasia). Illustration in Krebs 1976.**

synapomorphy (shared common ancestral feature) or something that evolved a number of times among different reptilian lineages.

In overall lifestyle, the aetosaurs must have paralleled other herbivorous tetrapod "tanks": pareiasaurs of the Permian, or the armoured scelidosaur, nodosaur, and ankylosaur dinosaurs that were to appear and diversify in the succeeding Jurassic and Cretaceous periods; and even the armadillos and the giant glyptodontid edentate mammals of the South American Cenozoic era. As is often the case with evolution, we see an example of a particular form, evolving and flourishing for millions of years, then eventually dying out, to be replaced tens of millions of years later by another, unrelated line, which independently evolves the same basic form, and again flourishes before it too dies out, to be replaced again later by yet another evolutionary line.

Aetosaur scutes (bony armour plates) can be readily distinguished from scutes of other armoured Archosauria. They are characterized by a flat, rectangular shape, presence of an anterior articulating surface, and lack of anteriorly- or posteriorly- projecting lappets (Heckert *et al*, 1999). Different aetosaur genera have differently shaped scutes, and this can be used as a diagnostic feature (Heckert & Lucas 1999)

Aetosaur systematics is still controversial; a serious problem is the frequent lack of adequate material [Heckert & Lucas 2003]. There is even a disagreement over whether a certain species is a synonym of another species or a whole different genus! The following systematic arrangement therefore is extremely speculative and armchairish, and should not in any way be taken as a formal statement on aetosaur phylogenetics! (MAK 000608 and 030803).

Descriptions

Suchia: aetosaurs + crocs [P93]

Range: from the Early Triassic.

Characters: Rauisuchiformes **:** Rauisuchia + * **:** Aetosauridae + (*Euscolosuchus* + (*Gracilisuchus* + (*Erpetosuchus* +

Crocodylomorpha))).

Characters: quadratojugal contacts postorbital [$P93]; ventral ramus of squamosal short or absent, with triangular lower temporal fenestra [$S91] **[3]**; foramina for cerebral branch of internal carotid on lateral surface of basisphenoid [$G02] **[1]**; occipital margin of parietals straight in dorsal view [**p**$03]; exoccipital with clear lateral vertical crest anterior to *hypoglossal foramen* [**p**$03]; exoccipitals extend further laterally than ventral ramus of opisthotic [**p**$03]; ventromedial surfaces of exoccipitals do not meet on floor of cranial cavity [**p**$03]; elongate region between *fenestra ovalis* and posterior of occipital condyle [**p**$03]; perilymphatic foramen with completely ossified border [**p**$03]; perilymphatic foramen transmits *perilymphatic duct* out of otic capsule more laterally than posteriorly [**p**$03]; foramina for *trigeminal nerve* & middle cerebral vein at least partially separated by prootic [**p**$03]; tibial facet of astragalus with a prominent posteromedial excavation that forms a posteriorly directed concavity" [$P93] [**p**$03] **[2]**; osteoderms sculputred [**p**$03].

Notes: [1] synapomorphy of clade uniting Prestosuchidae with Suchia [G02]. **[2]** "[**p**03]" refers to our own analysis of published data. **[3]** Sereno posits this as a synapomorphy of a broader "Suchia" equivalent to our Rauisuchiformes less Onithosuchidae. As to this taxon, he is wrong, since the prestosuchids plainly have an extended ventral ramus of the squamosal. He may be correct that the rauisuchids and poposaurs do not. However, this appears to be more similar to the condition in *Doswellia* in which fenestration is reduced generally, the skull is flat, and the squamosal ventral process is absorbed into a broad, laterally-facing squamosal lamina. The state in Suchia is rather different: the temporal fenestrae remain large, and the squamosal simply lacks any significant ventral development.

Links: Lecture 10 - Triassic: Newark, Chinle.

References: Gower 2002 [G02], Parrish (1993) [P93], Sereno (1991) [S91]. ATW040117.

Aetosauridae: (= Stagonolepididae, Aetosauria): Armoured Suchia.

Range: Late Triassic (Late Carnian to Rhaetian) of North America, South America, Greenland, & Europe. (also, scutes known from Madagascar)

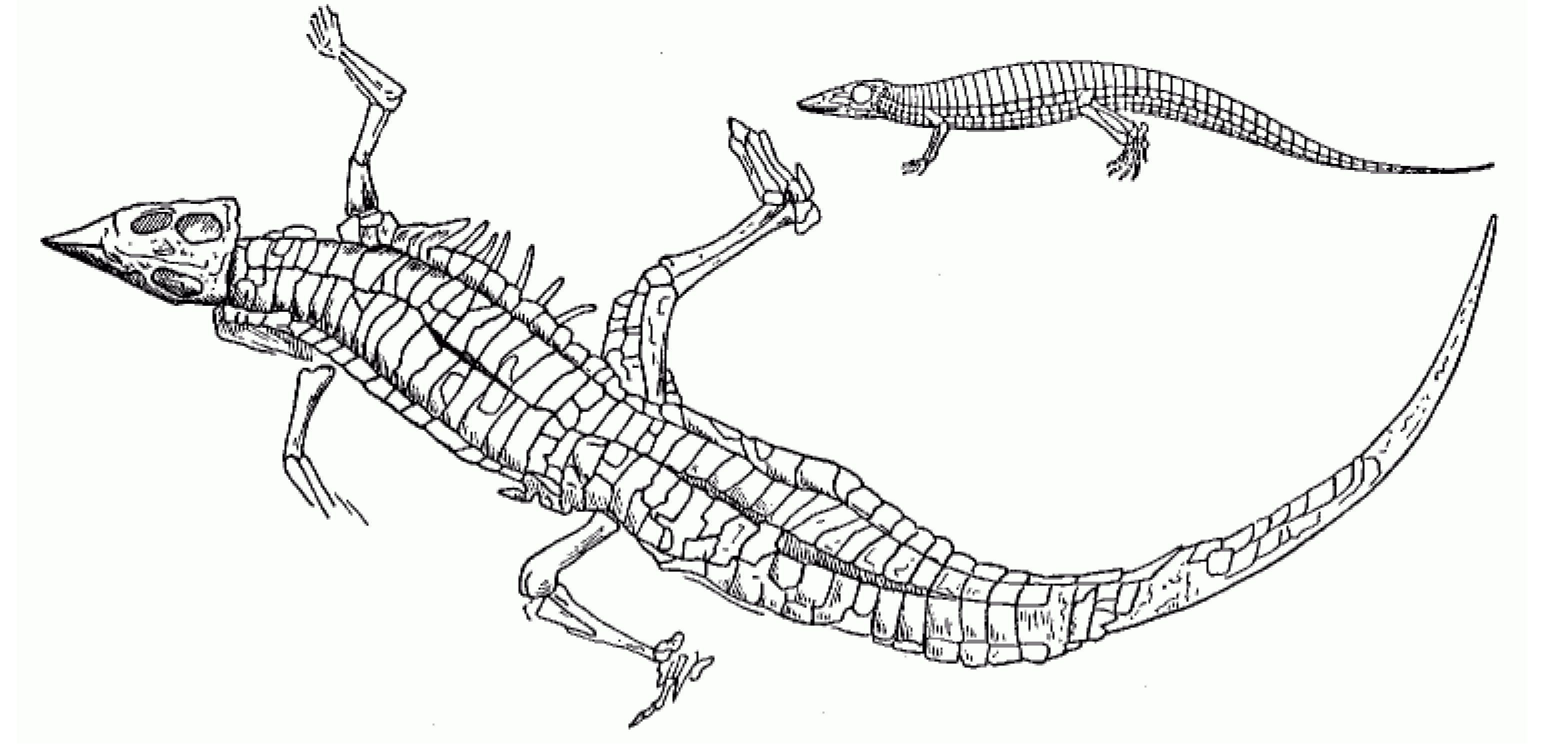
Phylogeny: Suchia **:** (*Euscolosuchus* + (*Gracilisuchus* + (*Erpetosuchus* + Crocodylomorpha))) + * **:** *Aetosaurus* + "Stagonolepia"

Characters: Small head; premaxilla upturned, anteriorly flattened [$P93]; premaxilla without teeth anteriorly [$P93]; descending process of prefrontal absent [**p**$03]; lower temporal fenestra reduced & triangular [**p**$03]; braincase similar to rauisuchian/crocodylomorph condition [GW02]; exoccipital with lateral crest lying anterior to *hypoglossal foramen* [$G02]; leaf-shaped teeth; teeth small & nearly conical [$P93]; herbivorous; limb bones very stout, with hypertrophied trochanters (*deltopectoral crest*, *4th trochanter*, intercondylar ridge of tibia & *iliofibularis trochanter*) [$P93]; manus IV with <4 phalanges [**p**$03]; pelvis generally primitive, but great ventral extension of pubis; pubis length <3x acetabulum width (reversal) [**p**$03]; acetabulum open ventrally [**p**$03]; femoral 4th trochanter absent [**p**$03] **[2]**; tibia distally expanded, with rectangular distal end [**p**$03]; crocodyloid tarsus with large calcaneal tuber; heavily armored; complete carapace with lateral & ventral armor [$P93]; scutes flat, rectangular, with anterior articulating surface, but anteriorly- or posteriorly- projecting lappets absent [H+99]; two pairs of *paramedian* dorsal osteoderms, with more dorsal series often bearing spines [S92]; paramedian scutes wider than long, sculptured, & without *lappets* [$P93]; dorsal osteoderms with ornament typivally radiating from a boss near posterior margin [S92];

Notes: [1] "[**p**03]" refers to our own analysis of published data. **[2]** This directly contradicts [P93], as noted. The data used in our analysis for this character were taken from [B99].

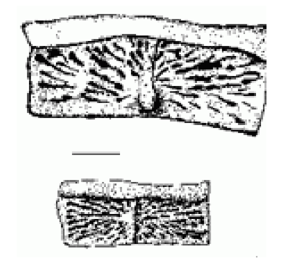
Links: Introduction to the Aetosauria (UCMP: **Best on the Web**); Aetosaur Introduction / Translation and Pronunciation Guide.

References: Benton (1999) [B99], Gower (2002) [G02], Gower & Walker 2002 [GW02], Heckert *et al*, 1999 [H+99], Parrish (1993) [P93], Sues (1992) [S92]. MAK030803, ATW031220.



***Aetosaurus ferratus*, a small and very primitive aetosaur, showing the complete animal as preserved, and a reconstruction of skeleton and armor. Length 80 cm. Norian of central Pangea (Laurasia - today, Stubensandstein of Germany). Composite of two individuals figured by O. Fraas; small image restoration after Marsh. Note - the animal in life had a more erect posture than shown here. Image from Gregory 1951**

***Aetosaurus*:** (= Aetosaurinae): *Aetosaurus* O. Fraas, 1887



***Aetosaurus* dorsal view of paramedian plates, scale bar 1 cm from Lucas 1998.**

Range: Late Triassic (Early to Mid Norian) of North America, Greenland, & Europe. (also, scutes known from Madagascar)

Phylogeny: Aetosauridae **:** "Stagonolepia" + * **:** *Aetosaurus ferratus* + *Aetosaurus arcuatus*

Characters: Small (up to 1.5 meters); skull relatively large, triangular, acuminate in front. Orbit large; antorbital fenestra fairly large, separated from the nares by narrow ascending process of the maxilla. 25 presacral vertebrae; back completely covered with short and broad bony plates; dorsal and ventral armor of radially ornamented scutes, ventral scutes smaller than dorsal ones, almost square in shape. [Zittel, 1932]

Comments: A widespread early-middle Norian index fossil [Lucas 1998], known from Eastern USA (Newark Supergroup) the German Middle Keuper, Italy and Greenland. According to Harris *et al* 2003, *Aetosaurus* is the sister taxon of all known aetosaurs

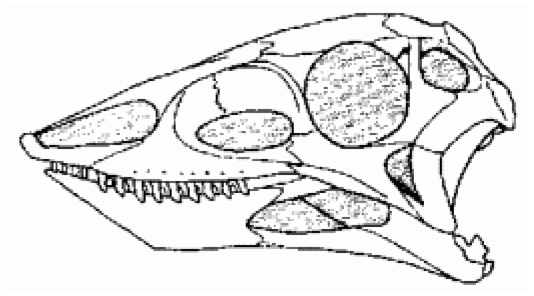
Links: Aetosaurus sketch.

***Aetosaurus ferratus*:** Western Aetosaurus - *Aetosaurus ferratus* O. Fraas, 1887

Range: Late Triassic (Early to Mid Norian) of Europe. (Germany & Italy)

Phylogeny: *Aetosaurus* **:** *Aetosaurus arcuatus* + *Aetosaurus crassicauda* + *

Characters: small (85 cm [Zittel, 1932] or 1.5 meters); scute with high W:L (Width to Length) ratio.



***Aetosaurus ferratus*, skull. Stubensandstein (Norian) of Germany**

Comments: Based on a slab of two dozen complete but slightly crushed individuals from the Stubensandstein, Middle Keuper, near Stuttgart [Zittel, 1932].

illustration in Krebs 1976, p.79.

Links: . Aetosaurus ferratus - University of Milan Vert Paleo page

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***Aetosaurus crassicauda*:** Western Aetosaurus - *Aetosaurus crassicauda* O. Fraas, 1887

Range: Late Triassic (Early to Mid Norian) of Europe. (Germany)

Phylogeny: *Aetosaurus* **:** *Aetosaurus ferratus* + *Aetosaurus arcuatus* + *.

Characters: small (1.5 meters in length); scutes with dorsal boss extending anteriorly past the middle of the scute as a longitudinal keel

Comments: from the Middle Keuper of Pfaffenhofen [Zittel, 1932]

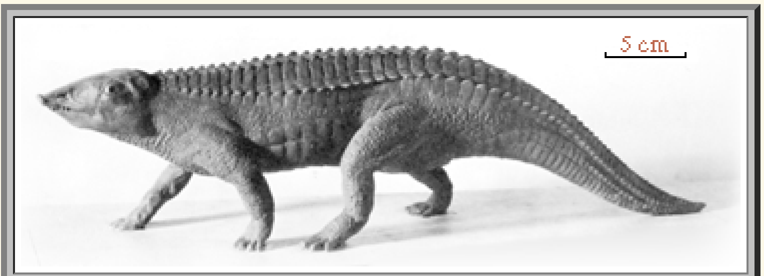
***Aetosaurus arcuatus*:** Eastern Aetosaurus - *Aetosaurus arcuatus* (= *Stegomus arcuatus* - [Heckert & Lucas, 1999])

Range: Late Triassic (Early to Mid Norian) of North America (New Jersey and Connecticut) & Greenland

Phylogeny: *Aetosaurus* **:** *Aetosaurus ferratus* + *Aetosaurus crassicauda* + *.

Characters: scutes more weaker sculpted [Creisler, 1996]

Comments: formerly known as *Stegomus*, and found in various localities of early or mid Norian age in the Newark Supergroup, this animal is now included in the genus *Aetosaurus* [Lucas 1998, Heckert & Lucas, 1999].



***Aetosaurus arcuatus*, model of animal. Newark Supergroup (Norian - equatorial Pangea). From Professor Paul Eric Olsen Lecture 11 - Triassic: Newark, Chinle; photo by Donald Baird of Rush Studio model.**

"Stagonolepia": = Higher Aetosaurs

Range: Late Triassic (Late Carnian to Rhaetian) of North America, South America, & Europe.

Phylogeny: Aetosauridae **:** *Aetosaurus* + * **:** "Stagonolepidinae" + "Desmatosuchia"

Characters:

aetosaurs more derived than *Aetosaurus* - ref Parrish, 1994, Harris *et al* 2003

Comments: Includes all higher aetosaurs, the majority of the family. There are two family names for the Aetosauridae Nicholson & Lydekker, 1889, Aetosauridae (ex Aethosauridae) Baur, 1887 and Stagonolepididae Agassiz, 1844 (see Re: quick dino-related question) Usually these families are considered synonymous, so that only the family Stagonolepididae is used. However, if *Aetosaurus* is given its own family ranking as Aetosauridae, then the clade Stagonolepia would correspond to the Stagonolepididae *sensu stricto*

"Stagonolepidinae": *Stagonolepis* > *Desmatosuchus*

Range: Late Triassic (Late Carnian) of North America, South America, & Europe.

Phylogeny: "Stagonolepia" **:** Desmatosuchia + *: *Coahomasuchus* + *Stagonolepis*

Comments: the less specialized of the higher aetosaurid clades. Although widely distributed, the stagonolepines did not survive the end of the Carnian. Corresponds to the "Stagonolepidini" of "Mikko's Phylogeny" [Aetosauria]

Coahomasuchus: *Coahomasuchus kahleorum* Heckert & Lucas, 1999

Range: Late Triassic (Early Late Carnian (Otischalkian)) of North America

Phylogeny: "Stagonolepidinae" **:** *Stagonolepis* + *

Characters: small (less than 1 meter); "dorsal paramedian plates considerably (3.25:1) wider than long, unflexed, lack keels or horns, and bear faint sub-parallel to radial ornamentation, and lateral scutes that are also unflexed, fiat, and bear a faint radial pattern of pits and grooves" [Heckert & Lucas, 1999], although scute lacks strong pitting [Heckert *et al* 1999]

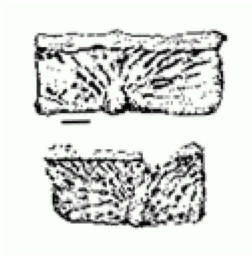
Comments: I'm following "Mikko's Phylogeny" [Aetosauria] in including this form in the tribe "Stagonolepidini".

Reference: Heckert & Lucas, 1999

Stagonolepis: *Stagonolepis* Agassiz, 1844

Range: Late Triassic (Late Carnian) of North America, South America, & Europe (Scotland).

Phylogeny: "Stagonolepidinae" **:** *Coahomasuchus* + *: *Stagonolepis robertsoni* + *Stagonolepis wellesi*/*Stagonolepis scagliai* (synonyms?)



***Stagonolepis* paramedian plates, scale bar 3 cm**
from Lucas 1998.

Characters: Large (length 2.5 to 2.7 metres); body is long and narrow; vertebrae with extensive transverse processes (Long & Murry, 1995); scutes either radial (ray-like) ornamentation - although this may be indistinct in some parts of the body [Murry 1986 p.123] - of the shallow drop-shaped pits on the dorsal surface; dorsal paramedian scutes lack ventral keel, scutes wide and thin (have low width:length (W:L) ratio), anterior bar present, [Heckert *et al* 1999]; caudal paramedian scutes gently arched transversely (Long & Ballew, 1985), dorsal boss quite pronounced and contacts the dorsal margin of the scute (Long & Ballew, 1985: figs. 13-14; Long and Murry, 1995: figs. 69-72).

