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Synapsida

Abbreviated Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EURETILIA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

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The Permian archetypal pelycosaur *Dimetrodon* surveys its domain

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Synapsida: Overview

Abbreviated Dendrogram

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AMNIOTA
|--+--ANAPSIDA
|  `--EURETILIA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

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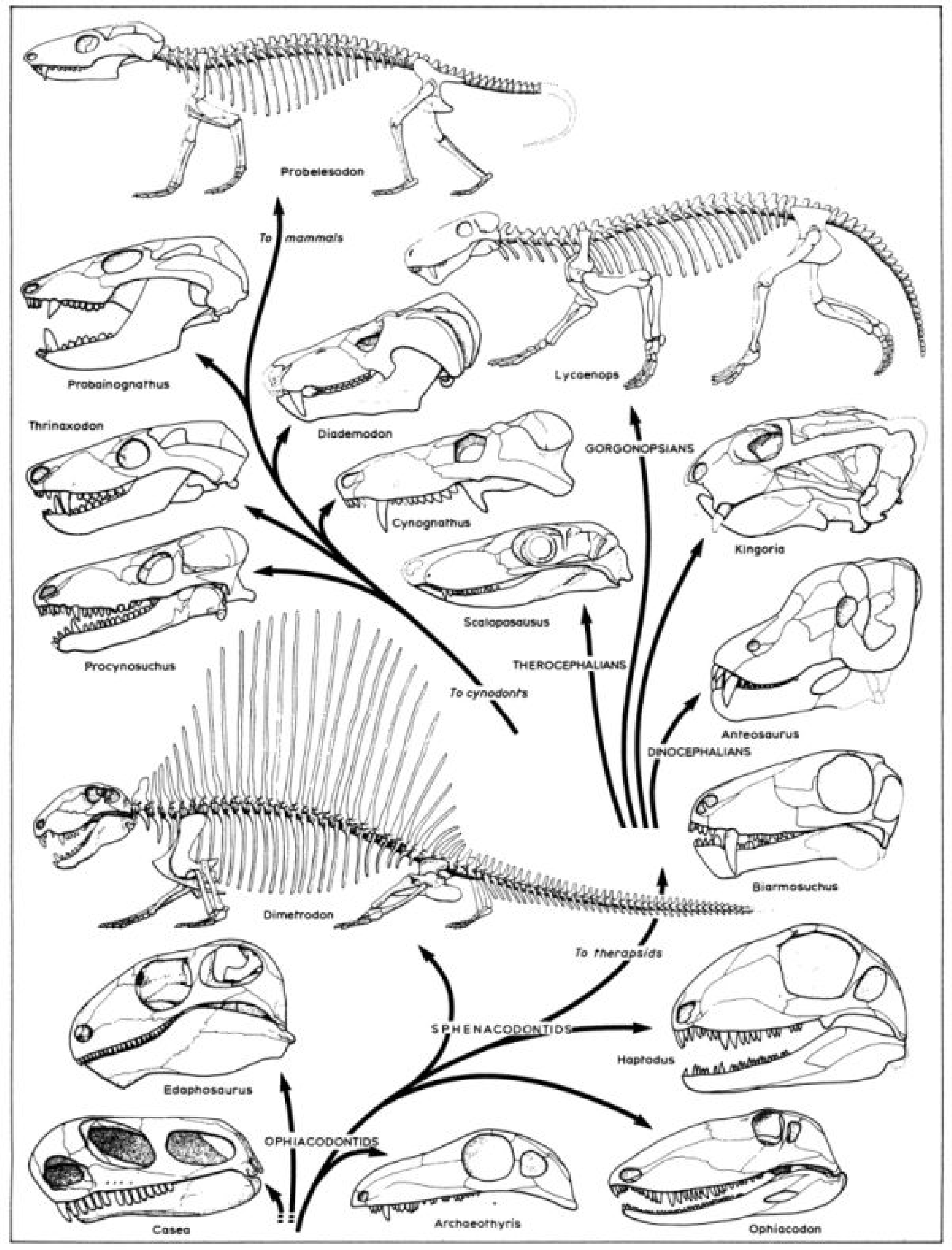


Synapsid evolution, after Thomas Kemp, showing changes in the shape of the skull and skeleton. At the bottom are pelycosaurs, in the middle and upper right therapsids, and on the upper left cynodonts, the most advanced clade of therapsids, from which true mammals evolved. Diagram copied from Mammal-like Reptiles (Korean)

Synapsida (=Theropsida)

Evolution

The Theropsids or "beast (mammal) faces" constitute an evolutionary lineage that developed a special opening, the synapsid arch, for attachment of jaw muscles, giving a superior bite and permitting adaptive radiation during the late Carboniferous. These basal forms evolved through the primitive pelycosaur stage, to the therapsids or mammal-like reptiles, and finally the mammals themselves. Pelycosaur, therapsid, and mammal represent three evolutionary grades in a single progressive evolutionary axis. The therapsids, as forms transitional between basal amniote and mammal, can be thought of as occupying the same evolutionary space as the dinosaurs, which are transitional between reptiles and birds, do.

When we look at the history of the Theropsids we see that the lineage can be further understood in terms of evolutionary "pulses", each pulse corresponding to a major biota. The following diagram and associated text, from Janis & Damuth (1990), shows the major pulses (although two Permian ones have been left out!), and other tetrapods that were contemporary.

'Pulses' of synapsid evolution.

"Note: Taxa illustrated are designed to give a flavour of the range of types of mammal and other vertebrates in each time period, and are not meant to be a comprehensive listing. Body mass ranges are approximate estimates based on overall body size.

Pulse 1 (Permian): Pelycosaurs. Unspecialized medium- to large-sized amniotes (20-100 kg). Sprawling posture, ectothermic, tropical distribution.

Pulse 2 (Early to Middle Triassic). Therapsids. Probably higher metabolic rate than pelycosaurs: 'improved' posture (more of a para-sagittal stance) and greater volume of jaw musculature. Wider geographical distribution (tropical and temperate zones). Size range 10-500 kg.

Pulse 3 (Late Triassic): Cynodont therapsids. Evidence for at least some degree of endothermy: diaphragm, secondary palate, differentiated dentition, masseter muscle in jaw. Size range 0.5-30 kg.