Comments: The aetosaur *Stagonolepis* was a prominent and widespread animal of the latest Carnian. It is distinguished from the contemporary desmatosuchines by somewhat smaller size, armour lack of spines, and ornamentation of dermal armor. Depending on one's choice of systematics, two or three species, included in one or two genera, are known, one from south-west Pangea (Argentina), one from north-central Pangea (Scotland), and one from the north and west equatorial Pangea (Arizona and New Mexico), although the ranges may have overlapped [Lucas 1998 p.368], and so possibly these may all only be subspecies or variations of the same cosmopolitan form. This is the first unnamed clade described in Parrish, 1994 (includes "Aetosauroides" and *Stagonolepis*.). Likewise according to Harris *et al* 2003, "Aetosauroides" is the sister taxon to *Stagonolepis robertsoni*

Links: .Stagonolepis; Stagonolepis (short description); Dinosaurios, tutorial interactivo - Stagonolepis; Dinowelt-Stagonolepis

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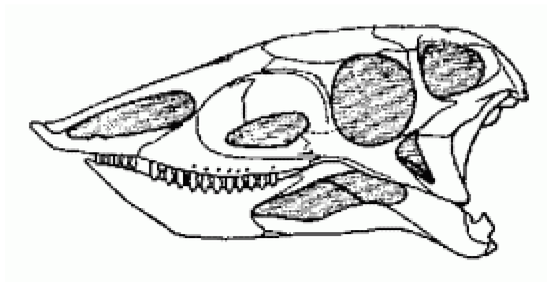
Stagonolepis robertsoni: Western Stagonolepis - *Stagonolepis robertsoni* (Agassiz, 1844)



***Stagonolepis robertsoni*, skull.**
illustration in Krebs 1976, p.79.

Range: Late Triassic (Latest Carnian) of Scotland

Phylogeny: *Stagonolepis* **:** *Stagonolepis wellesi*/*Stagonolepis scagliai* + *

Comments: The type specimen (consisting of dermal scutes) was originally mistaken for the scale of a large ganoid fish, but in 1859 Thomas Huxley correctly identified it as reptilian. [Creisler, 1996]. Fragmentary skeletons of about 20 individuals are known from the Lossiemouth Beds, Elgin, Scotland. In life the animal was a bit under 3 meters in length. Scroll up for skeleton and armor

---

Stagonolepis wellesi: Eastern Stagonolepis - *Stagonolepis wellesi* (Long & Bellew, 1985) Murray & Long, 1989 [= *Calyptosuschus wellesi* Long & Bellew, 1985)

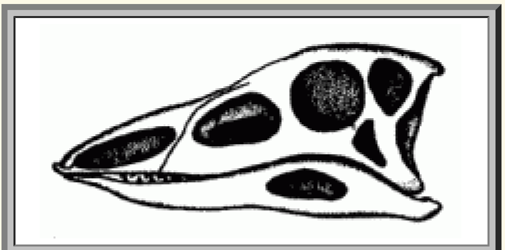
Range: Late Triassic (Latest Carnian) of North America

Phylogeny: *Stagonolepis* **:** *Stagonolepis scagliai* (synonym?) + *Stagonolepis robertsoni* + *

Characters:

Comments: Known from the Lower Blue Mesa member, Petrified Forest Formation, Arizona and New Mexico, this species is extremely similar to *Stagonolepis robertsoni*, and hence serves as a useful index fossil [Lucas 1998 Heckert & Lucas 2002]. According to *Aetosauroides scagliai* is a synonym. If so, the unusual shape of the type skull of the latter is due to post-mortem distortion. This species was formerly considered to be a separate genus, *Calyptosuschus* Long & Bellew, 1985

Stagonolepis scagliai: - *Stagonolepis scagliai* (Casamiquela, 1960); (= *Aetosauroides scagliai* Casamiquela, 1960]



***Stagonolepis scagliai* / *Aetosauroides* skull (part of the type specimen) illustration in Bonaparte 1971, p.671.**

Range: Late Triassic (Late Carnian - Ischigualastan) of South America (Argentina)

Phylogeny: *Stagonolepis* **:** *Stagonolepis robertsoni* + *Stagonolepis wellesi* + * (may be synonymous with one of the other two species)

Characters: *S. scagliai* retains a number of primitive features which distinguish it from other members of the group. The skeleton is very similar to the European *Aetosaurus*. (Bonaparte 1971, p.671). The type specimen skull, if not post-mortomly deformed, is unusually elongate

> "The genus it very well represented. The type is an incomplete skeleton with most of the skull and jaws (see image); other specimens have most of the postcrania. The primitive condition of this genus is seen in its elongated skull, the slender jaws and the small and conical teeth which distinguish it from other aetosaurs. The postcranium is very similar to other primitive aetosaurs. The dorsal armour lacks the spikes found in the North American genera. A good variation in size has been recorded, front 120 cm up to 250cm in total length. It has been found in levels bearing cynodonts, dicynodonts and other archosaurs."
> Bonaparte (1971: 671).

Comments: This species is known from skull and jaws, and several skeletons from the Ischigualasto Formation, San Juan Province, Argentina. The taxonomic status of this species seems to be rather confused. Parrish, 1994 and more recently Harris *et al* 2003 retain this species under the old name *Aetosauroides*, while Heckert & Lucas 2002 relate this to the genus *Stagonolepis*. It may or may not be the same as the North American species *S. wellesi*. On the basis of similarities with other global fauna Spencer G. Lucas [1998 pp.366-9) considers this part of the Adamanian faunal zone (latest Carnian). However radiometric dates for the Ischigualasto Formation put it in the early Carnian, which is , which is consistent with Bonaparte (1971). *S. scagliai* would seem to be a little smaller than the two other species. *Argentinosuchus bonapartei* Casamiquela, 1960 may or may not be a synonym. Scroll up for life reconstruction

Links: Stagonolepi scagliai sketch.

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

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Archosauria: Suchia (Aetosauridae): "Desmatosuchia"

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     |  |--"Stagonolepidinae"
                     |  `--"Desmatosuchia"
                     |     |--Neoaetosauroides
                     |     `--"Desmatosuchinae"
                     |        |-
-"Desmatosuchini"
                     |        |  |-Longosuchus
                     |        |  `--+-
-Desmatosuchus
                     |        |     `-
-Redondasuchus
                     |        `-
-"Typothoraxini"
                     |           |--Typothorax
                     |           `-
-Paratypothorax
                     `--CROCODYLOMORPHA
```

Contents

Taxa on This Page

(names of taxa in "inverted commas" are suggested here and have not been formally recognized)

1. "Desmatosuchia"
2. "Desmatosuchinae" X
3. "Desmatosuchini" X

4. *Desmatosuchus* X
5. *Longosuchus* X
6. *Neoaetosauroides* X
7. *Paratypothorax* X
8. *Redondasuchus* X
9. *Typothorax* X
10. "Typothoraxini" X

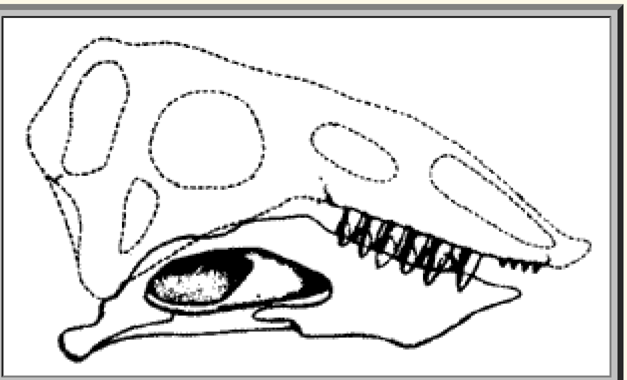
Descriptions

"Desmatosuchia": *Desmatosuchus* > *Stagonolepis*

Range: Late Triassic (Late Carnian to Rhaetian) of North America, & Europe.

Phylogeny: "Stagonolepia" **:** Stagonolepidinae + * **:** *Neoaetosauroides* + "Desmatosuchinae"

Neoaetosauroides: *Neoaetosauroides engaeus* Bonaparte, 1967



***Neoaetosauroides engaeus*, skull.**
illustration in Bonaparte 1971, p.671.

Range: Latest Triassic (Coloradean) of South America (Argentina)

Phylogeny: "Desmatosuchia" **:** "Desmatosuchinae" + *.

Comment: Despite the name, this form does not appear to be very close to *Aetosauroides* (= *Stagonolepis*,). This relatively primitive aetosaur nevertheless lived right at the very end of the Triassic period, being one of the last of its kind.. The following passage is from Jose Bonaparte's (1971) description:

> This genus was published with preliminary descriptions. The type includes most of the articulated postcranium, with the jaws, but no trace of the skull. However, in another very incomplete specimen some diagnostic fragments of the skull are present. The jaw is short and rather heavy, with no teeth in site anterior region. The upper jaw bears 4 small "incisors" in the premaxilla, and robust maxillary teeth. It has no spikes or projections in the carapace. The tail is formed by 26 rows of osteoderms. It has been found in levels with melanorosaurids [prosauropod dinosaurs].

Links: UCMP Mystery Fossil Number 33; Introduction to the Aetosauria; Aetosauria Translation and Pronunciation Guide; JVP 22(3) September 2002—ABSTRACTS 31A (DeSojo abstract) ATW030925.

References: Bonaparte (1971).

"Desmatosuchinae": *Desmatosuchus* and friends

Range: Late Triassic (Late Carnian to Rhaetian) of North America, & Europe.

Phylogeny: "Desmatosuchia" **:** *Neoaetosauroides* + * **:** "Desmatosuchini" + "Typothoraxini"

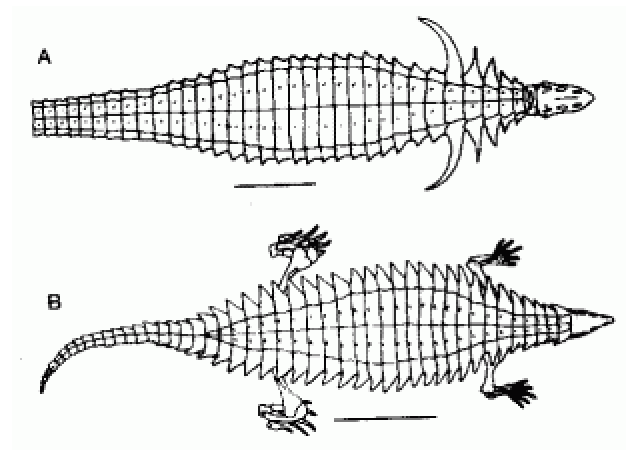
Comments: this is the second unnamed clade described in Parrish, 1994 (includes *Longosuchus*, *Desmatosuchus*, *Typothorax*, and *Paratypothorax*.). According to Harris *et al* 2003, *Longosuchus* and *Desmatosuchus* are more closely related than either is to *Neoaetosauroides*. This subfamily includes the most specialized and also many of the last surviving of the aetosaurs. Some forms have large backwardly curved spines, others very broad bodies and ovoid dorsal shields.

"Desmatosuchini": *Desmatosuchus* and friends

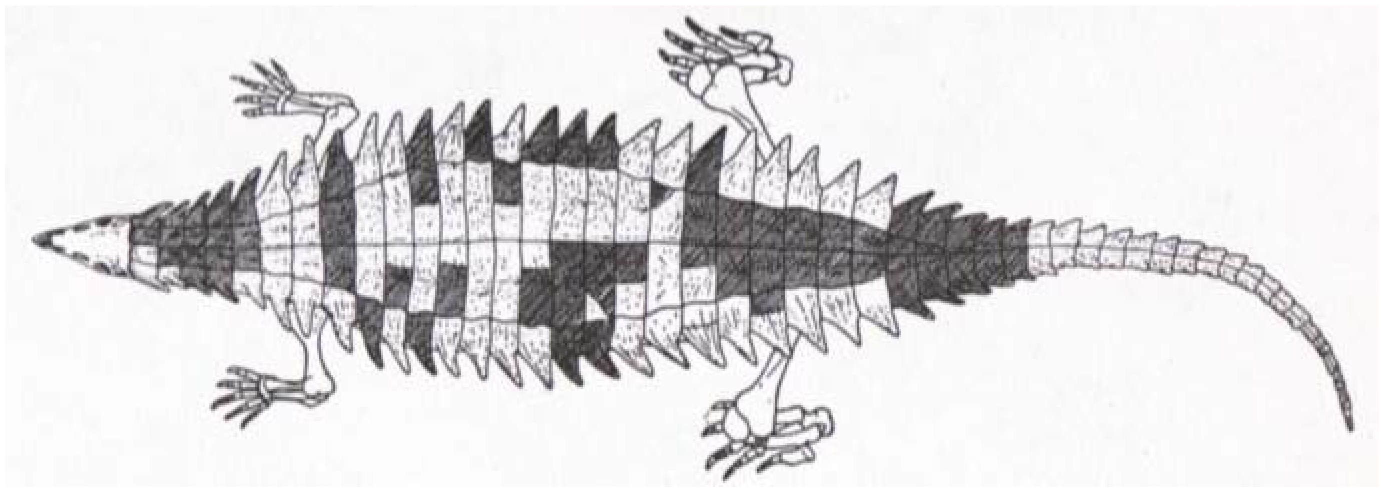
Range: Late Triassic (Early Tuvalian / Late Carnian to Rhaetian) of North America

Phylogeny: "Desmatosuchia" **:** "Typothoraxini" + * **:** *Longosuchus* + (*Desmatosuchus* + *Redondasuchus*)

Comments: Small to very large aetosaurs, often with backwardly curved spines. Unlike the Typothraxini, the body is narrow and crocodile-like. The phylogeny presented here is very tentative. It is proposed that the three genera represent an approximate evolutionary succession. This lineage appears to have been limited to equatorial west Pangea.



Desmatosuchine aetosaurs of west equatorial Pangea, showing arrangement of armor. *Desmatosuchus* (top) and *Longosuchus* (bottom). Scale bar 50 cm. Illustration, from Murry 1986 p.180

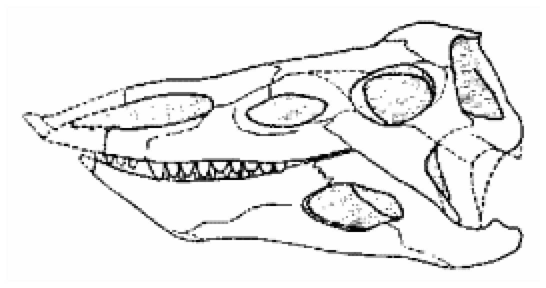


***Longosuchus meadei*, top view, showing arrangement of armour illustration in Krebs 1976, p.81 after H.J. Sawin 1947**

Longosuchus: *Longosuchus meadei* Hunt & Lucas, 1990 (= *Typothorax meadei* Sawin 1947= *Lucasuchus* Long & Murry 1995)

Range: Late Triassic (Early Tuvalian / Late Carnian (Otischalkian)) of North America

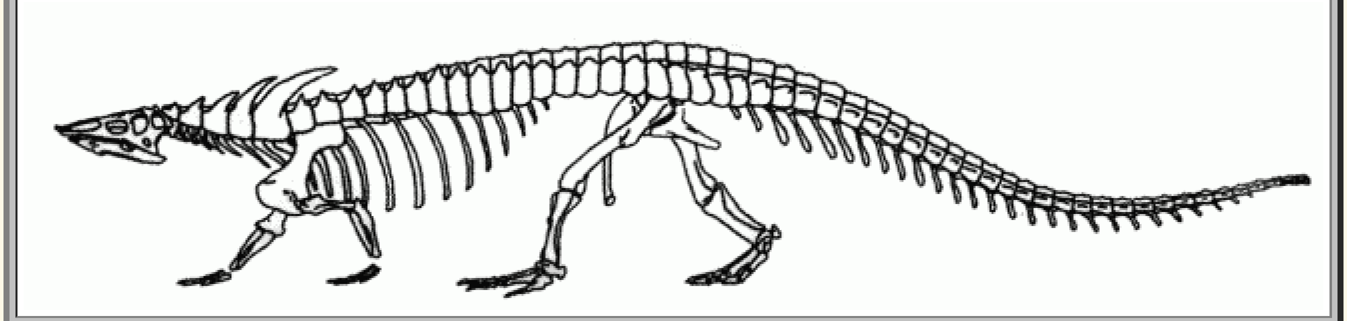
Phylogeny: "Desmatosuchini" : (*Desmatosuchus* + *Redondasuchus*) + *



***Longosuchus meadei*, skull. illustration in Krebs 1976, p.79.**

Characters and comments: A large (almost 3 meters) form; dorsal armor consists of broad discoidal shield or carapace of armour plates ridged with spines, but lacking the huge shoulder spines of its later cousin *Desmatosuchus*. Head relatively small; orbits small; paramedian plates pyramid-shaped [p.79] The limbs are quite gracile and the armour ornamentation is radiate [Murray 1986 p.123]. The In early books it is described under the name *Typothorax* (sometimes in inverted commas), however it is somewhat distinct from the type species *Typothorax coccinarum* Cope, 1892 and so was placed by Hunt and Lucas in a distinct genus. This is an Otischalkian index fossil.

References: Parrish, 1994



***Desmatosuchus haploceros*, drawing of skeleton. Length of original 4 or 5 meters**
(image from Mt. Blanco fossil catalogue - original source unknown)

***Desmatosuchus haploceros*, photo of head and part of body. photo © Robert Gay**

Desmatosuchus: *Desmatosuchus haploceros* (Cope 1892) (= *Acaenasuchus* Long & Murry 1995 - juvenile [Heckert & Lucas, 1999])

Range: Late Triassic (latest Carnian (Adamanian) to Early/Mid Norian) of North America

Phylogeny: "Desmatosuchini" : *Longosuchus* + (*Redondasuchus* + *)

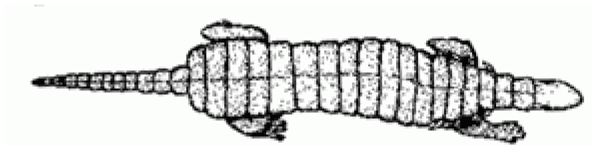
Characters: extremely large (up to 4 or 5 meters); back completely covered with dermal plates with a broad median paired series and a smaller lateral paired series; the latter plates coming to a prominent point; the first five rings covering the foremost ten vertebrae, each other ring covering one vertebra [Zittel, 1932]. cervical paramedian scutes elongate and rectangular with raised boss or bar, postcervical not as elongate and without anterior bar. Scute ornamentation consists of randomly placed pits and grooves with little if any radiate pattern [Murray 1986 p.122],

Comments: This enormous, narrow-bodied aetosaur possessed, in addition to the normal complement of armour plates, a pair of huge, backwardly turned shoulder horns, preceded by several pairs of smaller spikes on the side of the neck. This is the largest and most impressive of the aetosaurs, and hence there are a number of pages on the web dedicated to it (mostly with just a simple illustration and brief description).

References: see also Small 2002.

Links: Desmatosuchus (drawing, by Rob Gay); Desmatosuchus, an aetosaur (photo); Desmatosuchus (short text description); Desmatosuchus Desmatosuchus; Desmatosuchus - sketch; Dinowelt - Desmatosuchus; Dinosaurios, tutorial interactivo - Desmatosuchus.

Redondasuchus:



***Redondasachus*; from Lucas 1998.**

Range: Late Triassic (Rhaetian (Apachean) of North America

Phylogeny: "Desmatosuchini" :: *Desmatosuchus* + *.

Characters: medium sized (about 2 meters long); scutes with ventral keel.

"Typothoraxini": *Typothorax* and *Paratypothorax*

Range: Late Triassic (Late Tuvalian/Late Carnian to Rhaetian) of North America & Europe.

Phylogeny: "Desmatosuchinae" : "Desmatosuchini" + *: *Typothorax* + *Paratypothorax* + *

Characters: large (length to 3 meters); ovoid/discoidal dorsal shield; strap-like paramedian scutes (high W:L (Width to Length) ratio) [Heckert *et al* 1999; Murray 1986 p.122], ornamented with deep pits

Comments: Advanced large aetosaurs; the broad bodies indicate a large gut and hence specialized adaptation to fermenting plant material

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Paratypothorax: *P. andressorum* Long & Bellew, 1985 (= *P. ornatus*, *P. andressi*)

Range: Late Triassic (latest Carnian (Adamanian) of North America (Dockum Fm); Early-Mid Norian of North America, Greenland, and Europe. (Stubensandstein); to Rhaetian (Upper Chinle / Apachean)) of North America

Phylogeny: "Typothoraxini" : *Typothorax* + *

Characters: flat and regularly pitted dermal scutes; ornamentation consists of "prominent grooves and ridges that radiate from posteromedially placed bosses. These large, posteriorly hooked eminences have sharp anterodorsal margins and concave posterior margins" Murray 1986 p.122

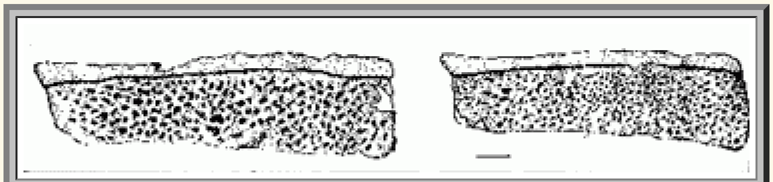
Comments: Advanced large (c. 3 meters) aetosaurs with a broad dorsal shield, the scutes marked by ridges and bumps. Scutes from the Stubensandstein of Heslach, Germany, were originally misidentified as belonging to the phytosaur *Nicrosaurus kapffi* [Murray 1986, Creisler, 1996]. During the Norian at least, this animal and *Aetosaurus* shared the same distribution. This species survived right up until the Rhaetian age (Apachean land fauna zone) [Heckert & Lucas, 1999]

Typothorax: *T. coccinarum* Cope, 1892

Range: Late Triassic (Early/Mid Norian (Revueltian)) of North America

Phylogeny: "Typothoraxini" : *Paratypothorax* + *

Characters: Scutes with ventral keel



***Typothorax* paramedian plates, scale bar 3 cm from Lucas 1998.**

Comments: Advanced large broad-bodied aetosaurs. This is a Revueltian age index fossil.

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

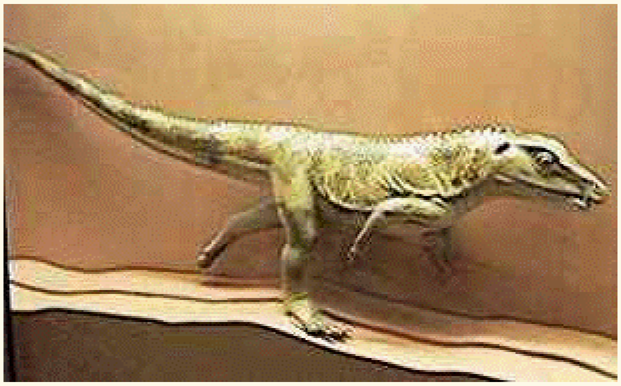
checked ATW060119

Archosauria: The Thecodonts

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
`--ARCHOSAUROMORPHA
   |
   `--ARCHOSAURIA
      |--Proterosuchidae
      `--+--Erythrosuchidae
         `--+--Euparkeriidae
            `--+--Proterochampsidae
               `--Crown Group Archosauria
                     |--Ornithodira
                     |  |--PTEROSAURIA
                     |  `--DINOSAUROMORPHA
                     `--Crurotarsi
                        |--Phytosauridae
                        `--Rauisuchiformes
                           |--Rauisuchia
                           |  |-
-Ornithosuchidae
                           |  `--+-
-Prestosuchidae
                           |     `-
-Rauisuchidae
                           `--Suchia
                              |--Aetosauridae
                              `-
-CROCODYLOMORPHA
```

Contents



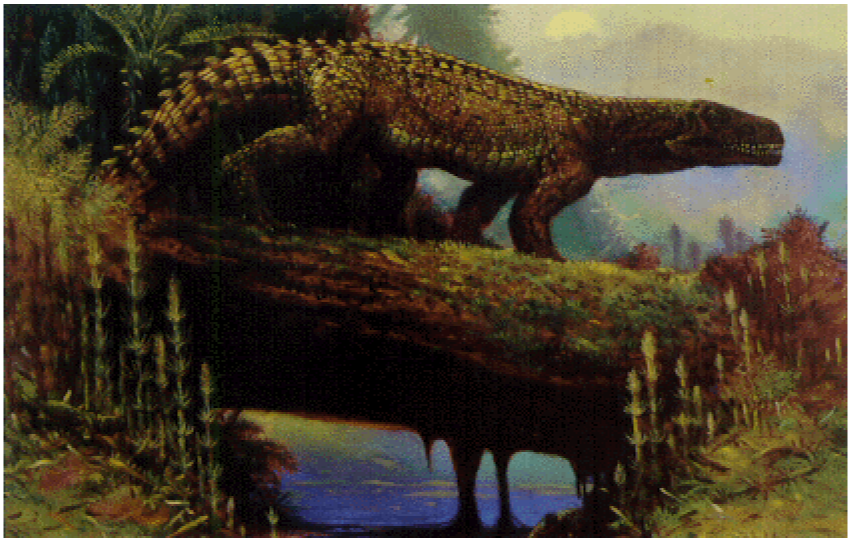
The classic (mid 20th century) image of the "pseudosuchian" thecodont, a small, bipedal reptile (*Ornithosuchus*). Up until the 1970s, animals like this were considered to be ancestral to both birds and (separately) dinosaurs. This model would seem to be based on a juvenile. More recent reconstructions present *Ornithosuchus* as a much larger (over 3 meters), carnosaur-like animal (see for example Walker 1964). This photo is of a model from the Elgin Museum

The "Thecodonts" - Masters of the Triassic

During the Triassic period, at the start of the Mesozoic era, there lived a whole lot of animals that were no longer small and insignificant lizard-like forms, but not actually crocs, dinosaurs, pterosaurs, or birds. These are the "thecodonts".