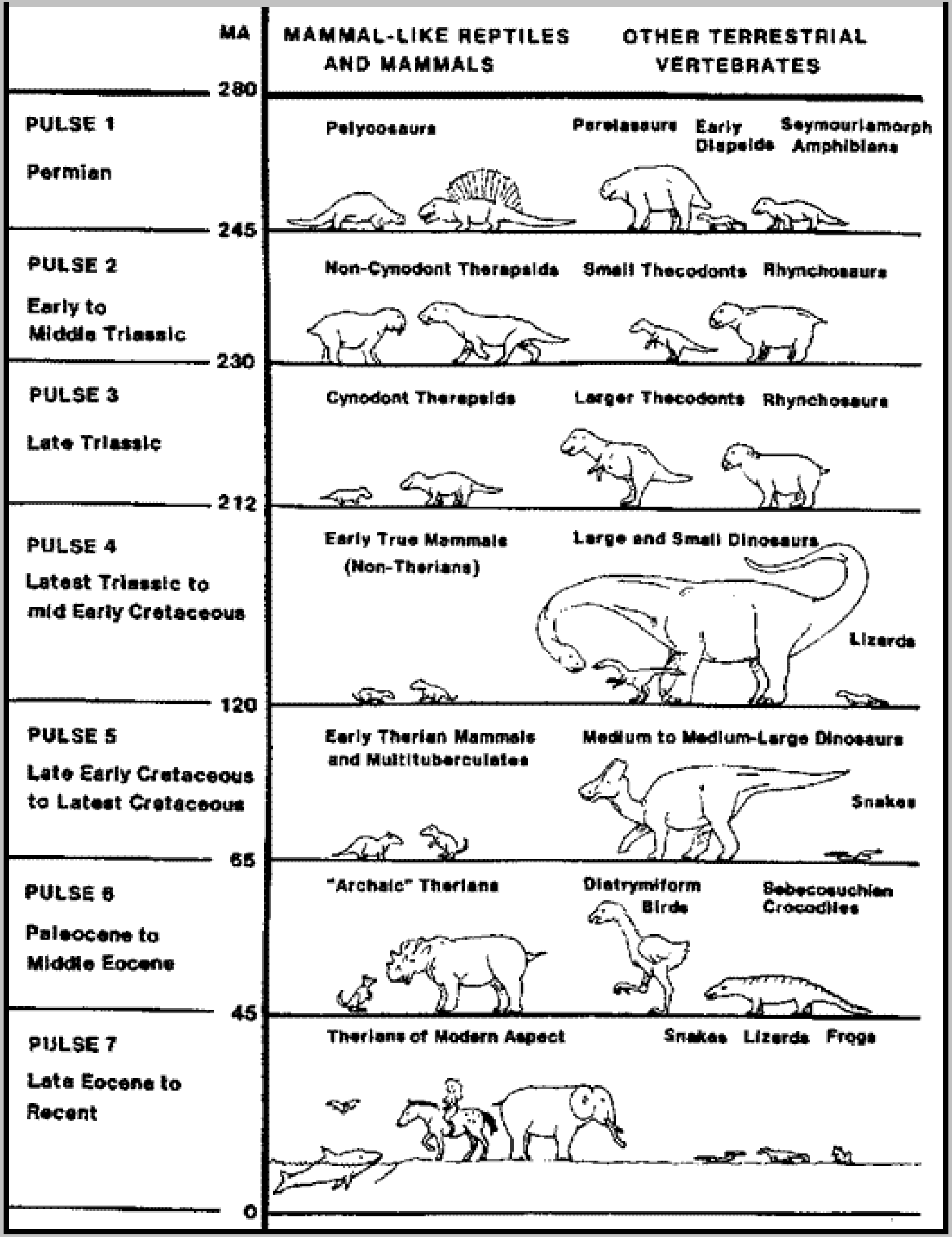
Pulse 4 (Latest Triassic to mid-Early Cretaceous): Early true mammals. Endothermic, widespread geographically but low diversity. Size range 0.03-0.5 kg

Pulse 5 (late Early Cretaceous

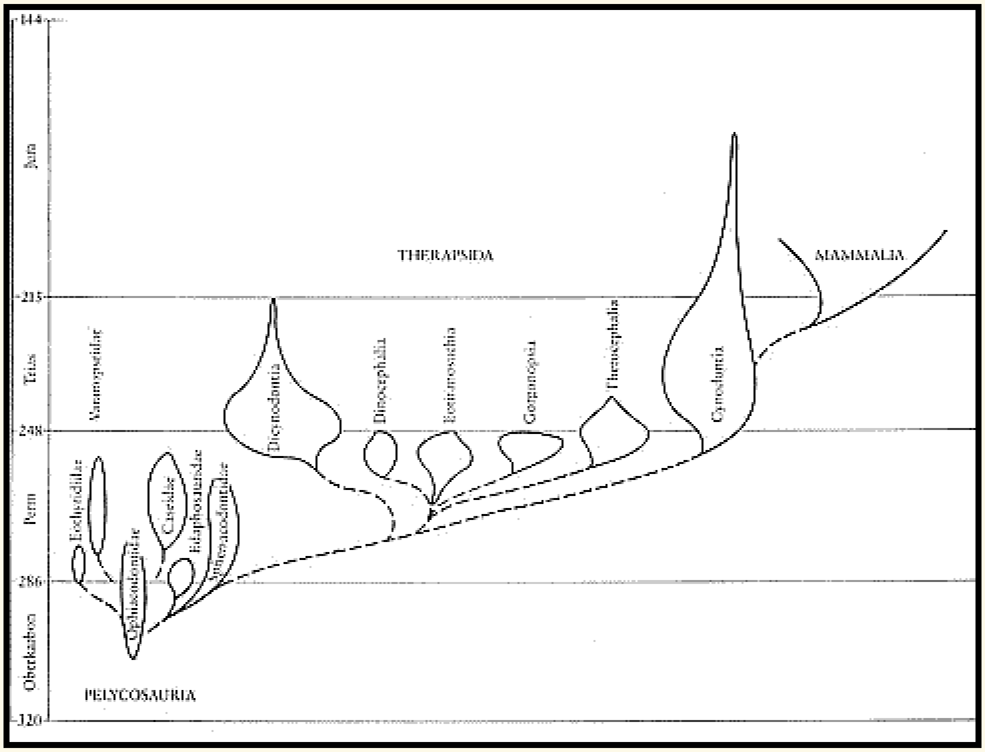
to latest Cretaceous): First therian mammals. Concurrent with radiation of angiosperm plants, see appearance of therians with tribosphenic molars (cheek teeth that can crush as well as shear). Split of therians into placentals and marsupials happens at this time. Multituberculates(non-therians) also diversify and obtain more complex cheek teeth. Size range up to 5 kg.

Pulse 6 (Early Paleocene to Middle Eocene): 'Archaic' therians plus didelphoid marsupials. Taxa seem mainly characteristic of tropical-type forest habitat world-wide. See first true carnivores and semi-aquatic herbivores. Size range up to 1000 kg.

Pulse 7 (Late Eocene to Recent): Modern therians, marsupials confined to Australasia and South America by Middle Miocene. Mammals inhabit diverse habitats, radiation of specialized groups such as bats, whales, cursorial mammals, hominoids. Size range 0.002-5000 kg (terrestrial) or to 100000 kg (aquatic)."



Each of these pulses is a major evolutionary radiationof the Theropsid lineage. And each follows the other sequentially.



The evolutionary systematic diagram to the right from Carroll (1988) shows how this works (*note* - time shown the opposite direction (bottom is oldest) to the preceding diagram). The branches of only the first two pulses mentioned here, the pelycosaurian and the Therapsid (the cynodonts and mammals are indicated but the numerous sub-branches are not shown). The Permo-carboniferous sees the flourishing adaptive radiation of the various pelycosaur groups (bottom left of the diagram). Then, as these decline due to changing environmental conditions (with only a few stragglers making it through to the middle Permian) the new adaptive radiation of the Therapsida takes off. This itself consists of a number of subgroups, one of which, the cynodonts, itself initiates a new adaptive radiation, from one line of which the mammals emerge. And so on.

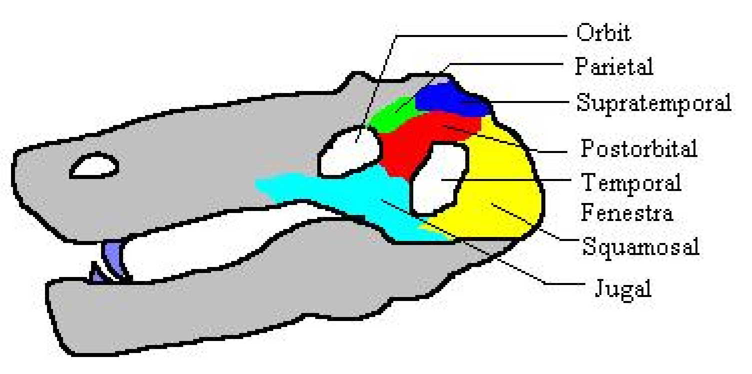
Speaking personally, I find few things more awesome than contemplating this vast and majestic process of evolution, the ebb and flow of successive biotas through geological time. Creationists and others who cannot for ideological or religious reasons accept the fact of evolution miss out a great deal, and are left with a claustrophobic little universe in which nothing happens and nothing changes.

Descriptions

Synapsida: defined as Confuscius > *Confusciusornis* (i.e. mammals > reptiles). Dilkes & Reisz (1996). *Varanosaurus*.

Range: from the Pennsylvanian.

Phylogeny: Amniota **:** Sauropsida + * **:** Caseasauria + Eupelycosauria.



Generalized synapsid skull showing arrangement of skull around temporal fenestra

Characters: Larger skull; septomaxilla columnar, with broad base straddling maxilla-premaxilla suture; **$** lower temporal fenestra present, bounded by postorbital, squamosal and jugal, with ventral margin formed by squamosal and jugal (excluding quadratojugal); **$** supratemporal and postorbital meet and exclude parietal from squamosal; postorbital extended posteriorly (probably related to reinforcing skull weakness caused by fenestration); post-orbital skull typically axially short and dorsoventrally tall; plate-like supratemporal retained; tabulars large; postparietals fused; occiput slopes and faces postero-dorsally; posttemporal fenestra small, bordered by supraoccipital, tabular & opisthotic; 2 coronoids retained on lower jaw; canine fangs; pectoral girdle tends to develop late and retain sutures between 3 centers of ossification (anterior & posterior coracoids, scapula); large medial centrale in pes; limited color vision (tendency to be nocturnal); glandular skin; complex, hardened forms of beta keratin absent; excrete urea (not uric acid).

Links: Introduction to the Synapsida; Schnellbestimmung anhand von typischen Schädelmerkmalen; Synapsids; Synapsida (ToL); Reptiles - Subclass Synapsida; Synapsida (Mikko's Phylogeny); Synapsida (basic lecture notes);

References: Dilkes & Reisz (1996); Reisz (1972). ATW081025.

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Synapsida

Caseasauria

Abbreviated Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EURETILIA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

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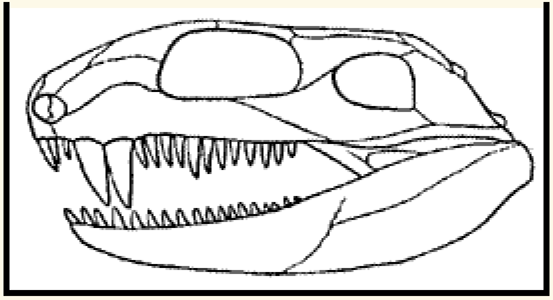
2. Caseidae X
3. Eothyrididae X

The Eothyrids

This family of very primitive pelycosaurs includes two species, known only from several skulls and limb bones from the Early Permian of North America. ***Eothyris***, from the Early Permian of Texas (Belle Plains formation, Artinskian age), is known from a single skull (right), 62mm in length. The teeth are simple conical structures, and there are distinct



caniniform teeth. ***Oedaleops***, from the Early Permian of New Mexico (Abo Cutler Formation, Sakmarian , is known from three partial skulls and some limb elements.