Thecodonts are defined by certain shared primitive or ancestral features, such as the suborbital fenestra (an opening on each side of the skull between the eye sockets and the nostrils) and teeth in sockets. The name Thecodont is actually Latin for "socket-tooth," referring to the fact that thecodont teeth were set in sockets in the jawbones; an archosaurian characteristic that was inherited by the dinosaurs.

From an evolutionary systematic point of view, the Thecodonts are a valid taxon of Triassic archosaurs. They include both the ancestors of dinosaurs and other animals, and a number of independent evolutionary lines that are important in their own right. And they dominated the Triassic. For as long as they were there, no crocodile or armored herbivorous or general carnivorous dinosaur could grow very big. It was only one of the accidents in the history of life on Earth, an impact by a wandering asteroid or comet, that wiped the thecodonts from the land and provided their successors, the dinos and crocs, to take their place


A large, *Ticinosuchus*-like thecodont. Graphic from Rare Resource - Thecodont

From the cladistic point of view, Thecodontia is a paraphyletic group, like cotylosaurs, the pelycosaurs, condylarths, and for that matter the colloquial as opposed to the cladistic definition of dinosaurs. Because they represent a "grab-bag" taxon for any archosaur that wasn't a crocodilian, a pterosaur, or a dinosaur, the term is considered to have no phylogenetic value.

The term *Thecodontia* is rarely used in current literature, but appears in evolutionary systematic-based books published pre-1990 or so, and in various on-line taxonomic lists based on them. The most recent version is Olshevsky (1991)'s "Superorder Thecodontia", which we have updated to Paraorder Thecodontia (the use of the para- suffix to indicate paraphyletic linnaean taxon was suggested by Olshevsky but did not catch on, prior to our adopting it).

In this context, "thecodont" remains a useful term as shorthand for "basal archosaur" and we will use it in that sense here. In fact, the term "thecodont" is more limited and usually refers to the basal archosaur*iforms*. These are reptiles in which the ankle has been somewhat simplified and reorganized to permit the more erect carriage mentioned above. Although very similar anatomically and clearly related to each other by common ancestry and many shared ancestral traits (plesiomorphies), the thecodonts are no longer considered a single taxon, but rather are divided along cladistic (phylogenetic) lines. (MAK)

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

Content MAK 991003 & 030730, updated MAK101007, last revised MAK120313

Archosauria: Thecodontia: Classification

Abbreviated Dendrogram

```
DIAPSIDA
|--LEPIDOSAUROMORPHA
`--ARCHOSAUROMORPHA
   |
   `--ARCHOSAURIA
      |--Proterosuchidae
      `--+--Erythrosuchidae
         `--+--Euparkeriidae
            `--+--Proterochampsidae
               `--Crown Group Archosauria
                     |--Ornithodira
                     |  |--PTEROSAURIA
                     |  `--DINOSAUROMORPHA
                     `--Crurotarsi
                        |--Phytosauridae
                        `--Rauisuchiformes
                           |--Rauisuchia
                           |  |-
-Ornithosuchidae
                           |  `--+-
-Prestosuchidae
                           |     `-
-Rauisuchidae
                           `--Suchia
                              |--Aetosauridae
                              `-
-CROCODYLOMORPHA
```

Contents

Order (or Paraorder) Thecodontia

Traditional classification

In applying an Evolutionary-Systematic, rather than a cladistic, classification scheme, Linnean taxonomy is employed. Instead of Basal or Stem Group Archosaur(omorphs), reference can be made to Order Thecodontia, a name that appears in text-books on palaeontology and evolution upto the 1980s, but rarely since.

The Thecodontia were traditionally (up to the 1960s) divided into four suborders, the Proterosuchia, Phytosauria, the Aetosauridae, and the "Pseudosuchia" (more or less equivalent to the Crurotarsi, minus the more derived forms). The Proterosuchia included various primitive ancestral types, the phytosaurs were crocodile like forms, the aetosaurs specialized armoured creatures, remarkably like the armoured ornithischian dinosaurs, and the Pseudosuchia were a sort of catch-all or "waste-basket" category for everything that didn't fit in any of the other suborders. This last group was also considered ancestral to dinosaurs, birds, and crocodiles. The Pseudosuchia as an artificial group, having the same "grab-bag" status within the Thecodontia as the Thecodontia have within the Archosauria. Robert Carroll in his book *Vertebrate Paleontology and Evolution* replaces the Pseudosuchia with the Rauisuchia and the Ornithosuchia, and moves the suborder Sphenosuchia (for small pseudosuchians) to the Crocodilia. The following arrangement relies mainly on Carroll 1988, with a few updates here and there

---

Infraclass Archosauromorpha Huene, 1946 (*cont.*)
 Order[1] Thecodontia Owen, 1859 Triassic archosaurs with teeth implanted in sockets
  Suborder Proterosuchia Broom 1906 primitive forms, Late Perm to Late Trias, cosmopolitan
   Family Proterosuchidae Huene, 1914 sprawling lizard or crocodile like, ancestral thecodonts, late Perm to Mid Trias, Cosm
   Family Erythrosuchidae large to huge, semi-sprawlingh terrestrial carnivores, Early to Mid Trias, S Afr, EEur, EAs,
   Family Euparkeriidae small faculatively bipedal types - Early Trias, S Afr, EEur, EAs
   Family Proterochampsidae specialised semi-aquatic types, Mid to Late Trias of SAm
  Suborder Suchia Huxley, 1875 (= Phytosauria Meyer, 1861) crocodile-like forms, L Trias of Eur, N Am, Ind, N Afr
   Family Phytosauridae Jaeger, 1828 (= Suchidae Lydekker, 1885)
  Suborder Ornithosuchia Huene, 1908 At one time considered ancestral to dinosaurs, now monotypal (Ornithosuchidae only)
   Family Ornithosuchidae Huene, 1908 medium-sized facultively bipedal carnivores, Late Trias of Eur & S Am
  Suborder Rauisuchia Huene, 1942, or Bonaparte, 1982 medium to very large terrestrial preditors, erect mamal, bird and dinosaur like posture, The phylogeny of the group and the status of some of the included families is uncertain. Some specialsied groups became herbivores. Early to Late Trias of Eur, EEur, N Am, Afr, E As
   Family Ctenosauriscidae Kuhn, 1964
   Family Doswelliidae Weems, 1980
   Family Lotosauridae Zhang, 1975
   Family Poposauridae Nopsca, 1928 (Postosuchidae)
   Family Prestosuchidae Romer, 1966
   Family Rauisuchidae Huene, 1936 (= Teratosauridae Cope, 1871)
   Family Shuvosauridae
  Suborder Aetosauria Lydekker, 1889 armoured herbivores, L Trias of Eur, N Am, S Am, N Afr
   Family Stagonolepididae Lydekker, 1887
  Suborder unspecified (proto-crocodylomorphs)
   Family Erpetosuchidae Watson, 1917
   Family Gracilisuchidae
  Suborder unspecified (Ornithodira)
   Family Scleromochlidae Huene, 1914

Hybrid classification

One alternative to the conventional linnaean classification that retains ranks (unlike strict cladistic-based phylogenetic nomenclature) is provided by Olshevsky 1991, who distinguishes between paraphyletic and monophyletic taxa. Whereas Olshevsky only used one prefix, para- in front of the rank of paraphyletic taxa (e.g. parafamily, monophyletic taxa being unmodified), we have used the following:

- **para-** for a paraphyletic (an ancestral or evolutionary grade defined only by shared primitive features and lack of specialised features) according to consensus opinion
- **holo-** for holophyletic (=monophyletic)
- **ambi-** for when different cladistic analyses dissagree as to whether a taxon is paraphyletic or monophyletic
- **mono-** for a monotypal taxon
- **evo-** for when a taxon is considered monophyletic according to current consensus cladistic studies, but morphologically and/or stratigraphically intermediate and so considered to have given rise to other taxa according to evolutionary systematics or a general gradistic perspective (which implies reversals (loss of original synapomorphies) and a non-parsimony-based phylogeny)

When no prefix is used, we haven't gotten around to assessing the taxon (or the current page is still under construction)

Hence, under this system, the Thecodontia consitute a Paraorder.

The following hybrid classification is the same as the linnaean one, but with additional suffixes. This system however is probably too complex and confusing to be practical, although we have include dit for the same of interst

Parainfraclass Archosauromorpha Huene, 1946 (*cont.*)
Paraorder Thecodontia Owen, 1859 Triassic archosaurs with teeth implanted in sockets
Parasuborder Proterosuchia Broom 1906 primitive forms, Late Perm to Late Trias, cosmopolitan
Evofamily Proterosuchidae Huene, 1914 sprawling lizard or crocodile like, ancestral thecodonts, late Perm to Mid Trias, Cosm
Evofamily Erythrosuchidae large to huge, semi-sprawlingh terrestrial carnivores, Early to Mid Trias, S Afr, EEur, EAs,
Evofamily Euparkeriidae small faculatively bipedal types - Early Trias, S Afr, EEur, EAs
Holofamily Proterochampsidae specialised semi-aquatic types, Mid to Late Trias of SAm
Holosuborder Parasuchia Huxley, 1875 (= Phytosauria Meyer, 1861) crocodile-like forms, L Trias of Eur, N Am, Ind, N Afr
Holofamily Phytosauridae Jaeger, 1828 (= Parasuchidae Lydekker, 1885)
Holosuborder Ornithosuchia Huene, 1908 At one time considered ancestral to dinosaurs, now monotypal (Ornithosuchidae only)
Holofamily Ornithosuchidae Huene, 1908 medium-sized facultively bipedal carnivores, Late Trias of Eur & S Am
Ambisuborder Rauisuchia Huene, 1942, or Bonaparte, 1982 medium to very large terrestrial preditors, erect mamal, bird and dinosaur like posture, The phylogeny of the group and the status of some of the included families is uncertain. Some specialsied groups became herbivores. Early to Late Trias of Eur, EEur, N Am, Afr, E As
Holofamily Ctenosauriscidae Kuhn, 1964
Monofamily Doswelliidae Weems, 1980
Monofamily Lotosauridae Zhang, 1975
Ambifamily Poposauridae Nopsca, 1928 (Postosuchidae)
Parafamily Prestosuchidae Romer, 1966
Ambifamily Rauisuchidae Huene, 1936 (= Teratosauridae Cope, 1871)
Holofamily Shuvosauridae
Holosuborder Aetosauria Lydekker, 1889 armoured herbivores, L Trias of Eur, N Am, S Am, N Afr
Holofamily Stagonolepididae Lydekker, 1887
Parasuborder unspecified (proto-crocodylomorphs)
Monofamily Erpetosuchidae Watson, 1917
Monofamily Gracilisuchidae
Monosuborder unspecified (Ornithodira)
Monofamily Scleromochlidae Huene, 1914

Notes

[1] In the interests of taxonomic continuity (Romer, Colbert, Carroll, etc), we have chosen not to follow Olshevsky (1991) in elavating Thecodontia to Superordinal rank.

Page Back | Unit Home | Page Top | Page Next

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Archosauria: Dendrogram

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

Contents

Cladogram

For taxa within Archosauria, this cladogram is based on a single most parsimonious tree generated from 133 characters for 20 taxa derived as follows:

1-73 from Benton (1999).

74-100 from Gower (2002).

101-133 from Olsen *et al*. (2000) As revised and corrected by Benton & Walker (2002).

Additional data for *Erpetosuchus* hand coded from Benton & Walker (2002)

Additional data for *Doswellia* hand coded from Weems, RE (1980).

The analysis was performed on PHYLIP, using the DNAPARS program. This program treats all characters as unordered and (as applied here) optimizes state changes in a manner similar to the DELTRAN option of PAUP. "Not applicable" characters were coded as such, rather than as unknown. In one or two cases, included taxa were assumed to have the same character states as a higher level taxon in order to promote comparability. Thus, *Batrachotomus* and *Saurosuchus* were assumed to have the "prestosuchid" states other than braincase characters, since they were scored separately by Gower, but not in the other sources. Other than this, the hand-coded *Doswellia* data, and the partially hand-coded *Erpetosuchus* data, no attempt was made to code characters not scored in the original reports. The data matrix is available on request -- but, frankly, you'd have to be out of your mind to rely on it.

There is some overlap between the characters from Olsen *et al*. (2000) and Benton (1999). No adjustment was made for the duplication. The objective of the study was largely to see if the close aetosaur - crocodylomorph relationship found by Gower (2002) could be disrupted by diluting the braincase data -- but without the overemphasis on tarsal (ankle) characters which marred studies such as Sereno (1990) and Parrish (1993) (concerning which, see Dyke, 1998). Since the inclusion of the duplicate characters effectively weighted cranial characters, other than braincase characters, a little more heavily, the minor duplication promoted the objectives of the test.

Gracilisuchus and *Euscolosuchus* were not included in this study. They have simply been interpolated for purposes of the cladogram below, as have various other taxa, including *Ticinosuchus* and Rauisuchidae. Various dinosaur and related taxa from Benton (1999) were included. We are aware of at least one study in which the failure to include a reasonable number of representatives from a deep branch within the study taxon led to arguably spurious results. *See*, Damiani (2001), discussed at Trematosauroidea. In any event, the topology within Ornithodira (not shown here) was conventional. For the same reason, a sphenosuchid was included in the study to help fill out the crocodylomorph branch.

Nodes have mostly been named in accordance with the definitions in Parrish (1993). So far as we know, no one has explicitly defined Suchia as *Alligator* > *Postosuchus* or equivalent. However, one common usage of the term is aetosaurs + crocs. This is close to what we need, so we have stretched a point in order to create a good node-stem triad: Rauisuchiformes = Rauisuchia + Suchia.

Despite these extensive efforts to break up the aetosaur-crocodylomorph relationship, only *Erpetosuchus* was more closely related to crocodylomorphs than aetosaurs. The degree of homoplasy between derived members of the Rauisuchia and Suchia is rather disturbing. Still, there are enough synapomorphies which look like true phylogenetic signal to suggest that this heterodox topology may be worth following, at least for the present. ATW031227.

REPTILOMORPHA

```
|--LEPIDOSAUROMORPHA
`--ARCHOSAUROMORPHA ToL
   |--Neochoristodera X
   |  |--Simoedosauridae •X
   |  `--Champsosauridae •X
   `--+--Rhynchosauria •X MH
      `--+--Trilophosauridae •X MH
         `--+--Prolacertiformes •X MH
            `--Archosauriformes MH
               |--Proterosuchidae •X MH
               |--Erythrosuchidae •X MH
               `--+--Euparkeriidae •X
                  `--+--Proterochampsidae •X
                     `--Archosauria MH, ToL Gauthier (1986) = "crown group archosaurs", i.e. crocs +
rocs [2]
                        |--Ornithodira MH rocs > crocs ˜ Avemetatarsalia Benton (1999).
                        |  |--Scleromochlus •X
                        |  `--+--PTEROSAURIA
                        |     `--DINOSAUROMORPHA
                        `--Crurotarsi MH crocs > rocs ˜ Crocodylotarsi Parrish (1993) = phytosaurs +
crocs
                           |--Phytosauridae X MH
                           |  |--Parasuchus •X
                           |  |--Paleorhinus •X
                           |  `--Euphytosauridae X
                           |     |--Angistorhinus •X
                           |     |--Brachysuchus •X
                           |     `--Rutiodontinae X
                           |        |--Rutiodon •X
                           |        |--Smilosuchus •X
                           |        `--Pseudopalatinae X
                           |           |--Pseudopalatus •X
                           |           |--Nicrosaurus •X
                           |           `--Mystriosuchus •X
                           `--Rauisuchiformes sensu Parrish (1993) = aetosaurs + Rauisuchia [1]
                              |--Rauisuchia X sensu Parrish (1993) = Rauisuchidae > aetosaurs
                              |  |--Ornithosuchidae X
                              |  |  |--Ornithosuchus •X
                              |  |  |--Venaticosaurus •X
                              |  |  `--Riojasuchus •X
                              |  `--+--Tarjadia •X
```

```
|     `--+--Prestosuchidae X
|        |  |--Saurosuchus •X
|        |  `--+--Ticinosuchus •X
|        |     `--Batrachotomus •X
|        `--+--Doswellia •X
|           `--+--Rauisuchidae •X MH
|              `--Poposauridae •X MH
`--Suchia MH used as aetosaurs > Rauisuchidae
   |--Aetosauridae X MH
   |  |--Aetosaurus •X
   |  `--+--+--Coahomasuchus •X
   |     |  `--Stagonolepis •X
   |     `--+--Neoaetosauroides •X
   |        `--+--+--Longosuchus •X
   |           |  `--+--Desmatosuchus •X
   |           |     `--Redondasuchus •X
   |           `--+--Typothorax •X
   |              `--Paratypothorax •X
   `--+--Euscolosuchus •X
      `--+--Gracilisuchus •X
         `--+--Erpetosuchus •X
            `--CROCODYLOMORPHA
```

[1]synonymous with Paracrocodylomorpha Parrish (1993) = Poposauridae + Crocodylomorpha

[2] = Avesuchia Benton

Page Back | Unit Home | Page Top | Page Next

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Archosauria: References

Abbreviated Dendrogram

```
ARCHOSAUROMORPHA
|
`--ARCHOSAURIA
   |--Proterosuchidae
   `--+--Erythrosuchidae
      `--+--Euparkeriidae
         `--Crown Group Archosauria
            |--Ornithodira
            |  |--PTEROSAURIA
            |  `--DINOSAUROMORPHA
            `--Crurotarsi
               |--Phytosauridae
               `--Rauisuchiformes
                  |--Rauisuchia
                  |  |--Ornithosuchidae
                  |  `--+--Prestosuchidae
                  |     `--Rauisuchidae
                  `--Suchia
                     |--Aetosauridae
                     `--CROCODYLOMORPHA
```

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Aetosaurus, *Desmatosuchus*, *Mystriosuchus*, *Nicrosaurus*

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

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Crocodylomorpha: Overview

Abbreviated Dendrogram

```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         `--Neosuchia
            |--Dyrosauridae
            `--Crocodylia
               |--Gavialidae
               `--+--Alligatoridae
                  `--Crocodylidae
```

Contents

The tropical Indo-Pacific apex predator *Crocodylus porosus* awaits its next meal. Males can easily grow to over 5 meters in length; before the coming of the white man, they were even larger

Photograph by Lepidlizard, Public Domian, Wikimedia

This unit is about the crocodiles, alligators, and their cousins and ancestors; in Linnaean taxonomy the Order *Crocodilia* [1]; in Cladistic nomenclature the Clade *Crocodylomorpha* (it doesn't matter what name we give them because both name smean the same). This very successful reptilian lineage includes is every bit as ancient as the dinosaurs (to which they are often compared). It includes everything from lightly built and even bipedal Sphenosuchia which rather resembled miniature dinosaurs and were previously refered to under the rubric of "pseudosuchians" ("false crocodiles") [2], to ocean going Metriorhynchids as well adapted to marine existence as any ichthyosaur or dolphin, to an extraordinary diversity of fully terrestrial forms, to narrow-snouted fish eaters and broad-muzzled semi-aquatic apex preditors, the largest of which - such as *Sarcosuchus* and *Deinosauchus* - surpassed in size even the carcharodontosaur and tyrannosaur theropod dinosaurs. At the other end of the size scale, some Jurassic crocodiles were no bigger than medium-sized lizards. MAK120201 120302

Notes

[1] More usually but incorrectly spelled Crocodylia with a "y" (see e.g. Carroll 1988 for only one authoritative textbook that usues this spelling). The original spelling used by Richard Owen (1842), the first to scientifically describe the group was Crocodilia. Crocodylia is incorrectly attributed to Laurenti 1768 (based on his naming of the genus *Crocodylus*) and Gmelin 1789 - Paleobiology Database. More recently, Crocodylia has been used in cladistics in a much more limited context to refer to the crown group crocodiles, and Crocodylomorpha to the stem group, which is directly equivalent to the evolutionary systematic Crocodylia (=Crocodilia). Actually Crocodylia is simply the nested clade within Crocodylomorpha. MAK120302

[2] In his pioneering work on cladistic paleontology, Gauthier (1986) used this term to refer to the clade to refer to Crocodiles and all other archosaurs closer to them than to birds. Thus true crocodiles are included under the heading of "false crocodiles". Perhaps because of this incongruance, Paul Sereno rejected the term Pseudosuchia and instead uses Crurotarsi (which we have also adopted).