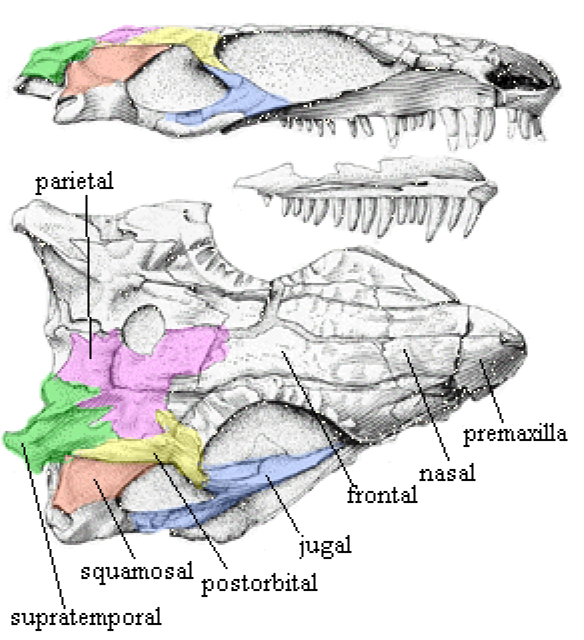
In terms of cranial morphology the eothyridids are the most primitive of any pelycosaur. For this reason they are, in modern cladistic classifications, considered a sort of ancestral group (or rather, the sister group to all other synapsids). However they appear quite late in the fossil record (they are one of the last groups of pelycosaurs to appear). This means either that they existed for a long time but in upland areas or isolated geographic regions away from any chance of fossilisation, or, alternatively, that they are only secondarily primitive. Either hypothesis is valid, and the answer, if it is ever known, must await further fossil discoveries.

The eothyririds share a few unique characteristics (synapomorphies) with the caseids, indicating they may be ancestral to the latter. The two groups are united in the clade (suborder?) Caseasauria. (MAK 000720).

-- and the Synapsid Skull

Sufficiently far back, all of us can trace our family tree back to some bad-tempered sail-back, *Dimetrodon*-like sphenacodont pelycosaur. Except for an annoying mess in the Late Jurassic to Early Cretaceous eras, the pedigree is fairly clear all the way from the Early Permian to my great-great grandfather, whose explanations of his ancestry and reason for being in Shanghai were (shall we say) a little unclear. However, aside from Mesozoic muddles and mendacious mercenaries, it is a remarkably straight line.

Moving beyond the Early Permian is much more difficult. A number of pelycosaurs are known from the Late Carboniferous, but they all seem rather specialized. A number of other scrappy specimens have turned out not to be pelycosaurs at all. The most morphologically basal synapsids we know reasonably well are the eothyrids from the Lower Permian of North America. The eothyrids consist of two adequately known specimens, *Eothyris* Romer and *Oedaleops* Langston.



Oedaleops campi: skull in dorsal and right lateral views, with isolated maxilla. Right squamosal is shifted medially and possibly rotated. Modified from Langston (1965).

The Eothyrids look more or less like Bob the Basal Amniote, whose osteological adventures are sometimes chronicled in the Bones section of this site. That is, most of the skull is composed largely of a series of long dermal bones, rather like the hull of a well-built sailboat. Pressure at any point is flexibly distributed over a wide area while the overall structure remains rigid. The eothyrids have none of the mammalian innovations. The skull is flat -- even depressed according to Langston (1965). The jaw articulation is at about the same level as the tooth row. In fact, there is almost nothing to suggest its distant mammalian affinities except perhaps the curvature of the lower jaw and the shape of the rostrum.

What is somewhat different about the skull is, of course, that it is a synapsid skull. That is, it has only one temporal opening on each side. The opening is defined very simply by the jugal, postorbital and squamosal -- at least it probably is. The squamosal is displaced or damaged on both sides of the skull and both posterolateral quadrants of the skull are somewhat distorted, as can be seen in the figure. (For this reason the quadratojugal appears to participate in the margin of the temporal fenestra.)

In diapsids, a second, dorsal fenestra opens at the junction of the squamosal, parietal and post orbital. No such junction exists in the eothyrids because the squamosal does not extend onto the top of the skull. Instead, an enlarged supratemporal intervenes and forms a sharp projection at the corner of the skull table. As if to compensate – and perhaps it did – both the orbits and the pineal foramen are greatly enlarged.

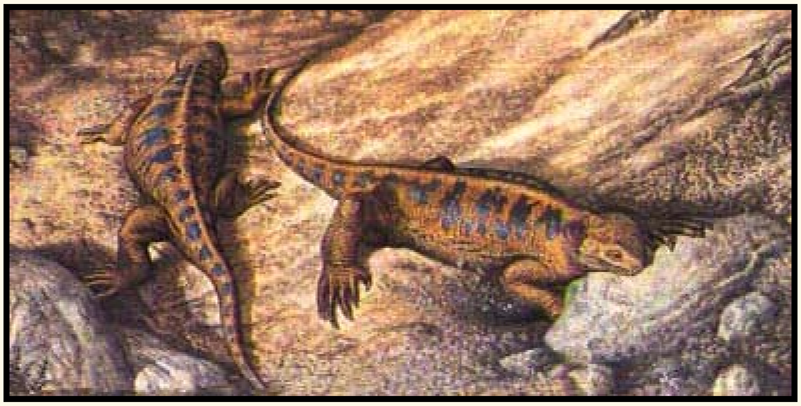
It would not be safe to assume that the synapsid temporal fenestra is strictly homologous to the lower temporal fenestra of diapsids. Although they occur at the same intersection, a number of lineages radiated from the ancestral amniote stock with different patterns of fenestration (see, e.g. Procolophonia), and it is entirely possible that the synapsid and diapsid lineages are separately derived from within Amniota. In fact, that is the usual assumption. If anything, the synapsids seem more closely related to anapsids than diapsids. Upper Carboniferous amniote fossils are few and far between, so that the details of the amniote radiation have remained elusive.

If the diapsids were so successful with their comparatively light-weight, strongly fenestrated skulls, how were the Synapsids able to compete? After all, the earliest synapsids had not yet developed the jaw specializations which enabled sphenacodonts and more derived forms to make good use of the comparative solidity of the synapsid posterior skull. Thus, they had only half the tooth row and perhaps half the jaw muscle strength of a well-developed diapsid.

Here we enter a more speculative area. Perhaps the answer relates to the odd flange of the frontal that enters the margin of the orbit at the top of its arc, together with that other singular feature, the shortened, highly arched ("inflated") rostrum. In a somewhat different form, we have seen this "bulldog syndrome" before in odd creatures like the porolepiforms, guildayichthyiforms, sphenodonts, and perhaps in some of the anthracosaurs and cichlids. In each case, we find some combination of the following features: the tooth row is fairly short, the orbits are large, anterior, and closely spaced, caniniform teeth are found on the anterior tooth row, and the medial bones are strong, uncomplicated and sometimes fused medially. As Lund (2000) points out in the extreme case of guildayichthyiform fish, this syndrome is associated with skulls which are arched and transfer stress from the anterior jaws medially to the rear of the skull -- literally like bulldogs, which sacrifice speed and big jaws for incredible strength in the anterior jaw.

Perhaps what Langston sees as skull depression is actually the osteological remains of a peculiar skull kinesis which allowed the median arch of the skull to be laterally reinforced even as it flexed slightly and locked on to some food source too tough or too uncooperative for normal diapsid slash and gulp tactics. The lateral flanges of the frontals and parietals are then easily explained as stiff crossbars to keep the skull from collapsing inward too far. For these tactics, an eothyrid would need an upper temporal fenestra like -- well, like a hole in the head. ATW 010601

Caseidae



The caseids were a widespread and diverse group of herbivorous pelycosaurs, which appeared during the later Early Permian and persisted until the late Middle Permian. Although ranging in size from 1 to 6 meters in body length, caseids are surprisingly conservative in their skeletal anatomy and body proportions. All were massively built animals with small heads and barrel-like bodies. Animals like *Angelosaurus* and *Cotylorhynchus*, which exceeded 4 meters in length and were the largest of the pelycosaurs, seems to have played the same ecological role during the later early Permian that the pareiasaurs and herbivorous dinocephalians did during the Middle and Late Permian. Caseids and eothyridids share a number of specialised features associated with the morphology of the snout and external naris and it is likely that the latter evolved from the former. The two together form the clade Caseasauria.

The caseid skull is distinctive in the presence of relatively large temporal openings, enormous external nares (nostril openings, probably to house some kind of sensory or moisture-conserving organ), and large pineal opening, and a snout or upper jaw that dramatically overhangs the tooth row to form a forward projecting rostrum. The external surface of the skull is skulpted with rounded deep pits and sometimes crevice-like depressions. The marginal teeth are quite similiar to the teeth of parelasaurs.

In contrast to most other pelycosaurs, except *Edaphosaurus*, and as befits the herbivorous lifestyle, the teeth are remarkably uniform. There is a general reduction in the number of marginal teeth cheek teeth. All caseids, whether modest in size, or enormous, are characterized by small cervical vertebrae, bulky, barrel-shaped bodies and relatively massive limbs. There is reduction in the phalangeal formula, ranging from 2-3-4-4-3 to 2-2-2-3-2. In Corylorhynchus the claw bearing element is very large and broad, with apparently sharp edges on the sides. While in *Angelosaurus* the claw bearing phalanges are also massive, but more conservative in morphology, roughly triangular in outline. This may indicate adaptations to different types of terrain. MAK.

Descriptions

Caseasauria: *Nitosaurus?*

Range: lwP-upP of NAm, Eur & Russia.

Phylogeny: Synapsida **:** Eupelycosauria + * **:** Eothyrididae + Caseidae.

Characters: Dentary with long, ascending untoothed posterior process; **$** long external nares with external narial shelf ; short preorbital skull; pointed rostrum formed by dorsal process of premaxilla; frontal contribution to orbit small (primitive) through narrow lateral process; broad, low skull table; large pineal foramen; wide supratemporal (primitive); slanted occipital plate.

Links: Synapsid classification and autapomorphies; Biology 356; Introduction to the Pelycosaurs.

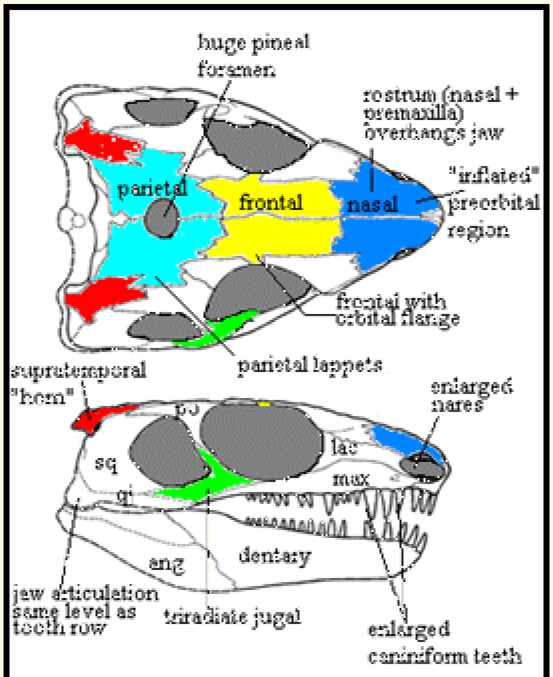
References: Langston (1965). 010531.

Eothyrididae: *Eothyris*, *Oedaleops*.

Range: Cisuralian (Sakmarian to Artinskian) of North America.

Phylogeny: Caseasauria **:** Caseidae + *.

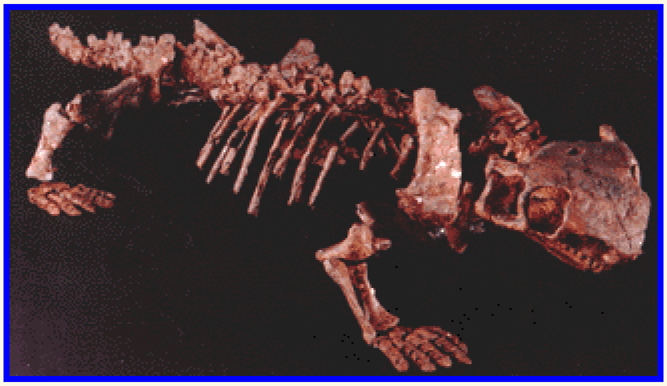
Characters: Small to medium (<1m?), primitive pelycosaurs, possibly polyphyletic as including caseids. Short antorbital region; teeth simple cones except **$** large caniniform teeth on premaxilla and near anterior of maxilla; groove and/or foramen above canines; tooth row horizontal and on same level as jaw articulation; ventral surface of lower jaw rounded; no retroarticular process; parasphenoid ventral plate broad; quadrate ramus of pterygoid has ventral shelf; pointed muzzle formed by a dorsal process of the premaxilla; rostrum formed by premaxilla & nasal overhangs jaw; nares large; maxilla with narial (**not** nasal) flange; lacrimal reaches nares anteriorly and jugal posteriorly; quadratojugal visible in lateral view; quadratojugal meets maxilla and excludes jugal from ventral margin of skull; postorbital large and extends far posteriorly; cranium generally broad and perhaps depressed (not domed); frontal has lateral process participating in orbit; parietal broad, with very large pineal foramen; parietal forms lappets into postorbital; broad supratemporal; supratemporal "horn"; postparietal not fully fused (??); broad supraoccipital; occiput formed from large, flat supraoccipital fused to paraoccipital; postcranium unknown except limb fragments; probably insectivorous and/or carnivorous.