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

Crocodilia: Overview

Abbreviated Dendrogram

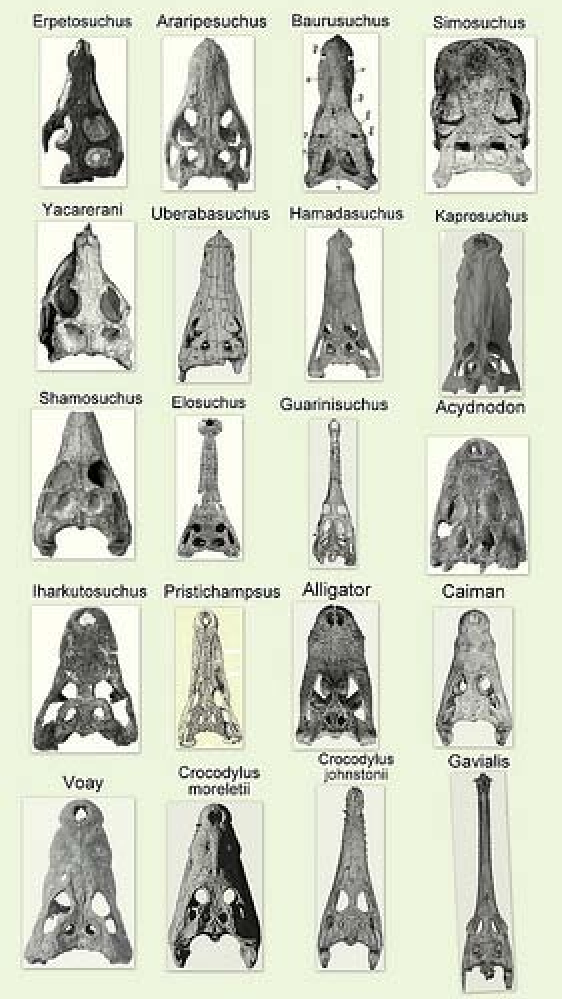
```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         `--Neosuchia
            |--Dyrosauridae
            `--Crocodylia
               |--Gavialidae
               `--+--Alligatoridae
                  `--Crocodylidae
```

Contents

Introduction

Today's crocodiles are mostly large reptiles are adapted to a semi-aquatic existence. This was not always the case. In fact the crodylomorph group began as small, gracile terrestrial predators. Crocodile scales are hard and square, and a few rows of raised scales down the back and tail contain knobs of bone. Every bit as old as the dinosaurs, to which they are fairly closely related, the crocodiles and their early predecessors (collectively, "Crocodylomorpha") are an ancient and venerable lineage of archosaurs. Although typically reptilian in their scaly integument and "cold blooded" (ectothermic - actually inertial homeothermic in large forms) metabolism, they nevertheless display advanced chracteristics such as a four-chambered heart (in efficency similiar to the bird and mammal heart) and maternal care of young.

During the late Triassic and early Jurassic these animals were mostly small, graceful, active terrestrial forms, quite unlike the way we think of crocodiles today. After flourishing for some 40 or 50 million years - almost as long as the age of mammals - these small active animals died out, either through competition with small theropod dinosaurs, or perhaps through a mass extinction (e.g. the Toarcian turnover that also eliminated the Prosauropod, Podokesaur and Heterodontosaur dinosaurs and a number of lines of marine reptiles and invertebrates). The surviving crocodilians were larger animals, more like the crocs we know today, but, curiously, mostly marine. Later in the Jurassic, these marine forms invaded fresh water and swamp environments as large semi-aquatic predators, and finally returned to the land again as small



Disparate cranial morphologies in Crocodylomorpha, collage by by Somasushumna, Crocodiles in the shadow of the dinosaurs

forms.

It was as large, semi-aquatic predators that they became most successful. Crocodiles are superbly adapted to life in rivers and swamps. A fold of skin closes the windpipe at the back, so that the animal can open its mouth under water and breathe with only its nostrils above the surface. The nostrils, like the eyes and ears, are placed high on the head. When crocodiles are completely submerged, the ears and nostrils are closed by valves, and the eyes covered by membranes. Crocodiles have no salivary glands and usually eat under water. Some species sweep their prey from the land into the water with their powerful, vertically flattened tails, a technique that was almost certainly also practiced by Phytosaurs of the late Triassic.

The warm balmy Mesozoic climate was kind to these prehistoric reptiles, and they flourished and diversified for many millions of years, attaining world-wide distribution. The larger semi-aquatic types lunched on dinosaurs and large lungfish and Lepidotids. Some, like the great *Sarcosuchus* and *Phobosuchus*, reached huge size, 10 to 15 meters in length and some 8 to 15 tonnes in weight, bigger than the largest *T. rex*.

Perhaps because of their ectothermic metabolism (which makes it possible to go without food for long periods) and their reliance on the fresh water carrion - detrivore foodchain, rather than the ocean plankton - based or the terrestrial plant - based foodchains, the crocodiles were unaffected by the comet/asteroid - impact end-Cretaceous mass extinction that eliminated most forms of life on Earth. They continued through to the Paleocene, and in the absence of large competitors evolved into large fully terrestrial preditors (Sebecosuchids, Pristochampsids).

The global cooling trend that began in the Oligocene epoch and accelerated in the Miocene and Pliocene was catastrophic for the crocodiles. Many types died out, unable to cope with the increasing cold, and the survivors retreated to the tropics and a life in swamps. The start of the modern epoch (Holocene epoch) saw 21 species distributed in (depending on how we draw the lines) one, two, or three families (four subfamilies). MAK

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

checked ATW031117, page last modified MAK120201

Crocodylomorpha

Abbreviated Dendrogram

```
ARCHOSAURIA
|
Crocodylomorpha
|Sphenosuchia
|  |--Trialestidae
|  `--Sphenosuchidae
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         `--Neosuchia
            |--Dyrosauridae
            `--Crocodylia
               |--Gavialidae
               `--+--Alligatoridae
                  `--Crocodylidae
```

Contents

Taxa on This Page

1. Crocodylomorpha
2. Sphenosuchia
3. Sphenosuchidae
4. Trialestidae

The Heart of the Crocodile

This essay replaces a small, cryptic paragraph previously included as "Crocodylia Notes." Like this effort, the previous note dealt with circulation. In fact, it is customary to accompany any discussion of crocodylians with a discussion of circulation for the simple reason crocs have a better, more flexible and more efficient heart than any other organism, alive or (presumably) dead. The croc system is also rather complex. Perhaps the idea is that if one can understand the croc heart, then anything else is a piece of cake.

Of course, more sinister motives may be at work. Students are most commonly introduced to croc circulation with a semi-schematic diagram which demonstrates what is surely a gleefully malicious intent to confuse. The left atrium and left ventricle are drawn on the right. This would be correct in ventral view, but the atria are on the bottom, which is contrary to the usual "valentine" representation of the heart, and also just plain wrong. Naturally, the left aorta emerges from the right ventricle, and vice-versa, while a connection between the aortas, the foramen of Panizza, is explained as creating a "right-to-left intercardiac shunt" when blood flows from the *left* aorta to the *right* aorta *outside* the heart. No reasonable student can view this representation without the deep suspicion that she is the butt of some bizarre, two-century-old practical joke handed down in the professoriate from one generation of cackling, gummy-eyed, misanthropic curmudgeons to the next.

Sadly, we are now probably doomed by nomenclature and convention endlessly to repeat this cycle of obfuscation, like a hideous parody of the circulatory system itself. However, in spite of the awful weight of history, an attempt will be made here, by casting off the shackles of nomenclature and concentrating on fundamentals. Nomenclature will, of necessity, be introduced as required, but not before.

The tetrapod circulatory system is essentially two circuits running off a single pump (**Fig. 1**). Blood alternates between picking up oxygen in the lung circuit and dropping it off in the body circuit. Because two circuits are involved, tetrapods functionally divide the heart into a left side (the body circuit) and a right side (the lung circuit). This functional division is manifested as a physical division in birds, mammals and crocs. However, turtles, lizards, and presumably pareiasaurs, mosasaurs, and so on achieve the same effect using partial separations and some rather neat hydrodynamic controls.

Each side of the heart is also divided, roughly, into an "in box" (atrium) and an "out box" (ventricle). In the conventional "valentine" representation of the heart, it is the atria which form the two upper lobes. With that symbol in mind, the figures here show the atria above the ventricles. In reality, the geometry of the heart is much more complex and somewhat variable.

Birds and mammals have a relatively simple two compartment design. (**Fig. 2**) The lung and body compartments of the heart are not interconnected at all. Each blood cell must make the rounds of both circuits sequentially. One aorta emerges from the left ventricle and pumps blood to the body, which eventually returns, spent and hung over, at the right atrium. The pulmonary artery takes this blood from the right ventricle into the lungs and returns it refreshed and oxygenated, to the left atrium. That is, essentially, all that birds and mammals can manage.

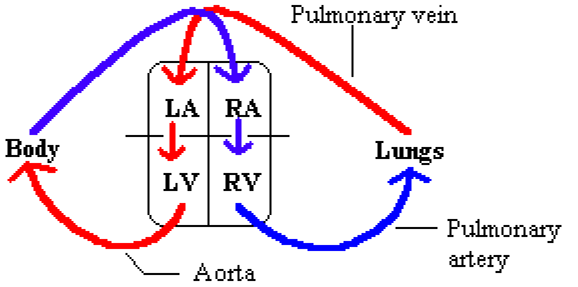


Fig. 2. Schematic circulation in mammals and birds. The central venous channel to the right atrium varies considerably amoung tetrapod groups.

Crocs have *two* aortas, one starting from the left side and one from the right. Unfortunately, the aorta leading from the left side bends to the right, and vice-versa. Thus the aorta connected to the left side of the heart is the "right" aorta. The aorta from the right side is the "left" aorta. The right aorta passes blood more directly to the brain and anterior circulation, although it also directs some to more visceral and posterior regions. The flow from the left aorta is directed more exclusively to the viscera and posterior circulation. However, the two aortas are connected at the base by a shunt, the Foramen of Panizza. **Fig. 3.** As a result, some rather complex patterns of regulation become possible. For reference, **Fig. 4** is included to illustrate a somewhat more realistic picture of the Crocodylian heart in dorsal view. Some of the vessels shown in this figure are discussed in more detail below.

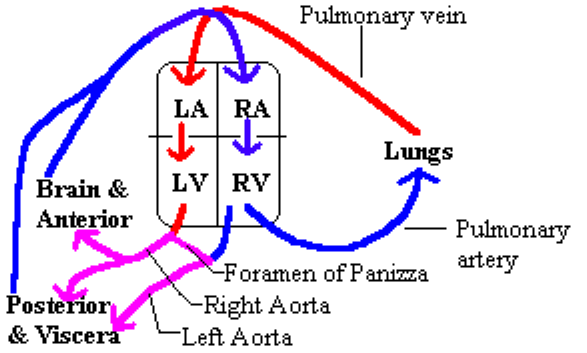


Fig. 3. Central circulation in the Crocodylia

When blood pressure in the left and right compartments is equal, as in a croc at rest on land, there is little movement through the shunt. Oxygenated blood is preferentially received by the brain. In addition, more acidic, deoxygenated blood is preferentially received by the viscera where it is apparently used to produce digestive acids.

When the animal is active on land, circulation approaches the mammalian or avian condition. Blood pressure is high in the left compartment and oxygenated blood is shunted to the left aorta. Deoxygenated blood in the right compartment is almost entirely routed to the lungs.

Finally, when the croc dives, the pulmonary system is partially shut down, causing higher pressure on the right than on the left. As a consequence blood from the right ventricle flows into the right aorta. Since the animal is not breathing, there is no fresh oxygenated blood. Thus the full ventricular output of the heart can be used to circulate nutrients and filter waste products -- particularly important functions when oxidative metabolism cannot be used to break down metabolic wastes. The increased flow through the Left aorta also tends to retain body heat in the central, visceral circulation.

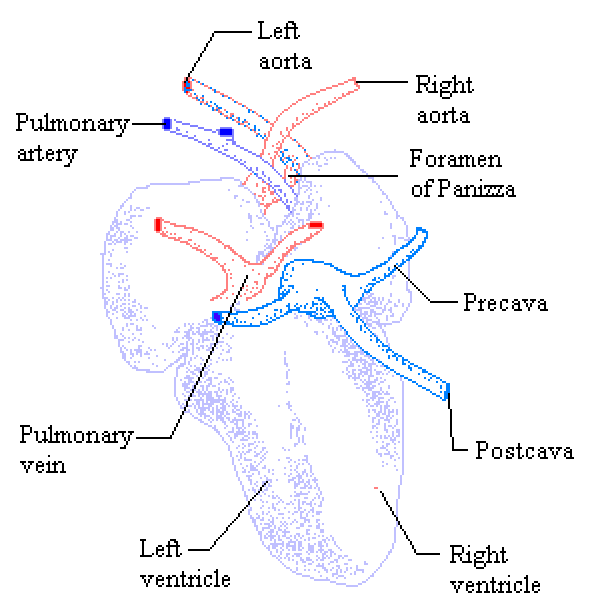


Fig. 4. Crocodylian heart, dorsal view. Vessel sizes have been reduced for clarity. In life, the Foramen of Panizza would not be visible from this perspective.

These are the conventional explanations for the probably circulatory states of the croc heart. As mammals, we are accustomed to think of blood primarily as an oxygen transport mechanism. Our metabolic needs for oxygen are very high, and this perception is not really unfair. However, in vertebrates other than mammals, birds and perhaps other dinosaurs, the respiratory functions of circulation are not as predominant. This requires a more balanced and complex regimen of circulatory regulation, as seen in the Crocodylia. Unfortunately, studies of croc circulatory regulation seem to have focused largely on respiration. As a result, we may be partially missing the point. The rationale and mechanisms of this regulation may actually lie in waste clearance and transport, immunology, regeneration, pH and ion balances, metabolic signaling, and all of the other functions of circulation. --ATW 000521

The basic vertebrate arterial system is based on a one compartment design. That is, the heart pushes blood through the gill arches, through the various organs, and back to the heart. Primitively, then, there was a one-to-one correspondence between aortic arches and gill arches. In fact, one of the more convincing demonstrations of the monophyly of the gnathostomes is that all vertebrates with jaws begin the development of the arterial system with six pairs of aortic and gill arches. The number in jawless vertebrates is much more diverse and is normally larger (eight pairs in lampreys, perhaps ten in ostracoderms). In truth, this evolutionary and embryological unity has a great deal of aesthetic appeal. However, in highly derived forms such as crocs, this basal architecture has been largely replaced with an irregular, asymmetrical flow pattern and these primordial symmetries have relatively little functional significance.

It may be more useful to think of the circulatory system in terms of its functional units. Every vertebrate circulatory system must accomplish at least the following two functions: **gas** transport and **nutrient** transport. For the (at least) two compartment tetrapod circulation, this may be broken down into a series of major sub-tasks as follows:

Gas Transport

1. carbon dioxide and oxygen transport between the heart and respiratory surfaces (usually the lungs);
2. gas transport and exchange with the major, mostly posterior, muscles of the body wall and limbs; and
3. gas transport and exchange with major anterior organs such as the brain and jaw.

Nutrient and Waste Transport

4. mobilization of nutrients from the digestive organs;
5. detoxification of digestive products in the liver; and
6. removal of soluble wastes in the kidneys.

In addition, of course, the circulatory system has critical

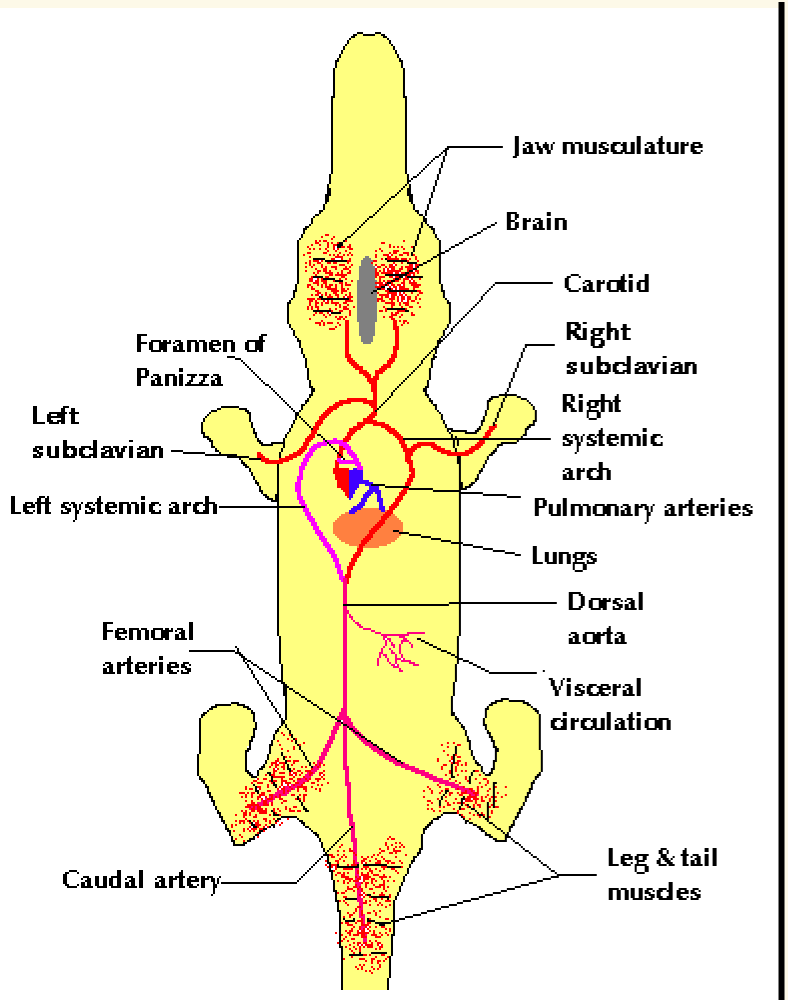


Fig. 1. Crocodylian arterial circulation

functions related to ion and water balance, transport and delivery of hormones and other chemical signals, and the efficient delivery of life-saving quantities of alcohol to grateful neural receptors. However, the foregoing six functions are sufficient to explain the main patterns of circulation for the present purposes. Following the functional outline above (see also figures 1& 2):

1. Gas transport in the heart-lung circuit is accomplished by the pulmonary aorta and pulmonary veins.

2. Gas transport to the posterior consumers occurs through both the left and right systemic arches as outlined in the prior essay. The left aorta joins with the posterior branch of the right aorta to form the dorsal aorta which curves posteriorly and trifurcates into the two femoral arteries and the caudal artery. Return circulation is through the caudal and iliac veins and either through the renal portal or through the lateral abdominal veins to the liver. In either case, the venous blood eventually reenters the heart through the postcava.