Oedaleops campi, skull in dorsal and right lateral views, modified from Langston (1965)

Links: PELYCOSAUR - Paleontology and Geology Glossary; Synapsid classification and autapomorphies; Biology 356; Schnellbestimmung anhand von typischen Schädelmerkmalen (German); reptiles; Oedaleops. .

References: Langston (1965); Lund (2000). ATW040124.



Caseidae: *Angelosaurus, Casea, Caseoides, Caseopsis, Cotylorhynchus, Ennatosaurus, Phreatophasma*.

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

Phylogeny: Caseasauria **::** Eothyrididae + *.

Characters: 1 to 4m herbivorous pelycosaurs with "slanted" skulls. Skull small; skull ornamented dorsally with small pits and some crevices; palatal denticles reduced; denticles (*not* teeth) absent on lower jaw; **$** marginal teeth generally foliate (bearing multiple cusps); no caniniform teeth; largest teeth anterior on both jaws; snout (premaxilla) strongly arched upward and overhangs tooth row to form anteriorly projecting rostrum; **$** large, high nares with external narial shelf; large pineal foramen; skull table broad & low; temporal opening very large; dorsal spines absent; small cervical vertebrae; very large rib cage and robust scapula; 3-4 sacral ribs; all limbs robust; phalangeal count reduced, as is size of feet; apparently successors to edaphosaurids as most common herbivorous pelycosaurs.

Image: *Ennatosaurus* from mathematical.com by permission.

Links: Introduction to the Pelycosaurs; PELYCOSAUR - Paleontology and Geology Glossary; Synapsid classification and autapomorphies; dinosaurs-ennatosaurus; Biology 356 (outstanding site!); Synapsida; Stars of the Show (A to I); Schnellbestimmung anhand von typischen Schädelmerkmalen (German); Caseidae (Mikko's Phylogeny); Stars of the Show (A to I) (*Ennatosaurus* skull).

References: Langston (1965). ATW030614.

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Synapsida: Ophiacodontidae

Abbreviated Dendrogram

```
AMNIOTA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      |  |--Archaeothyris
      |  `--Ophiacodon
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
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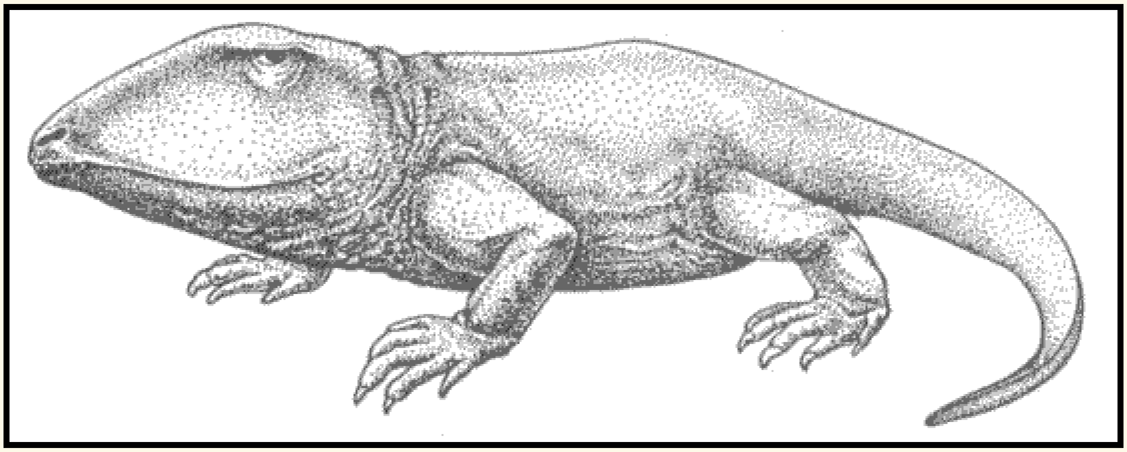
Ophiacodontidae



Ophiacodontids include small to very large carnivorous pelycosaurs distinguished by certain specialized cranial features. These were possibly semi-aquatic or fully aquatic animals, appearing early in the Carboniferous coal swamps.

There is a curious tendency to increase in the skull to trunk ratio, larger taxa having unusually large, awkward looking, elongate skulls. These animals also have relatively large, massive shoulder girdles, possibly to provide muscle attachment to support the weight of the huge head.

The modern cladistic paradigm unites ophiacodontids, edaphosaurids, and sphenacodontids by the possession of certain specialized features of the skull. However this is also the oldest family of pelycosaurs, and indeed of Synapsids/Theropsids, with the oldest known pelycosaurs - *Protoclepsydrops* and *Archaeothyris* - being included in this family (the former tentatively, the latter definitely).

From an ophiacodont stem, pelycosaurs evolved in two directions. One line of pelycosaurian development led to large aggressive, land-living carnivores, the sphenacodontids, the other to large plant- eating forms, the edaphosaurs. The ophaicodonts and edaphosaurs died out with the drying out of their swamp and pond-margin environments during the middle Permian, the sphenacodontids continued on a bit longer. (MAK 000720)

Ophiacodontidae: *Protoclepsydrops?*

Range: Pennsylvanian [RB86] to Guadalupian of North America & ?Europe

Phylogeny: Eupelycosauria :: (Edaphosauridae + Sphenacodontia) + * : *Archaeothyris* + *Ophiacodon*.

Characters: Semi-aquatic piscivores (per Romer. Reisz disagrees, based on the awkward length and height of the skull). Up to 4m. Head long & slender; deep jaw; numerous (40+) small teeth; well-developed lateral mandibular fenestra in notch of dentary; posterodorsal processes of premaxillae are long, thin & separated at midline by anterior process of nasal; angular with well developed ventral keel; lingual maxillary buttress above canines; **$** antorbital skull at least twice as long as postorbital skull; **$** nasal longer than frontal (at least twice as long as parietal); lacrimal elongated; orbit high on skull; ventral edge of skull concave postorbitally & includes jugal; relatively low skull table; braincase elements less fused than in other eupelycosaurs; **$** paroccipital process short, not extending to the cheek long tail; tabular with large medial process; dorsal centra relatively shorter than in sphenacodonts and edaphosaurids [RP40]; pectoral girdles large and massive; particularly broad anterior of scapulocoracoid; carpals & tarsals poorly ossified; claws blunted? absent?. Includes oldest known synapsid (*Protoclepsydrops*).

Image: *Ophiacodon* from The Synapsid Story (Ben Waggoner lecture)

Links: Paleontology and Geology Glossary: V; Synapsida; Biology 356. Schnellbestimmung anhand von typischen Schädelmerkmalen; Lecture 03 - Cont. Drift; Ophiacodontidae (Mikko's Phylogeny); Ophiacodon (German: interesting reconstruction); Ophiacodon, a pelycosaur with no fin.

References: Reisz & Berman (1986) [RB86]; Romer & Price (1940) [RP40]. ATW081024.

Archaeothyris: *A. florensis*. The oldest undisputed synapsid.

Range: Pennsylvanian (Kasimovian, possibly Moscovian) of North America (Nova Scotia) [TH04]

Phylogeny: Ophiacodontidae: *Ophiacodon* + *.

Characters: "true" synapsid skull

Introduction: *Protoclepsydrops* from the Middle Pennsylvanian of Joggins, Nova Scotia has been placed within the Ophiacodontidae, but its identity and taxonomic status is uncertain, partly because the known skeletal remains are fragmentary. *Archaeothyris*, from slightly younger sediments near Florence, Nova Scotia, is the oldest known diagnosable ophiacodontid. This was a more advanced animal than the contemporary protorothyrid captorhinomorphs. Its jaws were strong, and could be opened wide and snapped shut. Although its teeth were all the same shape - sharp and pointed - they were of different sizes, including a large pair of canines at the front of the jaws. Such teeth suggest a varied, carnivorous diet, and area distinguishing mark of the carnivorous pelycosaurs. MAK

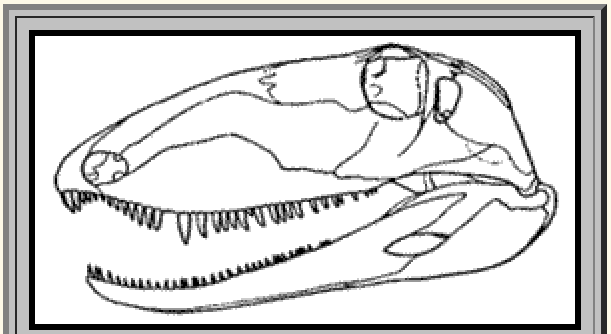
References: van Tuinen & Hadly (2004) [TH04].

Ophiacodon:

Range: Early Permian of North America

Phylogeny: Ophiacodontidae: *Archaeothyris* + *.

Introduction: *Ophiacodon*, a large Permian synapsid commonly 1.5 to 2.5 meters in length, was a specialized member of the ophaicodontid lineage. It is also the best known member of the family, represented by an extensive fossil record in North America, that has been subdivided, somewhat arbitrarily (based largely on stratigraphic position and size) into six species. The skull was very deep, with long jaws, these being provided with many sharp teeth. It has often been suggested that *Ophiacodon* was a fish-eating animal that lived largely along the shores of streams and ponds, although the high narrow skull would seem to mitigate against such a lifestyle. MAK



***Ophiacodon*: Early Permian of North America (Texas). Size: 1.5 to 2.5 meters, maximum size up to 3.6m long.**

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Synapsida: Varanopseidae

Abbreviated Dendrogram