3. Gas transport to anterior consumers occurs exclusively through the left systemic arch, which gives rise to the carotid arteries. Return circulation proceeds through the jugulars into the precava or common cardinal vein.*

4&5. Circulation to the digestive organs also occurs through the dorsal aorta. Dissolved nutrients are returned through the hepatic portal, across the hepatic filtration system, and into the postcava.

6. As noted in (2), posterior circulation may pass through the renal portal vein, across the kidneys and, after renal filtration, to the postcava. ATW 000603.

Descriptions

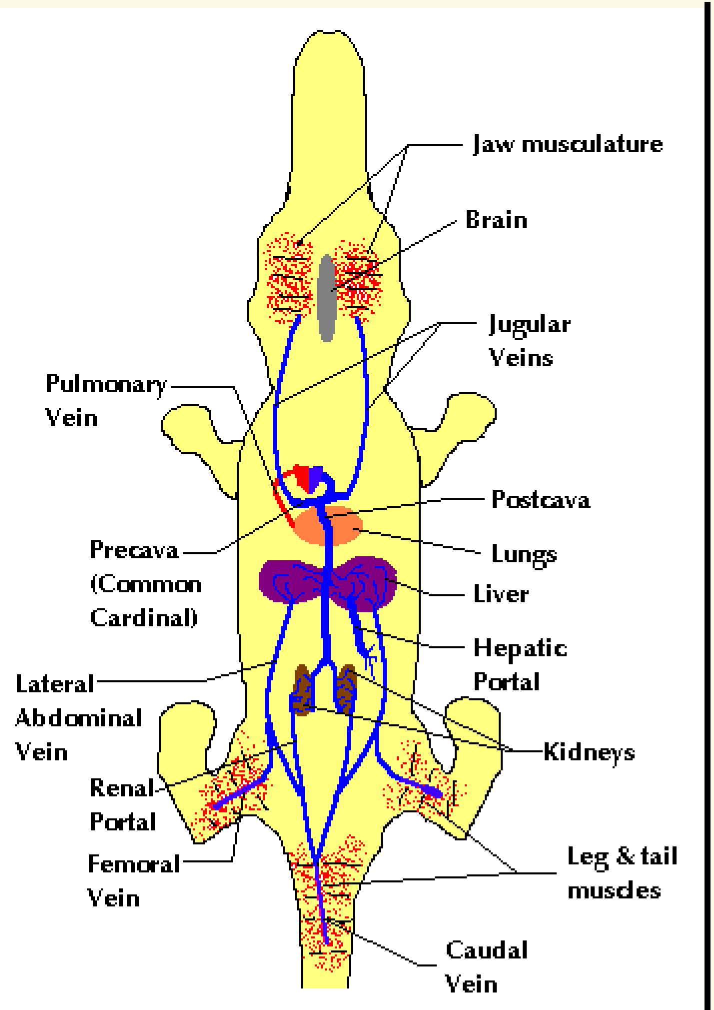


Fig. 2. Crocodylian venous circulation

Crocodylomorpha:

Range: from the Middle Triassic.

Phylogeny: Suchia ::: *Erpetosuchus* + * : Sphenosuchia + Crocodyliformes.

Characters: Skull massive and well-buttressed; no skull kinesis (skull absorbs force of strong, rapid bite); antorbital fenestrae small (closed in modern forms); descending process of prefrontal present [**p**$03]; postfrontals absent; descending process of squamosal absent [$P93] [**p**$03]; squamosal overhangs temporal region [**p**$03]; anterior extension of quadrate; quadrate complex; quadrate contacts prootic [**p**$03]; occiput solid, no or minor occipital fossae [**p**$03]; exoccipital with lateral crest lying anterior to *hypoglossal foramen* [$G02]; palate & braincase strongly integrated; ventral ramus of opisthotic makes extensive contact with prootic anteroventral to *fenestra ovalis* [**p**$03]; middle ear elements pneumatized [**p**$03]; *crista vestibuli* present [**p**$03]; lagenar recess visible externally as prominence on wall of otic capsule [**p**$03]; Eustachian tubes at least partially encased in bone [**p**$03]; prootic not in broad contact with anterior of paroccipital process [**p**$03]; external foramen for abducens nerve solely within basisphenoid [**p**$03]; epipterygoid absent; basipterygoid processes enlarged [**p**$03]; *pila antotica* ossified by basisphenoid and laterosphenoid so that these elements are in contact anterior to *trigeminal foramen* [**p**$03]; secondary palate formed by maxillae & vomers [$P93]; large anterior & posterior *pterygoideus* muscles, oriented horizontally; parasphenoid rostrum forms vertically expanded wedge [**p**$03]; skull bones pneumatized; 24 presacral vertebrae, 2 sacral vertebrae; accessory neural spine on mid-caudal vertebrae [**p**$03]; cartilaginous sternum (modern forms) separates posteroventral extensions of coracoids; no clavicle (all suggest obligate quadruped); elongated carpals (ulnare and radiale) perhaps involved in giving extra swing to foreleg [$P93]; manus IV with 5 phalanges (reversal) [**p**$03]; pubic shaft length >3x width of acetabulum [**p**$03]; pubis excluded from acetabulum since Late Jurassic; acetabulum semi-perforate [**p**$03]; femoral head without distinct neck, but bent medially with parallel medial & lateral sides [$P93]; metatarsal I length at least 85% length of Mt III [**p**$03]; pes IV with <5 phalanges [$P93]; pes V with 2 phalanges [**p**$03]; paramedial osteoderms sculptured [$P93]; osteoderms with anterolateral articulatory process & dorsolateral keel (as in *Euscolosuchus*) [S92].

Notes: [1] "[**p**03]" refers to our own analysis of published data.

Links: The Forgotten Archosaurs - infpormative blog dedicated to fossil crocs, gwu faculty clark image (cladogram); columbia; Crocodylomorpha; Crocodylomorpha -- The Dinosauricon; Reptilia.html; Basal Crocodylomorpha [Sphenosuchia] after Clark, Sues & Berman, ... (Mikko's Phylogeny); CROCODYLOMORPHA (basic systematics, with some references); CROC LINKS (some individual links and pointers to the Big Three croc sites); Those three sites are: Crocodilians: Natural History & Conservation: Crocodiles, Caimans, Alligators, Gharials (Crocodilian.com), The Bibliography of Crocodilian Biology (still extraordinary bibliograhical reference from Prof. Mason Meers, though now a bit dated), and Crocodile Specialist Group (mostly a conservation site); RAPID COMMUNICATION FIRST RECORD OF ERPETOSUCHUS (REPTILIA- .... (one of two relatively recent papers discussing *Erpetosuchus* -- the sister of Crocodylomorpha); Steve Turner's Crocodilian Link Page (another good links page, but also somewhat dated).

References: Gower (2002) [G02], Parrish (1993) [P93], Sues (1992) [S92]. ATW031223.

Sphenosuchia: *Gracilisuchus?* (like stem Archosauriforms), *Sphenosuchus*.

Range: Middle to Late Triassic

Phylogeny: Crocodylomorpha **:** Crocodyliformes + * **:** Trialestidae + Sphenosuchidae.

Characters: Apparently characterized by absence of derived characters(?!). Pneumatization limited; posterior process of prefrontal turns onto orbital surface of frontal where it inserts into a groove, rather than maintaining its usual superficial position on the dorsal skull roof; rim on lateral margin of supratemporal fossa; squamosal arcuate, flaring, with low-angle articular surface for the postorbital; squamosal with forked posterior process, straddling paroccipital process; quadrate does not contact lateral wall of braincase; little or no secondary palate.

Links: link; crocodylomorpha.

Trialestidae: *Trialestes* (= *"Triassolestes"*)

Range: Late Triassic of South America.

Phylogeny: Sphenosuchia **:** Sphenosuchidae + *.

Characters: small, lightly built animal; elongate limbs; fore and hind legs of equal size; elongate carpals [C+00]; digitigrade; well-developed supraacetabular crest (like dinosaurs) [C+00]; acetabulum perforate (like dinosaurs) [C+00]; medium-sized terrestrial insectivore/carnivore.

Note: may turn out to be a primitive dinosaur. The again, it may be a crocodylomorph, but not a sphenosuchian. The third possibility is that specimens from different taxa have been referred to this single species. See [C+00].

Links: Trialestes; New References; Trialestes.

References: Clark *et al.* (2000) [C+00]. ATW030625

Sphenosuchidae: *Dibothrosuchus* (Early Jurassic of China), *Pedeticosaurus* (Early Jurassic of South Africa), *Platyognathus* (Early Jurassic of China), *Sphenosuchus* (Early Jurassic of South Africa), Terrestrisuchus (Late Triassic of England).

Range: Middle Triassic to Early Jurassic of Europe, North America, South Africa and China(?).

Phylogeny: Sphenosuchia **:** Trialestidae + *.

Characters: Loss of postfrontal unites sphenosuchids to crocodiles; erect, bipedal posture; terrestrial.

Links: All About Archaeopteryx (historical interest); Biology 356; Nathis Fauna Krokodillen (Dutch). 020317.

Page Back | Unit Home | Page Top | Page Next

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Crocodilia: Crocodyliformes

Gobiosuchids, Teleosaurs & Metriorhynchids

Abbreviated Dendrogram

```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--+--Gobiosuchidae
      `--Mesoeucrocodylia
         |--Thalattosuchia
         |  |--Teleosauridae
         |  `--Metriorhynchidae
         `--Metasuchia
            |--Notosuchidae
            `--Neosuchia
               |--Dyrosauridae
               `--Crocodylia
                  |--Gavialidae
                  `--+--Alligatoridae
                     `--Crocodylidae
```

Contents

Taxa on This Page

1. Crocodyliformes
2. Gobiosuchidae X
3. Mesoeucrocodylia
4. Metriorhynchidae **X**
5. Protosuchia **X**
6. Teleosauridae **X**
7. Thalattosuchia X

Descriptions

Crocodyliformes:

Range: from Late Triassic.

Phylogeny: Crocodylomorpha: Sphenosuchia + *: Protosuchia + (Gobiosuchidae + Mesoeucrocodylia).

Characters: Maxilla shorter than jugal; occipital contacts ventromedial portion of quadrate to enclose carotid and form passages for cranial nerves IX-XI; basisphenoid forms a dorsoventral expanded ("cultriform") process; basisphenoid joint suturally closed; parietal extends dorsally to form ventrolateral edge of trigeminal foramen; antorbital fenestra smaller than orbit; quadrate hollow, with dorsal fenestra; dorsal head of quadrate contacts laterosphenoid; quadratojugal very broad; 2 large palpebrals; skull table flat in temporal region; tail surrounded by osteoderms; ventromedial expansion of coracoid; coracoid anteriorly concave; scapula broadens greatly dorsally (reversed in later forms); pubis at least partly excluded from acetabulum by ant process of ischium.

Links: Crocodylomorpha; NOVA: Outlasting the Dinosaurs; Crocodilian Locomotion (high walk); Clark (1994) cladogram; Crocodylomorpha -- The Dinosauricon.

Discussion: The phylogeny of the Crocodylomorpha is an interesting case study in the status of phylogenetic analysis. Until the mid-1980's the generally accepted phylogeny was essentially Linnaean. Sphenosuchids, Protosuchids, "Mesosuchids," and Eusuchids were believed to form different, and probably successive, suborders of the Order Crocodylomorpha. The exact evolutionary relationships among these groups were studied, but perhaps not a matter of great concern or interest. See, e.g., the treatment by Carroll (1988: 277-83). Then, in that same year, Benton & Clark published their landmark cladistic study which found the Mesosuchia to be *paraphyletic*. (For reasons to be discussed, this is the scheme that will eventually be adopted here). This was not an unexpected result, and it has widely been accepted as correct. Benton & Clark found that the sphenosuchids and protosuchids were indeed successive branches from the Crocodylomorpha. However, the next major division separated the Thalattosuchia from all other crocs. The Thalattosuchia consist of the well studied marine metriorhynchid and telosaur families (see, e.g. Hua & Buffetaut (1997)). Benton & Clark erected (a) the Mesoeucrocodylia to contain both thalattosuchids and their last common ancestor with living Crocodylia, and (b) the Metasuchia to contain the non-thalattosuchian branch of this clade.

The Thalattosuchia had already been widely recognized as having a close relationships, so this result was reasonably close to expectations. The exact branch point assigned by Benton & Clark, and the separation of, for example, *Sebecus* from the former "Mesosuchian" mainstream was not as predictable, but again not unreasonable. In fact, it is just this sort of insight that one might expect to get from a computer analysis of the fossil record.

Perhaps unfortunately for croc phylogeny, computers became vastly more powerful over the next few years. Clark (1994) then published a new study using a great deal more morphological data. The resulting cladogram is available, in part, at his home page. A variation is found at the Dinosauricon.

As Clark himself was the first to recognize, something is clearly odd about these results. Clark's analysis reunites all of the *Mesozoic* marine crocs: not only the Thalattosuchia, but the Dyrosaurs and other groups, which are found to be more basal. *Sebecus* is now basal to both living crocs and their extinct marine relatives. The problem is that this phylogeny is not only "discordant" with the stratigraphic record, as Clark notes, but it stands the stratigraphic record on its head. The Thalattosuchids are primarily Jurassic and disappear by the early Cretaceous. Dyrosaurs are found from the Upper Cretaceous to the end of the Eocene. *Sebecus* is restricted to the Eocene of South America. Yet Clark's phylogeny places these groups in the *reverse* order. Bluntly, it requires more *ghost lineages* than a Halloween film festival.

What might have gone wrong? Clark himself notes that the results depend on the non-correlation of "*longirostrine*" characters (the long, thin jaw frequently found in fish-eating forms). As he notes, this assumption is undermined by the presence of the same suite of adaptations in the living gavials, a group which clearly has only distant kinship with Mesozoic marine crocs. Clearly, if most marine piscivores on the croc model are likely to develop the same related group of adaptations, cladistic analysis will tend to group them without regard to actual relationships.

The problem may be more fundamental. Croc phylogeny has a number of features which make it a sort of worst case for cladistic analysis. First, crocs are notoriously conservative. The basic crocodylian design has changed very little in the last 200 million years. As a result, the phylogenetic signal is weak. There is simply very little phylogenetic divergence to detect. Second, the adaptations required by marine life are in fact rather stereotyped. For example, the long, thin piscivorous rostrum, polyphalangy, amphicoelous vertebrae, thickening (pachyostosis) of ribs and vertebrae; development of caudal spines or of a sort of bifurcated caudal "fin", and certain changes in the limb girdles are frequently encountered in all sorts of different organisms making the adaptation to open water life. These changes tend to swamp (perhaps a poor choice of wording in this context) the relatively weak phylogenetic signal in crocs. Third, and to make matters worse, crocs had numerous competitors as large marine predators in the Mesozoic and early Cenozoic: ichthyosaurs, turtles, plesiosaurs and their relatives, mosasaurs, champsosaurs -- not to mention sharks and other predatory fish. This was a contest that the crocs gradually lost. Eventually, crocs were largely restricted to the role of amphibious tropical predators in special environments. As a consequunce, crocs tended to become *less* marine as time progressed, making the later crocs *less* specialized than earlier forms. The net result is that Clark's 1994 phylogeny may well be measuring the degree of marine specialization, instead of a real phylogenetic signal, and doing so in circumstances under which the apparent phylogeny reversed the actual pattern of speciation.

If the thesis advanced here is correct, the story of croc phylogeny may have some significant lessons for phylogenetic systematics. Most notably, the assumption that characters are independent *cannot* be taken for granted. (See glossary entry on *parsimony* for discussion of this point). The original Benton & Clark (1988) study is preferable because the characters measured are fewer, but more diverse. This increases the chance that the measured attributes are actually independent. The seduction of computing power is in the temptation to measure the same thing many times. The more traits measured, the greater the chance that significant elements are correlated and that the presumption of independence is violated. Phylogenetic systematics has actually shown itself to be remarkably robust, despite the fact that independence cannot be proven in most cases and is probably violated frequently. Nevertheless, independence cannot be assumed away, nor does increasing the size of the character matrix avoid the necessity for validating the assumptions of the study. In fact it may, as here, simply make things worse.

Second, and correlatively, it is neither inappropriate nor unscientific to test the results of cladistics against common sense and stratigraphy. In fact, the assumptions which underlie the cladistic result can usually be tested in no other way. Not only are the assumptions of a study open to question, the quality of the data itself is not always clear. See Ahlberg & Clack (1998) for a recent report in which the inclusion of one poorly understood taxon in the character matrix nearly destroyed the value of an otherwise excellent study. (Indeed, the study is all the more excellent because the authors recognized and dealt with the problem). Unless and until phylogenetic systematics can incorporate the equivalent of a standard error bar in the matrix, it is too easy to claim accuracy when one has only achieved precision.

For reference, the (more or less) complete Benton & Clark (1988) cladogram is as follows [note that this arrangement has now been twice transformed from one format to another and may contain errors] :

```
Crocodylomorpha
|--Pseudohesperosuchus
|--Saltoposuchus
`--+--Dibothrosuchus
   |--Sphenosuchus
   `--+--"Kayenta form"
      `--Crocodyliformes
         |--Protosuchidae
         |  |--Hemoprotosuchus
         |  |--Protosuchus+
         |  `--Kayenta edontosuchus
         `--+--Odontosuchus
            `--+--Gobiosuchus
               `--Mesoeucrocodylia
                  |--Thalattosuchia
                  |  |--Pelagosaurus
                  |  `--+--Teleosauridae
                  |     `--Metriorhynchidae
                  `--Metasuchia
                     |--"Fruita form"
                     `--+--Notosuchus
                        `--+--Baurusuchus
                           |--Libycosuchus
                           `--+--Sebecus
                              `--Neosuchia
                                 |--+--Theriosuchus
                                 |  `--Alligatorium
                                 `--+--Dyrosauridae
                                    |--Pholidosauridae
                                    |--Goniophilidae
                                    `--+--Shamosuchus
                                       |--Bernissartia
                                       `--+--"Glen Rose form"
```

```
`--Eusuchia
   |--Hylaeochampsa
   |--Stromatosuchus
   |--Leidysuchus
   `--Crocodylia
```

Protosuchia: *Erythrochampsa* (Early Jurassic of South Africa), *Nothochampsa* (Early Jurassic of South Africa), *Orthosuchus* (Early Jurassic of South Africa), *Protosuchus* (Early Jurassic of North America).

Range: upT-upK(?).

Phylogeny: Crocodyliformes: (Gobiosuchidae + Mesoeucrocodylia) + *.

Characters: Reduced upper temporal and antorbital fenestrae; lower canine tooth (like Sphenosuchia) fits into recess between maxilla & premaxilla; basisphenoid larger than basioccipital; extensive ventral contact between quadrate and basisphenoid (quadrate integrated w lateral braincase); pneumatic pterygoid; well-developed secondary palate; quadrate condyles only slightly protruding beyond posterior margin of braincase, and lack of retroarticular process; parietals fused; post-orbital & post-frontals single ossification; post-cranial skeleton like Crocodylia except vertebrae shallowly amphicoelous. Terrestrial forms.

Gobiosuchidae: *Gobiosuchus.*

Range: upT?

Phylogeny: Crocodyliformes:: Mesoeucrocodylia + *.

Mesoeucrocodylia: Marine & amphibious crocs from the Mesozoic and Cenozoic.

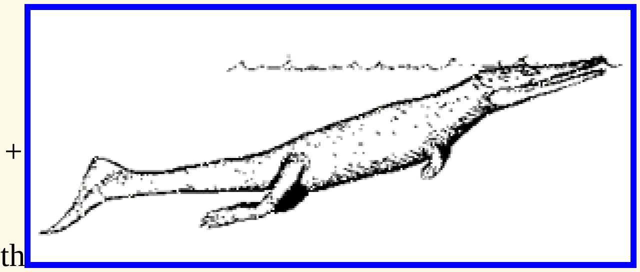
Range: fr lwJ.

Phylogeny: Crocodyliformes:: Protosuchia + *: Thalattosuchia + Metasuchia.

Characters: Posterior extension of palatines (secondary palate); vertebrae amphicoelous; some specialized marine forms with loss of dermal armor, forelimbs as paddles, and thin, elongated snouts.

Links: Paleoecology of the Metriorhynchidae; Crocodilian Biology Database - Locomotion (gallop) (relevance?); DINOSAUR-1995Apr: new Refs; DINOSAUR-1995Oct: Re: Crocodile program on Discovery channel; New ref - Carrier & Farmer; Re: postparietal fenestrae lost; Nathis Krokodillen (Dutch).

Thalattosuchia: *Pelagosaurus*



Range: lwJ-upEc (lwK??).

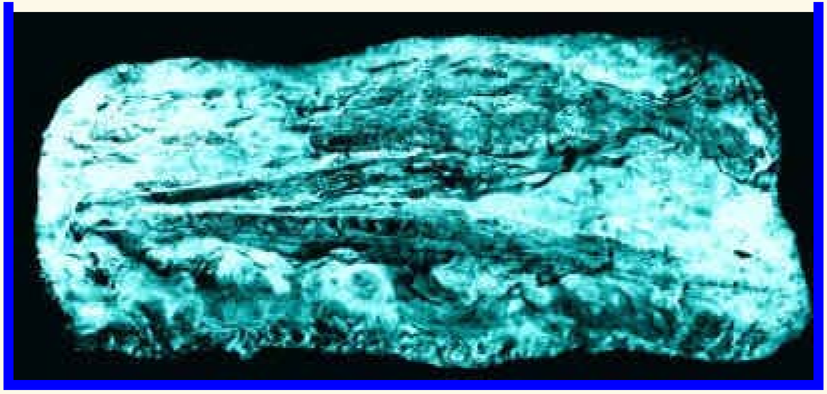
Phylogeny: Mesoeucrocodylia: Metasuchia + *: Teleosauridae + Metriorhynchidae.

Characters: highly adapted to aquatic life; long snout; long tail with a tail fin; padle-like limbs; marine.

Links: Paleontology and Geology Glossary: T; paleoecology of the Metriorhynchidae; Untitled Document; Chronologia prochesov (Russian).

Note: Perhaps the only archosaurs fully adapted for marine life. 011113.

Teleosauridae: *Machimosaurus*, *Mystriosaurus*, *Pelagosaurus*, *Steneosaurus*, *Teleosaurus* (middle Cretaceous of North America)



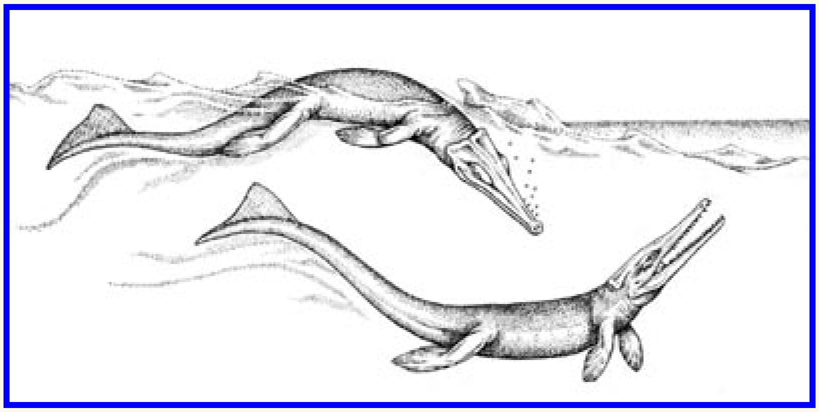
Introduction: One of several families of marine mesosuchian crocodiles.

Range: Early Jurassic to middle Cretaceous of Europe, North America.

Phylogeny: Thalattosuchia: Metriorhynchidae + *.

Characters: The body was long and slim, the back heavily armoured. The jaws extremely narrow and elongated, lined with sharp interlocking teeth from catching fish and belemnites. Forelegs only half the length of the hind limbs, and held flat against the body when swimming. Propulsion came from sinuous movements of the body and tail. Not highly specialized for marine life and may have retained amphibious habits.

Links: PANGEA, Untitled Document; Information: Krokodil (German); Teleosauridae; juras2.html (Spanish); Bone histology as a clue in the interpretation of functional ... (JVP abstract); SUI RESTI DI COCCODRILLO DEL ROSSO AMMONITICO VERONESE DI SASSO ... (article in Italian); reptiles (table); PANGEA (table); Fauna der Oberen Jura Deutschlands; Information- Krokodil; ATW031027.



Metriorhynchidae: *Geosaurus*, *Metriorhynchus*, *Teleidosaurus*.

Range: Early to Middle Jurassic of Europe and South America.

Phylogeny: Thalattosuchia: Teleosauridae + *.

Characters: Skull dorsoventrally flattened (quick lateral attacks); skull highly pneumatized; nares are not raised; osteoscutes absent; forelimbs with hydrofoil shape; generalist swimmers; epipelagic stalking predators

Links: paleoecology of the Metriorhynchidae; Untitled Document; cocodrilos marinos (Spanish. **Best on the Web**); PANGEA (Italian); Pelagosaurus typus (French); Information: Krokodil (German). 020317.

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checked ATW031027

Crocodilia: Metasuchia

Abbreviated Dendrogram

```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         |--+--Baurusuchidae
         |  `--Libycosuchidae
         `--+--Sebecosuchidae
            `--Neosuchia
               |--+--Dyrosauridae
               |  `--+--Terminonaris
               |     `--Sarcosuchus
               `--Crocodylia
                  |--Gavialidae
                  `--+--Alligatoridae
                     `--Crocodylidae
```

Contents

Taxa on This Page

1. Baurusuchidae X
2. Dyrosauridae X
3. Libycosuchidae X
4. Metasuchia
5. Neosuchia
6. Notosuchidae X
7. *Sarcosuchus* X
8. Sebecosuchidae X
9. *Terminonaris* X

Sebechosuchidae

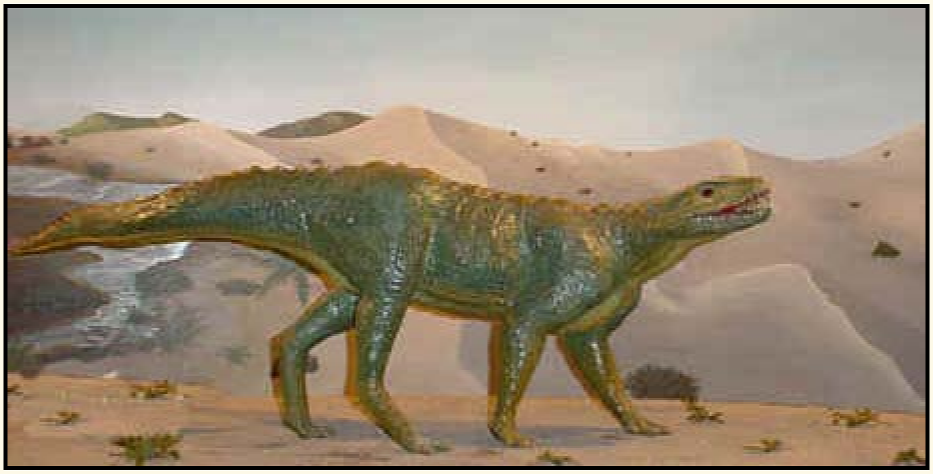
Not a great deal is known about the Sebecosuchidae. Indeed, the post-cranial skeleton is completely unknown. A few isolated vertebrae and osteoscutes have been found in association with Sebecosuchid remains. However, characterizing these fossils as Sebecosuchid is hazardous.

As a result, there is some controversy about the ecological place of these animals. Traditionally, it was supposed that the Sebecosuchids occupied a transitional top-predator niche after the extinction of the dinosaurs and before the arrival of carnivorous placental mammals in South America. This theory seems to have fallen into disfavor for two reasons. First, the Sebecosuchids disappeared a bit too early -- around the mid- to late Miocene, before placentals really got going in South America. Second, Sebecosuchids are almost always recovered from environments that were river and lake deposits in tropical forests: that is, jungle areas like the Amazon Basin today. This had led to speculation that they were semi-aquatic riparian predators like living Crocodilians.

However, Busbey (1986) points out that, even if this were the case, the Sebecosuchids cannot have hunted in the same manner that crocs do today. Modern crocs latch on to large prey and roll with it into the water, both to kill and to disarticulate. Sebecosuchids, with their long, thin, but very tall, rostrum, would be far less suited for this strategy. *See also*: Holtz (1997). Further, their jaw is specialized to maximize the strength of the jaw-*opening* muscles and the teeth are very similar to Theropod teeth, designed for slicing and tearing rather than as holdfasts. Busbey notes that the structure of the jaw is similar to Varanidae -- terrestrial ambush predators. However, this does not explain their distribution, nor the laterally thin, almost pisciverous, jaw.

Unfortunately, there is little good Sebecosuchid material. For this reason, it is entirely possible that the association with aquatic deposits is simply a taphonomic artifact. However, even it reflects an actual ecological association, the narrowness of the jaw may simply reflect the optimal mechanics for specialized prey: perhaps flightless birds. One could imagine, for example, *Sebecus* as a moderately long-legged ambush predator feeding on flightless or nearly flightless wading birds. It springs or rushes out of ambush, opening its jaws quickly and allowing them to slam together hard enough to snap the relatively fragile tibiotarsus of the bird. Unlike mammalian prey, this immediately immobilizes the victim, making a rolling, aquatic attack unnecessary.

Descriptions



Metasuchia: *Notosuchus* + *Crocodylus* [S+01].

Range: from the Early Cretaceous

Phylogeny: Mesoeucrocodylia : Thalatosuchia + * : Notosuchidae + (Baurusuchidae + Libycosuchidae) + (Sebecosuchidae + Neosuchia)

Characters: Small or moderate body size [S+01].

Image: *Notosuchus* from **www.neuquentur.gov.ar - default**

Links: Metasuchia after Sereno, Larsson, Sidor & Gado, 2001.

References: Sereno *et al*. (2001) [S+01].

Notosuchidae: *Notosuchus*.

Range: upK of SAm.

Phylogeny: Metasuchia **:** (Baurusuchidae + Libycosuchidae) + (Sebecosuchidae + Neosuchia) + *.

Baurusuchidae: *Baurusuchus*.

Range: Late Cretaceous, possibly surviving to Eocene, of South America & Europe.

Phylogeny: Metasuchia **::** Libycosuchidae + *.

Characters: Therapsid-like dog-sized terrestrial forms.

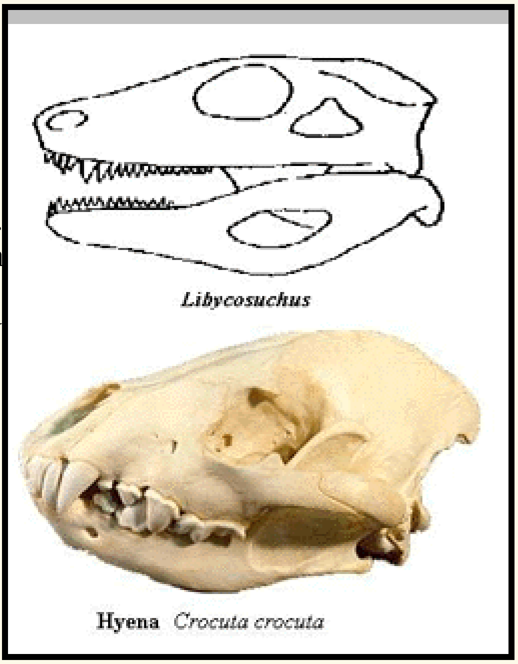
Links: reptiles; トミーの進化論 in どうぶつ大百科; Re- New Mesozoic vertebrate articles.   ATW030601.

Libycosuchidae: *Libycosuchus*.

Range: lwK-upK of Afr.

Phylogeny: Metasuchia **::** Baurusuchidae + *.

Characters: Small (~1 m) terrestrial croc, with very strong jaw muscles. Very short, rather tall rostrum (shorter than post-orbital region); diastema absent; deep lower jaw; large pterygoid "wings" (related to adductor muscle development); **$** maxillae excluded from margins of pterygoid vacuities by palatine and "transverses" (= ectopterygoids?); choanae have been variously placed and actual position unknown; nares placed laterally on rostrum; orbits large; antorbital fenestra present only as unperforated depression; very large mandibular fenestra; sharp angle between dorsal and posterior ("ventral"?!) faces of the occiput (*i.e.* a very sharp or abrupt angle between the top & back of the head); quadrate strongly curved, with large ventral process, displacing jaw articulation anteriorly; post-cranial skeleton known only from fragments.



Links: Buffetaut, E.

Image: The comparison with hyena skulls is instructive. Lycaon sp. Hyena Skull from Skulls Unlimited; Image of *L*. from Buffetaut (1982); Hyena skull © 1998 Kronen Osteo, by permission.

Note: As Buffetaut (1982) points out, the skull shows numerous adaptations for an *exceedingly* strong & fast bite.

Sebecosuchidae: *Sebecus*, *Ayllusuchus*.

Range: Pc-Mc of SAm, Eur? Afr?.

Phylogeny: Metasuchia **:::** Neosuchia + *.

Characters: Active terrestrial predators. Tall, narrow rostrum; sides of rostrum tall and nearly vertical; teeth long, curved, laterally compressed and se (very similar to theropod teeth); 4 teeth on premaxilla; 10-11 teeth on maxilla; no enlarged maxillary teeth; teeth widely spaced, intercalate; posterior ends of maxillae meet on palate anterior to palatine; broad maxilla forms sides of rostrum, and narials forms flat dorsal portion, terminating in a premaxilla with substantial diastema; maxilla and premaxilla do not overlap; no maxillary fenestra; nares face antero-laterally or dorso-laterally; maxilla and, especially, premaxilla deeply sculptured with deep pits connected by channels; rostrum widens abruptly in front of orbits; orbit relatively small; angular and surangular large, long and strongly curved dorsally; axial skeleton largely unknown.

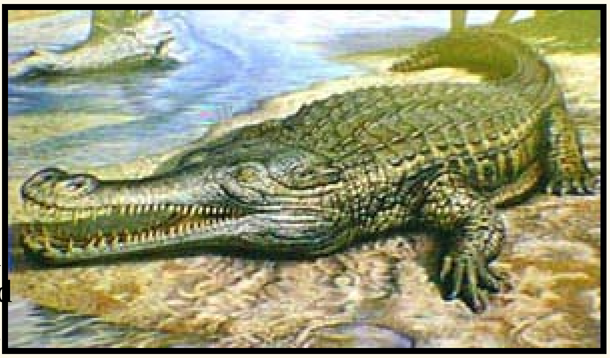
References: Busbey (1986); Gasparini (1984).

Image: life reconstruction of a juvenile *Sebecus* altered from an image of *Alligator* © John White with permission.

Neosuchia:

Range: fr lwK.

Phylogeny: Metasuchia **:::** Sebecosuchidae + * **:** Crocodylia + (Dyrosauridae + (*Terminonaris* + *Sarcosuchus*)).



Dyrosauridae: *Atlantosuchus, Dyrosaurus, Hyposaurus, Phosphatosaurus, Rhabdognathus, Sokotosuchus, Tilemsisuchus*.

Range: Late Cretaceous (Maastrichtian) to Early Eocene worldwide.

Phylogeny: Neosuchia **::** (*Terminonaris* + *Sarcosuchus*) + *.

Characters: ~4m longirostrine forms; external mandibular fenestra reduced; tall neural spines; lateral area of tail expanded by elongated chevrons; appendicular skeleton not reduced; limbs relatively long (~1.5 - 2 times longer than in the image); limbs subequal, with no polydactyly or hyperphalangy; osteoderms reduced; strong swimmers & possibly walkers with lightly built snout, favoring shallow marine and some freshwater habitats.

Links: Treasures of the Earth Ltd. Dyrosaurus; AMBAR; Ablauf der Evolution: Mesozoikum; Kreide (German); Re: K/T impact.

References: Hua & Buffetaut (1997). ATW021015.

Terminonaris: *T. browni* Osborn, 1904; *T. robusta* Mook, 1934.

Range: mK of NAm.

Phylogeny: Neosuchia **:::** *Sarcosuchus* + *.

Links: An abstract of a paper supporting our phylogenetic placement can be found at *Terminonaris*. Very recent finds confirm the placement, as stated at Crocs in CJES. Other DML entries also touch on some anatomical aspects of the genus. *See* New in Palaeontology, 48, 2 and Re- Gnathosaurus question. German summaries of some of the most recent work can be found at Literaturbericht. We have not been able to locate any other worthwhile links on *Terminonaris*. However, the many links relating to *Sarchosuchus* compare the two, closely-related forms.

Note: for list of characters uniting *Terminonaris* with *Sarcosuchus*, see *Sarcosuchus*.

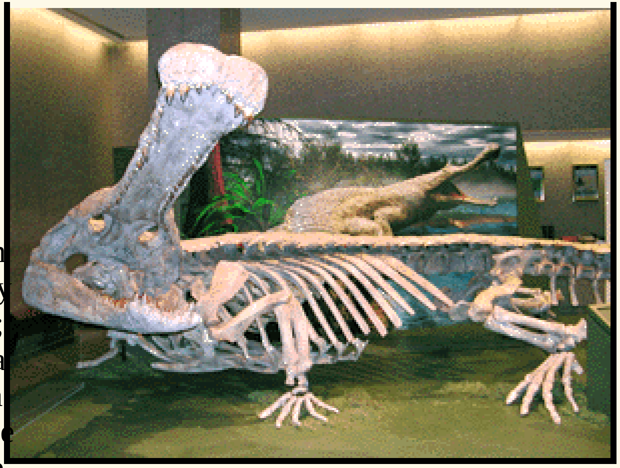
References: Sereno *et al.* (2001), X-C Wu, AP Russell & SL Cumbaa (2001), **J. Vert Paleontol.** 21: 492. 011128. ATW050804.

Sarcosuchus:

Range: middle Cretaceous of Africa (Niger)

Phylogeny: Neosuchia **:::** *Terminonaris* + *.

Characters: Up to 11m & 8000 kg; snout 75% of skull length, very



long but much wider than usual longirostrine forms; premaxilla form expanded bulla around undivided nares; large choanae separated by narrow pterygoid septum; choanae bordered by palatines & pterygoids; 5 premaxillary, 30 maxillary, 31 dentary teeth; premaxilla 3-4, maxilla 10 & dentary 3-4 enlarged; teeth stout, conical, sharp-pointed, with small anterior & posterior keels; all dentary teeth occlude inside maxillary toothrow; dentary also 10 cm shorter than maxilla; large diastema; no teeth insert into diastema; no maxillary fossae; very long, narrow anterior rami of nasals remains in medial contact with premaxillae; orbits dorsal & moderately telescoped; trapezoidal supratemporal fossa slightly larger than orbit; cervical vertebrae with shallow ventral keel and overlapping cervical ribs; all vertebrae amphicoelous; dorsal vertebrae with long transverse processes & short, stout neural spines; scapulae, coracoids & pubes flare widely & sacrum provides very broad dorsal surface; continuous, broad line of osteoscutes from neck to tail; immature specimens appear conventionally longirostrine, & snout broadens late in development; generalized fresh water ambush predator.

Note: Synapomorphies of unnamed *Sarcosuchus* + *Terminonaris* clade per [S+01]: premaxillary palate with circular paramedian depressions; premaxillary teeth and alveolar margin angled postreoventrally; premaxillary tooth row angled posterolaterally; last pmx tooth lateral to 1st mx tooth; premaxillary toothrow ventrally offset; distal dentary transversely expanded. Now that's interesting! Almost *all* the characters joining the two species are, according to Sereno's work, features acquired by *Sarcosuchus* individuals late in ontogeny. This decoupling of dentary and maxillary development might require some significant genetic novelties. See Meckel's Cartilage.

Links: National Geographic SuperCroc--Sarcosuchus imperator, photos, maps, bios, tour information; African Fossil Find: 40-Foot Crocodile (washingtonpost.com); Geological Society - News - Giant croc and a right load of bulla; RP-Online - Wissenschaft (German); Untitled Document. Too many good sites to list them all.