```
AMNIOTA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   |  |--Mycterosaurinae
   |  |  |--Mycterosaurus
   |  |  `--Elliotsmithia
   |  `--Varanodontinae
   |     |--Aerosaurus
   |     `--Varanops
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

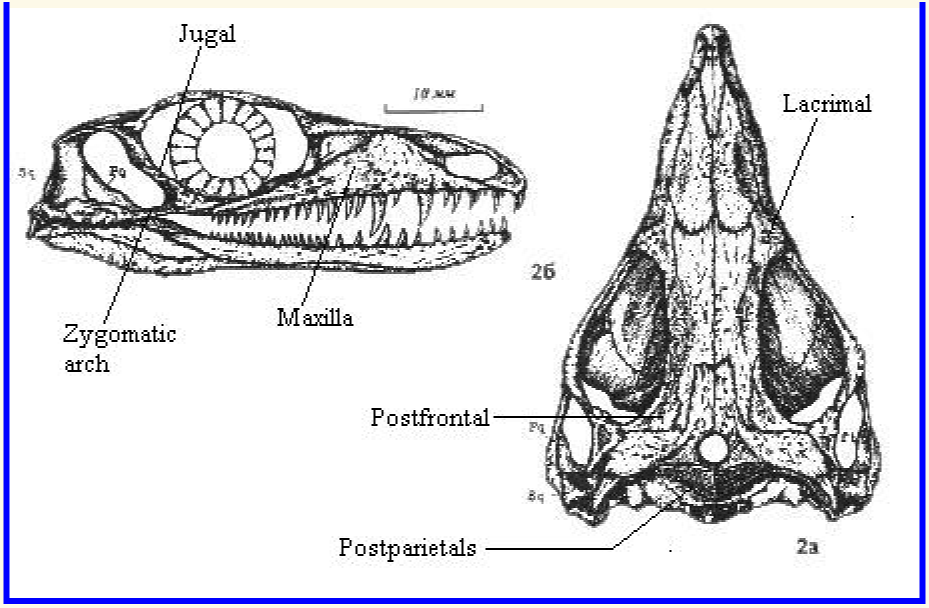
Taxa on This Page

1. *Aerosaurus* X
2. *Elliotsmithia* X
3. Mycterosaurinae X
4. *Mycterosaurus* X
5. Varanodontinae X
6. *Varanops* X
7. Varanopseidae X

Varanopseidae: Relatively small (~1 m), lizard-like, basal carnivorous (piscivorous? insectivorous?) eupelycosaurs, resembling monitor lizards.

Range: upC-upP(mP?) of NAm, Eur. & Afr.

Phylogeny: Eupelycosauria: (Ophiacodontidae + (Edaphosauridae +



Sphenacodontia)) + *: Mycterosaurinae + Varanodontinae.

Introduction: Of all the pelycosaurs, the varanopseids in appearance most resemble large modern varanid (monitor) lizards. None developed the distinctive sail that distinguished many pelycosaur groups. All are of small to medium size (none more than about 1.5 meters), with slender, lightly built skulls and a slender, very typically lizard-like body, fairly slender limbs, and a long tail. In fact, we might say that the varanopseids were lizardlike in its general aspect, though this must not be taken as an indication of any close relationships with the lizards.