References: Sereno *et al.* (2001) [S+01]. ATW030803

Page Back | Unit Home | Page Top | Page Next

checked ATW050804

Crocodilia: Crocodylia

Abbreviated Dendrogram

```
ARCHOSAURIA
|--+--PTEROSAURIA
|  `--DINOSAUROMORPHA
|
`--CROCODYLOMORPHA
   |--Sphenosuchia
   `--Crocodyliformes
      |--Protosuchia
      `--Mesoeucrocodylia
         |--Thalattosuchia
         `--Metasuchia
            |--Notosuchidae
            `--Neosuchia
               |--Dyrosauridae
               `--Crocodylia
                  |--Gavialidae
                  `--+--Alligatoridae
                     `--Crocodylidae
                        |--Crocodylinae
                        `--Tomistominae
```

Contents

Taxa on This Page

1. Alligatoridae
2. Crocodylia
3. Crocodylidae
4. Crocodylinae
5. Gavialidae
6. Tomistominae

Descriptions

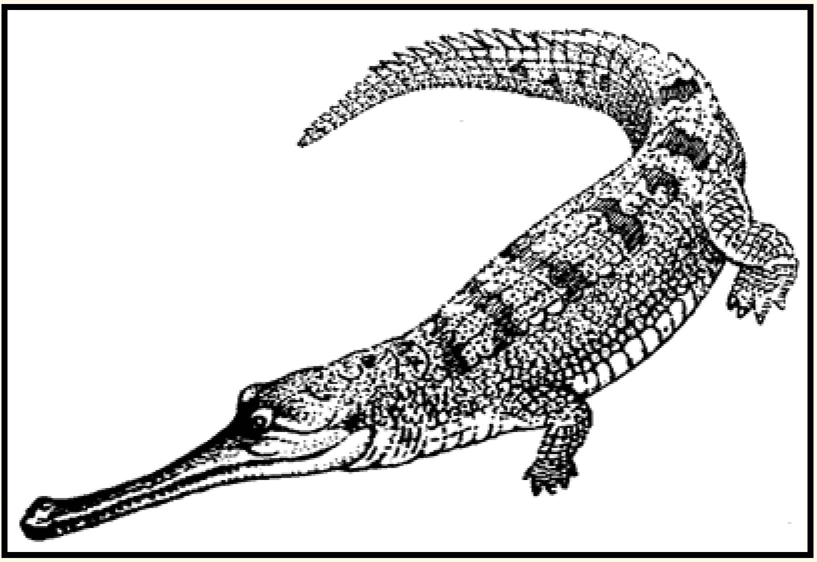
Crocodylia: for our purposes, we can consider Crocodylia as the crown group including all of the living crodiles, alligators, gharials and *Tomistoma*.

Range: From the Late Jurasic, fl Late Cretaceous.

Phylogeny: Neosuchia **:** (Dyrosauridae + (*Terminonaris* + *Sarcosuchus*)) + * **:** Gavialidae +

Characters: Internal nares completely surrounded by pterygoids; centra of almost all vertebrae procoelous. Did not begin decline until climate deteriorated in ~Pc. 4-chambered heart, but effectively 3 compartments.

Image: Two gharials from the Repti-Page. ATW020318.



Gavialidae: *Gavialis* > *Crocodylus niloticus*. *Eogavialis* (Eocene-Oligocene of Africa), *Eotomistoma* (Late Cretaceous of Mongolia), *Gavialis* (from Pliocene of India, Asia & South America), *Gryposuchus* (Pliocene to Pleistocene of Brazil), *Ramphosuchus* (Pliocene of India -- possibly a tomistomid), *Thoracosaurus* (Late Cretaceous to Eocene of Europe & North America).

Range: from Late Cretaceous.

Phylogeny: Crocodylia **:** (Alligatoridae + Crocodylidae) + *.

Introduction: These crocodylians developed a very slender snout, with very small nasal bones, which reduce resistance in the water. There is also a change in the set of jaw muscles being emphasized. All long-snouted crocodyliforms reduce the pterygoideus musculature and enlarge the temporalis assemblage. This is evident even in extinct forms in which the supratemporal fenestra (openings) in the skull are enormous. For these fish eaters, there is little need for the crushing blow the heavy crocodylid skull could potentially produce. A fast, snapping action is far more important. This tendency developed independently in a variety of crocodylian lineages.

This line of long-snouted fisheaters first appeared when dinosaurs still ruled the Earth. The genus *Thoracosaurus*, only distantly related to modern forms, appeared in the Maastrichtian epoch and continued through to early Eocene, inhabiting Europe and eastern North America. It was formerly included under the Tomistoninae. The Mongolian species *Eotomistoma multidentata* is even earlier (Turonian?), and did not survive the end of the dinosaurs. There is no guarantee that *Eotomistoma* really belongs to this group. It had as many as 48 pairs of straight, pointed teeth on each jaw (hence the name *multidentata*).

Modern gavials seem to have evolved in Africa during the Eocene, with the Egyptian species *Eogavialis africanus* (middle to late Eocene) and *E. gavialoides* (late Eocene to Early Oligocene).

As with all the crocodile tribe, the Gavaliadae were much more diverse and widespread in the past than they are today. The gigantic *Ramphosuchus crassidens* from the Pliocene of India may have been as much as 15 to 18 meters in length. The group was common not only in Asia but in Central and South America as well, where they persisted until the Pliocene. Only one species of this lineage survives, the gavial or gharial, *Gavialis gangeticus*, also known as the 'true' or 'Indian' gavial. It lives in the Indus, Ganges and Brahmaputra river systems, feeding on fish. Despite its large size (upto 6 meters in length) it is harmless to man. The elongate snout has 27-29 teeth on each side, and a long narrow snout that widens at the nostrils. (MAK) 020318.

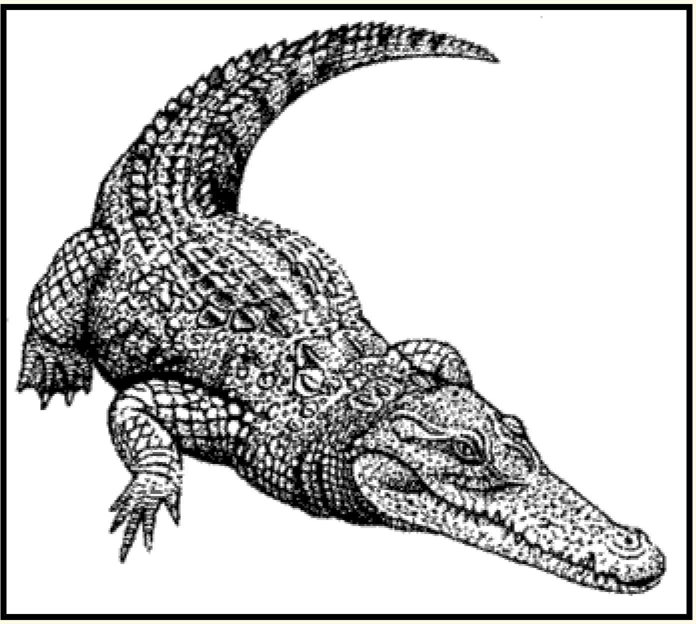
Alligatoridae: *Alligator*, *Caiman*, *Melanosuchus*, *Paleosuchus*

Range: from Late Cretaceous (Campanian)

Phylogeny: Crocodylia:: Crocodylidae + *.

Introduction: This important and long-lived family of large tropical reptiles (suborder Eusuchia) first appeared during the Campanian epoch of the later Cretaceous period. This group includes the alligators (upto 3 or 4 meters, in the past to 5 or 6 meters) and their smaller and more primitive cousins the caimans of South America, along with a lareg number of extinct (late Cretaceous and Cenozoic) forms. The snout is broad and only moderately elongated, and not demarcated from the rear of the skull. The nasal bones extend forward to meet the premaxillae (snout / upper jaw bones). There are 17-22 teeth on either side of each jaw. The fourth tooth of the lower jaw fits into a pit in the upper jaw and is invisible when the mouth is closed. During the past this group ranged widely through Europe, Asia, North and South America. There are 7 living species, most of which are endangered. (only the American alligator, *A. mississippiensis*, is relatively secure). 020318.

Crocodylidae:



Phylogeny: Crocodylia:: Alligatoridae + *: Crocodylinae + Tomistominae.

Introduction: There is some dispute over what taxa to include in this family of relatively unspecialised eusuchians. A.S. Romer (*Vertebrate Paleontology*, 1956) placed here three subfamilies - Alligatorinae, Crocodylinae, and Gavialinae. Rodney Steel (1973) in *Encyclopedia of Paleoherpetology* vol 16 (Crocodylia) included five subfamilies - Crocodylinae, Alligatorinae, Gavialinae, Thoracosaurinae / Tomistominae (false gavials), and the extinct terrestrial Pristichampsinae. Sometimes the Gavialidae was considered a distinct family, as in the wonderful (and long out of print) natural history book *The Living World of Animals*, (1970, The Reader's Digest Association). Robert Carrol in his important work Vertebrate Paleontology and Evolution (1988, the last great pre-cladistic book on vertebrate phylogeny) elevates the Alligatorines to family rank as well, while *The Fossil Record* II (1993, edited by Michale Benton) entry on Reptiles has the Pristichampidae as a seperate family rank, and further distinguishes the extinct Thoracosaurinae from the living false gavials (Tomistominae). Finally, modern cladistic representations undertake further taxonomic inflation by making the Alligators, Crocs, and Gavial groups each superfamilies (-oidea). And what was formerly family Crocodylidae now becomes the clade "Crocodylia"; formerly the ordinal name for the entire group, but now used to define all recent species and all extinct descendents of their most recent common ancestor.

Such a high taxonomic ranking (three superfamilies) is surely unwarranted. There is very little difference among the so-called "crown group crocodylia". All these animals display a relatively conservative form and a pretty basic morphological pattern, although they do differ greatly in skull proportions and shape and distribution of the teeth. (MAK) 020318.

Crocodylinae: *Crocodylus, Euthecodon, Osteolaemus, Tomistoma?*

Range: from Early Miocene

Phylogeny: Crocodylidae: Tomistominae + *.

Introduction: The Crocodylinae, or true crocodiles, include 12 living species. These crocodiles have 14 or 15 teeth on each side of the mouth. The fourth tooth fits into a pit in the upper jaw, but remains visible when the mouth is closed. Among the largest speceis of thios subfamily (and the whole Crocodylidae group), the Nile crocodile, *Crocodylus niloticus* (illustrated above) reaches 5 meters. It is found in southern and central Africa and Madagascar. It lives in lairs dug out of river banks and feeds mainly on fish, though it also eats land animals. There are seven surviving subspecies. The stratigraphic range is Early Miocene? - Pliocene to Recent. The Australasian salt-water crocodile *Crocodylus porosus* is even larger, reaching over 6 meters in length and 2 to 3 tonnes in weight, although nowadays anything approaching 5 meters and 1 tonne would be extraordinary. As it's name indicates, this species is quite capable of swimming out to open sea and migrating between islands of south east asia and far north Australia. Like the Nile crocodile it is an ancient and long-lived species, ranging from the Pliocene to Recent. MAK; ATW040208.

Tomistominae: *Gavialosuchus, Tomistoma*

Range: From Miocene.

Phylogeny: Crocodylidae: Crocodylinae + *.

Introduction: The Tomistominae, or false gavials are so called because these long-snouted forms resemble Gavials, to which they are only distantly related. The "longirostrine" adaptation to long narrow snouts has appeared a number of times among the Crocodylimorphs. Tomistomines have 20 or 21 teeth on each side side, and, as with the Crocodylinae, the fourth tooth remains visible when the mouth is closed. This is a relatively recent group, appearing suddenly during the Miocene epoch (earlier specimens attributed to this subfamily probably pertain to different groups) and flourished on both sides of the Atlantic. The gigantic *Gavialosuchus americanus* from the late Miocene and early Pliocene of Florida, attained 14 meters, but other members of this subfamily are smaller. There is only one recent species, the south-east Asian *Tomistoma schlegelii* (maximum length 5 meters) (now limited to Indonesia and Malysia). 020318.

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

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

Crocodilia: Dendrogram

Abbreviated Dendrogram

```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         `--Neosuchia
            |--Dyrosauridae
            `--Crocodylia
               |--Gavialidae
               `--+--Alligatoridae
                  `--Crocodylidae
```

Contents

```
ARCHOSAURIA
|
CROCODYLOMORPHA MH
|--Sphenosuchia X
|  |--Trialestidae •X
|  `--Sphenosuchidae •X
`--Crocodyliformes MH
   |--Protosuchia •X MH
   `--+--Gobiosuchidae •X
      `--Mesoeucrocodylia
         |--Thalattosuchia X
         |  |--Teleosauridae •X
         |  `--Metriorhynchidae •X
         `--Metasuchia
            |--Notosuchidae •X
            |--+--Baurusuchidae •X
            |  `--Libycosuchidae •X
            `--+--Sebecosuchidae •X
               `--Neosuchia MH
                  |--+--Dyrosauridae •X MH
                  |  `--+--Terminonaris •X
                  |     `--Sarcosuchus •X
                  `--Crocodylia •
                     |--Gavialidae •
                     `--+--Alligatoridae •
                        `--Crocodylidae
                           |--Crocodylinae • MH
                           `--Tomistominae •
```

Page Back	Unit Home	Page Top	Page Next

Crocodilia References

Abbreviated Dendrogram

```
ARCHOSAURIA
|
CROCODYLOMORPHA
|--Sphenosuchia
`--Crocodyliformes
   |--Protosuchia
   `--Mesoeucrocodylia
      |--Thalattosuchia
      `--Metasuchia
         |--Notosuchidae
         `--Neosuchia
            |--Dyrosauridae
            `--Crocodylia
               |--Gavialidae
               `--+--Alligatoridae
                  `--Crocodylidae
```

Contents

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

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Clark, JM, H-D Sues & DS Berman (2000), *A new specimen of* ***Hesperosuchus agilis*** *from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs*, **J. Vert. Paleontol.** 20: 683-704. Trialestidae.

Gasparini, Z (1984), *New Tertiary Sebecosuchia (Crocodylia: Mesosuchia) from Argentina.* **J. Vert. Paleontol.** 4: 85-95. Sebecosuchidae

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

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Pterosauria

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--DINOSAUROMORPHA
   |
   `--PTEROSAURIA
      |--Dimorphodontidae
      `--+--Campylognathoidea
         `--+--Rhamphorhynchoidea
            `--Pterodactyloidea
               |--Ornithocheiroidea
               `--+--Ctenochasmatoidea
                  `--+--Dsungaripteroidea
                     `--Azhdarchoidea
```

Contents

Introduction

The Pterosaurs may or may not belong here, between the crocs and the dinosaurs. There is a strong minority opinion that they are more basal archosauriforms -- or perhaps an even earlier diapsid clan. Like birds, much of the body and its skeleton have been highly modified for flight. Also like birds, the skull has also been reengineered, perhaps to an even greater degree than in birds, but for reasons which are much less easy to determine. Fortunately, the sequence of events *within* the pterosaurs is somewhat easier to work out than in modern birds, or even bats. (ATW 020327)

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Pterosauria

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--DINOSAUROMORPHA
   |
   `--PTEROSAURIA
      |--Dimorphodontidae
      `--+--Campylognathoidea
         `--+--Rhamphorhynchoidea
            `--Pterodactyloidea
               |--Ornithocheiroidea
               `--+--Ctenochasmatoidea
                  `--+--Dsungaripteroidea
                     `--Azhdarchoidea
```

Contents

Taxa on this Page

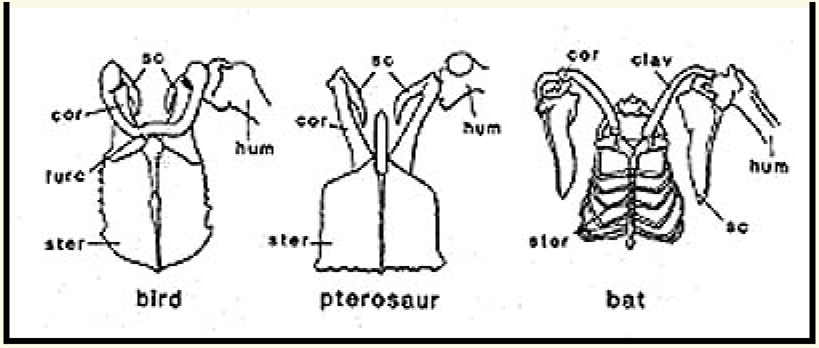
1. Azhdarchoidea X
2. Campylognathoidea X
3. Ctenochasmatoidea X
4. Dimorphodontidae X
5. Dsungaripteroidea X
6. Ornithocheiroidea X
7. Pterodactyloidea X
8. Pterosauria X
9. Rhamphophynchoidea X

Descriptions

Pterosauria: *Scleromochlus* may be in stem group.

Range: Middle Triassic?-Late Cretaceous.

Phylogeny: Ornithodira:: dinosauria + *:



Dimorphodontidae + (Campylognathoidea + (Rhamphorhynchoidea + Pterodactyloidea)).

Characters: large eyes; sizeable brains; hollow long bones; sternum (but small or no ossified keel); long retroverted scapula as in birds; ventral edge of coracoid articulates with sternum as in birds and supports pectoral girdle [P97]; expanded sternum with keel [P97]; humerus longer than sternum [P97]; big deltopectoral crest on proximal. humerus for flight stroke muscles [P97]; primitively, deltopectoral crest has straight edges [P&S]; forearm longer than humerus [P97]; pteroid bone in wrist; hand with elongate digit 4 supporting wing membrane; manus 1-3 retained, with unguals, and at least sometimes robust [U99]; wing membranes with fibers for stiffening [P97] (*contra* [U99] who suggests that wings were supported largely by physical attachment to legs, cranium, etc.); short pubis with pre-pubic bones; highly mobile hip joint [U99]; femur bowed and shorter than tibia [P97]; fibula reduced and fused to tibia [P97]; mesotarsal ankle [P97]; 4 elongated, closely appressed metatarsals plus reduced 5th [P97] (*contra*, Bennett (1997), who states that the metatarsals were flexible: closely appressed in flight, but spread in walking); pes with 5 digits; pes 5 small & without claws [U99]; longish penultimate phalanges on feet (not digitigrade?) [U99]; wing membrane extends to leg in some or all groups, even between rear legs (uropatagium); pteroid supports additional membrane to neck; fibers in membrane; typical gait may have been quadrupedal and plantigrade, with limbs at least partly sprawling [U99]; bones generally highly pnematic or hollow & supported by internal struts [P97]; integument possibly with hair-like pilosity [P97] (widely disputed).

Links: Pterosauria; Pterosauria Translation and Pronunciation Guide; Pterosauria -- The Dinosauricon; Pterosauria; Dinosaurier-Interesse - Saurierart: Ordnung der Pterosauria (German); Science News: Flat-footed fossil; ??? Pterosauria (Japanese); Pterosauria; PTEROSAURS- Enchanted Learning Software; Literature - Pterosauria; Amazing Fossil Treasures of the Canadian Museum of Nature - Frame Setup for Research; PterosaurSite - TITELSEITE (German); Comparative Anatomy Topic 6 - Archosaurs; Pterosaurs @ nationalgeographic.com.

References: Bennett (1997), Padian (1997a) [P97]; Padian & Smith (1992) [P&S]; Unwin (1999) [U99].

Image: comparison of bird, bat & pterosaur pectoral girdles from Padian (1997a).

Note: Padian (1997a) identifies several features as synapomorphies, but then states that most are shared with dinosauromorphs. 011010.

Dimorphodontidae: *Dimorphodon*, *Nesodactylus?*, *Peteinosaurus*, *Sordes?*

Range: Late Triassic (Norian) to Early Jurassic (Sinemurian) of Europe for *Dimorphodon*. Inclusion of *Sordes* extends range to Asia and the Late Jurassic. Various unconfirmed bits and pieces suggest a worldwide distribution.

Phylogeny: Pterosauria: (Campylognathoidea + (Rhamphorhynchoidea + Pterodactyloidea)) + *.

Introduction: *Dimorphodon macronyx*, from the Lower Lias of Lyme Regis, Dorset, and Aust Cliff, Gloucestershire is the only certain member of the family Dimorphodontidae. Only a few specimens are known; all but one (the one illustrated) coming from the Sinemurian of the Dorset Coast of England.

This primitive pterosaur had quite a large, deep skull that was also very lightly built, consisting of large openings separated by narrow strips of bone. The tail was long, with the first five or six vertebrae short and flexible, and the rest elongated and stiffened against each other by long strips of bone. The tail was thus a long stiff rudder, flexible only at the base, and used for stabilization in flight. The overall length was up to 100 cm, with a wingspan up to 1.4 metres. The hind legs were long and powerful, indicating that *Dimorphodon* was able to walk competently on land, bird or dinosaur fashion. (MAK 991008)

Characters: medium-sized; large, deep skull; maxilla does not extend posteriorly to the level of the orbit; nasal breaks contact between ascending process of maxilla and lacrimal; cranial struts very thin; cervical ribs tiny; tail long; first five or six caudal vertebrae short and flexible, and the rest elongated and stiffened against each other by long strips of bone (tail used as rudder, flexible only at base); sternal complex wider (laterally) than deep; *deltopectoral crest* with bulbous distal expansion [P&S]; metacarpals roughly equal in length; large wing claws; legs long; metatarsals tightly appressed; *brachiopatagium* attached to ankles and *uropatagium* even to toes in *Sordes* [U99].

Notes: [1] the name is derived from the dimorphic teeth: large conical stabbing teeth anteriorly, and tiny pointed teeth posteriorly. However, many types of pterosaur developed similar specializations and this particular trait may be characteristic of the pterosaurs as a whole. **[2]** *Sordes* is variously classified as just basal to this group, as a dimorphodontid, or as a rhamphorhynchoid (U&B). *Nesodactylus* is known from a rather incomplete specimen from the Late Jurassic of Cuba. **[3]** *Sordes* has also been at the heart of the controversy relating to wing attachment, with Unwin and others using some of these beautifully preserved specimens to show that the wing was attached far down the ankle, as well as extending between the legs, making bipedal locomotion almost impossible.

Image: This specimen, from the Late Jurassic of Kazakhstan, is one of the *Sordes* specimens which caused all the ruckus about pterosaur "hair." The current thinking is that these are elastic fibers from *inside* the wing membranes, and not integumentary hair. The image is said to be © Prismatic Productions. However I am very dubious of this claim. Further, the links to this entity and the alleged authors are not functional. So sue me.

Links: **DinoData Flying Reptiles Dimorphodontidae**; Nesodactylus; Dinosaurs- Sordis pilosus; Pterosauria -- The Dinosauricon; De Pterosaurus Site Dimorphodontidae (German); Best Vertebrates, Dimorphodon (very nice links); Kinder-Index (German); PANGEA (Italian); Dinosaurs- Sordis pilosus; 16; Dinosaurier Interesse.de - Suker-Dimorphodon (German: student page, but nicely done).

References: Padian & Smith (1992) [P&S]; Unwin (1999) [U99]; Unwin & Bakhurina (2000) [U&B]. ATW030607.

Campylognathoidea: *Campylognathoides, Eudimorphodon* (Eur, India, Greenland?)

Range: Late Triassic to Early Jurassic of Europe, India, Greenland, & possibly North America

Phylogeny: Pterosauria:: (Rhamphorhynchoidea + Pterodactyloidea) + *.

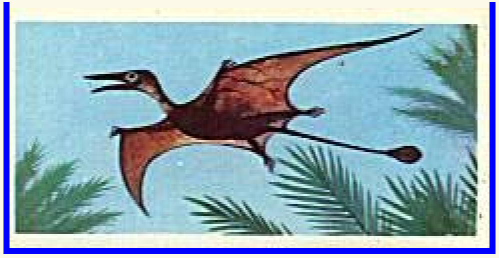
Characters: medium to large (wingspan 1-6 m); long jaws, slightly curved anteriorly; numerous sharp teeth; relatively short neck; long tail with terminal diamond-shaped flap.

Links: Campylognathoidea; Campylognathoides -- The Dinosauricon; Paleontology and Geology Glossary: C; Pterosauria Translation and Pronunciation Guide; Dinosaur fossil plaques.; campylognathoides (Rachel Clark); New Page 1; Eudimorphodon -- The Dinosauricon; eudimor (Spanish); eudimorphodon (German); Eudimorphodon; Dimorphodon- Enchanted Learning Software; Dinosauri- (Italian); The Aerodynamics of Pterosaurs; PANGEA; Dinosaurier-Interesse - Saurierart: Ordnung der Pterosauria (German); Dinosaurios, tutorial interactivo; Museo Civico di Scienze Naturali \Enrico Caffi\.; Campylognathoides; Pterossauro (Portuguese); DinoData Flying Reptiles Campylognathoididae; Re: Pterosaur Help; Eudimorphodon; Nuova pagina 1; Pterossauro (Portuguese); DinoData Flying Reptiles Eudimorphodontideae.

Notes: *Eudimorphodon* (pictured) had multi-cusped teeth. ATW030223.

Rhamphorhynchoidea: *Rhamphorhynchus, Scaphognathus*. Definition: *Rhamphorhynchus* > *Pterodactylus.*

Range: Early Jurassic to Late Jurassic



Phylogeny: Pterosauria::: Pterodactyloidea + *.

Characters: **$** skull more than three times longer than deep (U&B); bony mandibular symphysis; **$** very large, protruding anterior teeth; **$** mandibular teeth not dimorphic (?!) (U&B); **$** tip of lower jaw (predentary?) dorsally deflected, toothless and very sharp; **$** premaxillae separate frontals (U&B); **$** orbits larger than nasal and preorbital openings (U&B); **$** prepubes ventrally oriented; long, stiffened tail, sometimes with "rudder"; deltopectoral crest with bulbous distal expansion [P&S]; 5-6 carpals; **$** metatarsal 4 reduced in length (U&B); loosely appressed metatarsals; pes 5 retains 2 phalanges & is hooked or retroverse. Tail probably provided stability, but less maneuverability.

Image: *Rhamphorhynchus*, from the Brooke Bond tea cards -- traditional, but many are very well done.

Notes: Many sources use the traditional notion of Rhamphorhynchoidea as including almost all Jurassic pterosaurs.

Links: Rhamphorhynchus; Pterosauria Translation and Pronunciation Guide; Image -- The Dinosauricon; Earth History Graphics; Prehistoric Products Co. - fossil replica specimens; PTEROSAURS- Enchanted Learning Software; sh: Prehistoric Animals; What do fossils tell us about the history of Big Bend National Park?; Ville Rantapuska - Dinosaurs (Finnish); Rhamphorhynchus; PTEROSAURIA; forelasning8.pdf (Swedish); Digimorph - Rhamphorhynchus sp. (pterosaur); RÉPTEIS VOADORES; RE- Reading material on Pterosaurs; 16 ; D. weintraubi.

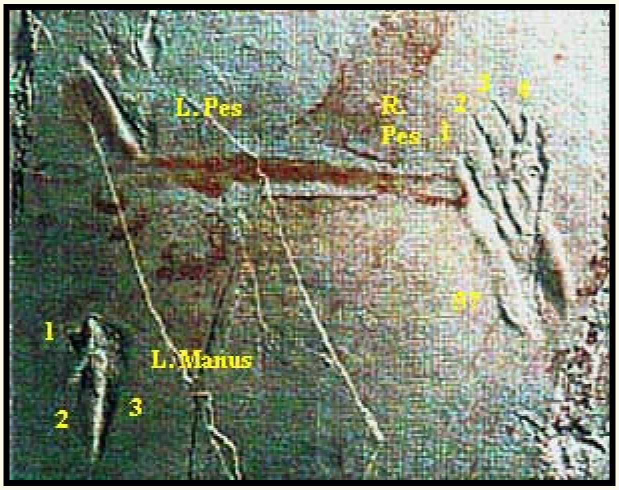
References: Padian & Smith (1992) [P&S]; Unwin & Bakhurina (2000) (U&B). ATW030413.

Pterodactyloidea: mostly Cretaceous forms

Range: upJ-upK.

Phylogeny: Pterosauria::: Rhamphorhynchidae + *: Ornithocheiroidea + (Ctenochasmatoidea + (Dsungaripteroidea + Azhdarchoidea)).

Introduction: advanced forms from the Late Jurassic and Cretaceous. Small to very large. Short tails. The neck is longer (although with the same number of vertebrae) and the brain is larger. In some forms a head crest developed to aid in manoeuvourability during flight. The teeth are reduced and sometimes absent.



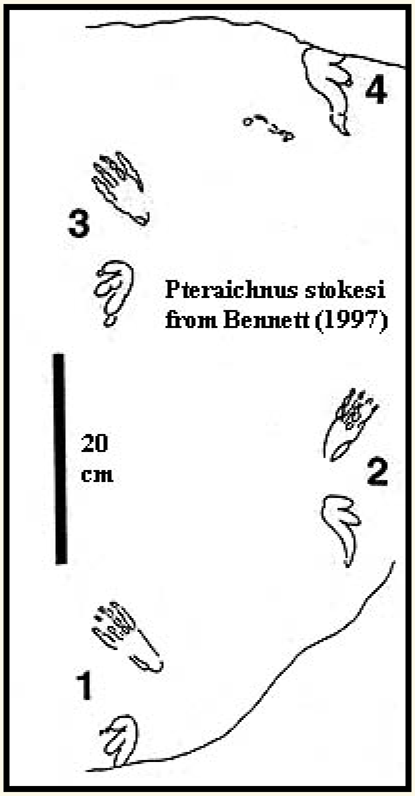
Pteradoctyloid prints, probably from Crayssac, analyzed as in Bennett (1997)

Characters: all relatively large as adults [B96]; skull elongate & laterally compressed [K&L]; cranial bones usually fused in adults; **$** jaws triangular with tendency to lose teeth [P97]; premaxilla usually forms anterodorsal portion of skull, including at least part of rostrum [K&L]; maxilla lies below premaxilla and forms sides of upper jaw and anteroventral margin of nasoantorbital fenestra; **$** nares absent or confluent with antorbital fenestra [K&L][P97]; cranial crests [B96]; articular condyles of quadrate helical in some large forms [K&L]; anterior trunk vertebrae fused into notarium; tail reduced or absent (maneuverability); scapula curved inward and articulated with notarium (stronger flight stroke) in larger species [P&S]; glenoid directed posterolaterally (rather than laterally) since scapulocoracoids now formed parts of a ring structure with sternum and notarium; metatarsals flexible --appressed for flying & spreadout for walking [B97]; outer layer of bones 1-2 mm in large forms, supported by internal struts [K97]; integument very thin, probably without scales or "hairs" [K97]; at least small forms probably quadrupedal, using manus digits 1-3 spread laterally or retrograde [B97].

Links: Pterodactyloidea -- The Dinosauricon; Prehistoric Products Co. - Dinosaur and fossil replica specimens; Pterodactyloidea; Page11; PTEROSAURS- Enchanted Learning Software.

Discussion: In the brief period between about 1980 and 2000, dinosaurs evolved from long-extinct, slumbering mountains of swamp-dwelling flesh -- barely swifter than continental drift -- to hot-blooded athletes who dominate the skies even today. We will pointedly ignore the question of whether this reinvention of the taxon has gone just a shade too far. The astounding success of the general reinterpretation can legitimately cause us to wonder whether even the most outlandish claims for the abilities, metabolism, prowess and intelligence of the dinosaurs might not turn out to be well founded after all. But every success breeds imitators, and not every imitation matches the quality of the original. The pterosaurs, who underwent a parallel transformation in the scientific literature, now seem to be devolving back into a more traditional mold.

For a while, in the early 1990's, it seemed that pterosaurs were almost more birdlike than birds. They were characterized as active, deep-keeled, flapping flyers in the air and as lithe bipedal runners on land. They were covered with hair and distinctly warm-blooded. Their wings were narrow and held in place by keratinous rods of some unique and advanced design. They were loving parents who engaged in extended care of their chicks **[1]**. They finished the **Times** crossword before their second cup of coffee went cold. The name of Kevin Padian **[2]** is frequently invoked for this interpretation, although it would be unfair to ascribe the more extreme expressions of these views to Prof. Padian.



It all seemed a little too good to be true -- and it probably was. One stumbling block is *Pteraichnus*, probable pterosaur footprints from Arizona and Wyoming. Similar prints have been found in France. Actually, the track maker was not stumbling, but it was certainly not a biped. Nor does it appear to have been an ordinary quadruped. Images of these tracks are found at right (from Bennett (1997)) and under the main heading for this taxon. Padian showed that similar tracks could be generated by crocodilians, specifically by *Caiman*, under appropriate experimental conditions. However, the appropriateness of these conditions has been criticized, as has the similarity of the prints. See, e.g., Bennett (1997) and Unwin (1999). It has been reported that Padian has also recently stated that certain similar trace fossils are probably pterosaurian.

If this is correct, then pterosaurs were not only quadrupeds, but probably somewhat sprawling quadrupeds who walked a bit awkwardly on plantigrade feet and almost retrograde fingers. Perhaps this proves too much, since it is hard to see how a really large pterodactyloid could have moved in this manner. But, then again, it is hard to see how something like *Quetzalcoatlus* could have moved in *any* manner on the ground. It is probably safe to say that pterosaurs were not cursorial bipeds, but distinctly hazardous to say much more than that.

Another difficulty has been the beautifully preserved remains of *Sordes* from Sölnhofen and of more exotic species from the Brazilian Santana Formation. The pterosaur "hair" is probably internal membrane fibers, the main wing membrane (*brachiopatagium*) was fastened well down the leg, and a distinct cruropatagium joined the legs, held in place by the retroverted fifth toe. If pterosaurs ran, they did so in heavy floor-length gowns. As any reasonably articulate feminist will be happy to explain, the whole point of such attire is to make it more difficult either (a) to get anywhere or (b) to accomplish any useful work. I hasten to disclaim any opinion on the politics and intent, if any, of gender-specific fashion statements -- although it is interesting that traditional academic garb is designed along the same lines – but one is forced to concede the practical consequences. A fully accoutered pterodactyloid might manage a stately pavan, but was clearly not designed for the ptango.

Unwin goes so far as to suggest that this deconstruction of the pterosaurs might require us to place pterosaurs back among the basal archosauromorphs or even in the basal diapsids, a theory that was worked out in some detail by Peters in the sadly missed Pterosaur Home Page and various JVP abstracts. Unfortunately almost *all* pterosaur phylogenetic work is published in the form of JVP abstracts, so it is difficult to comment. Unwin cites work by Bennett for the idea that only characters of the hind limb place pterosauria among ornithodires. However, this is a little unfair since Ornithodira, as well as the clades it contains, largely reflect key transitions in hind limb locomotion. The growth of this whole branch of the Tree seems to have been driven by hind limb design. See, e.g., Hutchinson & Gatesy (2000), Novas (1996), and review by White (2001). Thus, it may be meaningless to speak of ornithodires without ornithodire hind limbs. It is only a slight exaggeration to say that ornithodires *are* all archosauromorphs with the specialized ornithodire hind limb. However, it may be possible that the ornithodires are cursorial descendants of little gliding or even flying archosaurs, and that the pterosaurs were an early radiation of that line. This is sheer speculation, of course, but it has the advantage of accommodating all schools of thought and even providing a little vindication to the much reviled work of John Ruben. See, e.g., Jones *et al*. (2000).

[1] Oddly enough, this part is still very likely true. See Bennett (1997).

[2] In the interests of full disclosure, I should state that I hold, and have strongly expressed, negative opinions about Dr. Padian's statements on certain subjects. These subjects are not among those discussed anywhere in **Palæos**, but the reader is duly warned of a potential bias. (ATW 011012.)

References: Bennett (1996) [B96]; Bennett (1997) [B97]; Hutchinson & Gatesy (2000); Jones *et al*. (2000); Kellner (1997) [K97]; Kellner & Langston (1996) [K&L]; Novas (1996); Padian & Smith (1992) [P&S]; Peters (1997) (P97); Unwin (1999); White (2001).

Ornithocheiroidea: *Anhanguera*, *Ornithocheirus*, *Pteranodon*

Range: lwK-upK probably worldwide.

Phylogeny: Pterodactyloidea: (Ctenochasmatoidea + (Dsungaripteroidea + Azhdarchoidea)) + *.

Characters: **$** mandibular symphysis large, bearing substantial teeth (U&B); **$** symphysial teeth include 3 pairs of large, fang-like teeth (U&B); **$** symphysis with marked midline channel bounded by ridges (U&B); median palatal longitudinal ridge [K&L]; **$** saggital crests near ends of jaw (U&B); deltopectoral crest "warped" , i.e. not at right angles to shaft of humerus [P&S].

Links: Anhanguera -- The Dinosauricon; Behind the Scenes; ANHANGUERA; Australian Pterosaurs; Pterosauria Translation and Pronunciation Guide; ???? (Japanese); 110-million year old pterosaur flies again; BBC Online - Walking with Dinosaurs - Fact Files (also in Swedish,); Burger King España - Kids - Ficha Ornithocheirus (Spanish); Ornithocheirus (German); Pteranodon; PTERANODON-Enchanted Learning Software; UCMP Pteranodon ingens display information; Our Amazing Treasures: Discover the Amazing Story of Pteranodon longiceps.; Pteranodon; Pterosauria

References: Kellner & Langston (1996) [K&L]; Padian & Smith (1992) [P&S]; Unwin & Bakhurina (2000) (U&B). 011006.

Ctenochasmatoidea: *Ctenochasma*, *Pterodactylus*.

Range: upJ-mK.

Phylogeny: Pterodactyloidea:: (Dsungaripteroidea + Azhdarchoidea) + *.

Characters: generally shallow-keeled (P97), **$** feet plantigrade (P97).

Links: Ctenochasma -- The Dinosauricon; PterosaurSite - Fotos und Grafiken; il mondo dei dinosauri; Pterodactylida; Pterosaurs; Pachycephalosaurus and Pterodactylus; Pterodactylus (Portuguese); PTERODACTYLUS- Enchanted Learning Software.

References: Peters (1997) (P97).

Image: *Pterodactylus*. 011006.

Dsungaripteroidea: *Domeykodactylus*,

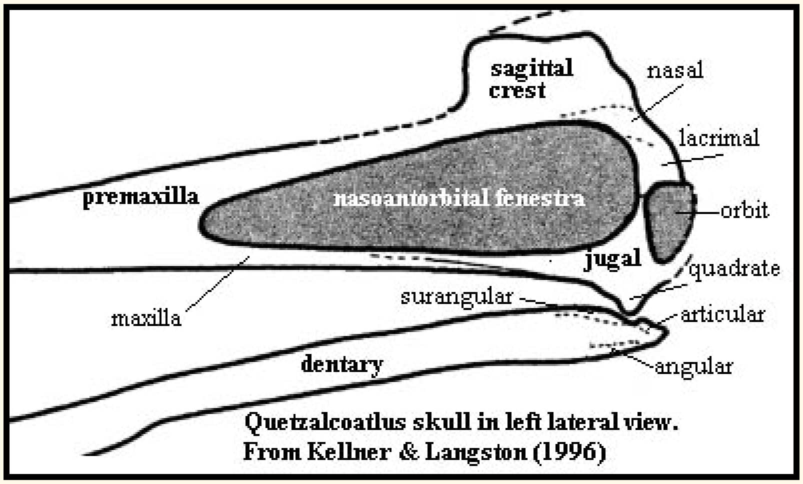
Dsungaripterus, Noripterus, "Phobetor"

Range: upJ-lwK of Asia, & SAm

Phylogeny: Pterodactyloidea::: Azhdarchoidea + *.

Links: Pterosauria Translation and Pronunciation Guide; Dsungaripteroidea; Dsungaripterus -- The Dinosauricon; Dsungaripterus- Enchanted Learning Software; Dsungaripterus; Dsungaripterus

Image: *Dsungaripterus* from PterosaurSite - Fotos und Grafiken. 011006.



Quetzalcoatlus skull in left lateral view.
From Kellner & Langston (1996)

Azhdarchoidea: *Arambourgiania, Azhdarcho, Doratorhynchus, Montanazdarcho, Quetzalcoatlus, Titanopteryx.*

Range: m(lw?)K-upK worldwide.

Phylogeny: Pterodactyloidea::: Dsungaripteroidea + *.

Characters: cranial crests small or absent; mid-cervical vertebrae highly elongate (U&B); large humeral head; tall, squarish deltopectoral crest on humerus, at right angles to humeral shaft and with outer (distal) edge concave [P&S]; deltopectoral crest lacks bulbous distal expansion; **$** 2nd wing phalanx has T-shaped cross-section due to pronounced ventral keel (U&B); outer layer of bones, esp. of largest forms, only 2mm thick.

Links: CHATTERJEE'S BIRD BOOK; Azhdarcho -- The Dinosauricon; Artist Joe Tucciarone Gallery 2; Quetzalcoatlus; Dinosaur Photo Index Library - Quetzalcoatlus; BBC Online - Walking with Dinosaurs - Fact Files; DinoData Flying Reptiles Azhdarchidae; Australian Pterosaurs; New Refs #19; BBC - Walking with Dinosaurs - Dig Deeper; Pterosauria Translation and Pronunciation Guide; Azhdarcho Views.

References: Kellner & Langston (1996) [K&L]; Padian & Smith (1992) [P&S]; Unwin (1999) [U99]; Unwin & Bakhurina (2000) (U&B).

Notes: *Quetzalcoatlus* is generally believed to be the largest flying vertebrate, as well as one of the last pterosaurs. 011007

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

checked ATW030607

Page Back | Unit Home | Unit Dendrogram | Unit References | Taxon Index | Page Next

Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Pterosauria References

Contents

Abbreviated Dendrogram

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ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--DINOSAUROMORPHA
   |
   `--PTEROSAURIA
      |--Dimorphodontidae
      `--+--Campylognathoidea
         `--+--Rhamphorhynchoidea
            `--Pterodactyloidea
               |--Ornithocheiroidea
               `--+--Ctenochasmatoidea
                  `--+--Dsungaripteroidea
                     `--Azhdarchoidea
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Page Back | **Unit Home** | **Page Top** | **Page Next**

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