In the skull Varanosaurus showed certain specializations that were the beginnings of some definite evolutionary trends typical of the more advanced pelycosaurs. For instance, the skull was rather narrow, deep, and elongated, with the eyes set far back. The jaws were very long, and the teeth were numerous and sharp. There was no indication of an otic notch (to support an eardrum), and the ear was located in the vicinity of the jaw articulation.

All varanopseids have specialized marginal dentition, and flattened curved teeth with anterior and posterior cutting edges. The skull, as mentioned above, is light, the temporal fenestra being enlarged and the lower jaw slender. The postcranial skeleton is also lightly built, giving varanopseids a sleek appearance, superficially similar to modern monitor lizards. The varanopseids were probably the most agile predators of their time. These successful animals outlasted all other carnivorous pelycosaurs as highly specialized lizard-like insectvores and small carnivores, and survived as late as the early late Permian (Capitanian epoch). The last forms were all small, and in the end they were probably outcompeted by the even more lizard-like younginiform diapsids

Varanopseids retain several primitive skull and skeletal features that indicate they are more primitive than other Pelycosaurs apart from the Eothyrids. For this reason modern cladistic paleontogists reject the opinions of earlier workers like Romer and Price (1940) who associated varanopseids with the advanced sphenacodontid family, and even suggested that *Varanops*, may have been closed to the ancestry of sphenacodontids. The most recent hypothesis places varanopseids within the Eupelycosauria, as its most primitive member, and close to the ancestral linneage from which the more advanced ophiacodontids, edaphosaurs, and sphenacodontids evolved.

Unfortunately the evidence of the fossil record contradicts this hypothesis. All of the really early pelycosaurs belong to the supposedly advanced ophiacodontid family. Rather then erect numerous "ghost lineages" to fill in the gaps, I would suggest instead that the Varanopseids, like the Eothyrids represent a secondarily primitive lineage that had lost certain specialised features. It is likely that both these groups evolved from Ophaicodontids during the great drought of the Kasimovian epoch, when the long period of aridity proved favourable to the reptiles, and not so good for the big basal tetrapods of the coal swamps. No doubt future discoveries will no doubt determine which theory is the correct one.

Characters: Compared to other pelycosaurs, sleek and streamlined [R+97]; skull deep and narrow, with relatively short antorbital region [RP40]; snout slender [RP40]; premaxilla with strong, deep maxillary process [R+97]; premaxilla maxillary process dorsolateral surface broad, smooth & gently curved [R+97]; premaxilla with shallow groove terminating in crescent-shaped depression (for nares) [R+97]; maxillae lengthened; lacrimal reaches nares (?); medial and orbital margins of frontal raised [R+98]; **$** parietals with medial anterior process bordered laterally by frontals and reaching level of orbit [R+98]; narrow zygomatic arch (implies possible primitive development of masseter muscle for chewing) [DR96]; maxilla contacts quadratojugal [DR96] and may exclude jugal from skull margin; lacrimal reaches nares [RP40]; orbits frontated (dorsal margin concave) [RP40]; slender posterolateral process of frontal [DR96]; in some, postfrontal may be reduced, and squamosal may have long anterodorsal process reaching dorsal process of jugal, excluding postorbital from temporal fenestra; **$** tuberous ornamentation on jugal, postorbital & prefrontal [R+98]; bars under orbit & fenestra usually very slender; suborbital and temporal fenestra usually large and **$** always tall, **$** bordered ventrally by thin bar from jugal, quadratojugal, with small maxillary contribution [DR96] [R+98]; occipital flange of squamosal reduced [DR96]; pineal foramen large & located near posterior end of skull table [DR96]; postparietals paired; tabulars slender [R+98]; otic notch absent; occiput concave in dorsal view [RP40]; plate-like occiput from supraoccipital fused to paroccipital processes; occiput may be strongly slanted forward; parasphenoid plate with large posterolateral wings [R+97]; quadrate and pterygoid floor middle ear cavity [R+97]; basisphenoid with large, laterally extended, tapering, pointed tubera [R+97]; jaw articulation posterior of occiput [RP40]; toothed area of premaxillae expanded; maxilla with longer posterior tooth row; dentary slender [M+01]; **$** marginal dentition strongly recurved [DR96] [R+97] [R+98]; **$** teeth mediolaterally flattened [DR96] [R+98] (*contra* [RP40]) with both anterior and posterior cutting edges formed by tapering (not ridges) [R+97]; teeth with slight lingual curvature at end [R+97]; tooth row horizontal & at same level as jaw articulation [RP40]; canines poorly developed [RP40]; elongate hyoid elements extending far behind skull [DR96]; ventral keel on vertebrae not much developed [RP40]; transverse processes short [RP40]; dorsal zygapophyses more lateral than in sphenacodonts and articular surfaces more horizontal [RP40]; neural spines short [RP40]; 2 sacral vertebrae [RP40]; deltopectoral crest in two parts, each with rugosity for muscle attachment [R+97]; proximal head of humerus relatively small (width 1/3 total humerus length) [R+97]; distal end width <50% humerus length [R+97]; ilac blade "low" (?) [RP40]; hind legs markedly longer than forelimbs [RP40].

Links: Paleontology and Geology Glossary: V; Synapsid classification and autapomorphies; Anatomy and relationships of Elliotsmithia; Biology 356; Synapsida; Schnellbestimmung anhand von typischen Schädelmerkmalen (German).

Image: *Mesenosaurus romeri* courtesy mathematical.com. Earliest fossil synapsid group. Note that this is not the best example, as some of the features mentioned above are not visible or simply not present. Here, and in some other varanopseids, the posterior process of the maxilla passes under a small shelf created by the jugal and quadratojugal in the zygomatic arch. Thus, in this specimen, the maxilla and quadratojugal may well articulate, but do not exclude the jugal from the skull margin. Similarly, the lacrimal does contact the narial margin, as can be seen in the dorsal view.

Note: [1] for detail of premaxilla, see *Mycterosaurus*. **[2]** As always, Romer's observations are of great value, but have to be understood in their context. Romer & Price erected the Varanopsidae in [RP40], believing it to be a grade of pelycosaur intermediate between ophiacodonts and sphenacodonts. Notwithstanding, their suppositions about what should go into this new box were startlingly correct, including *Varanops*, *Aerosaurus*, *Elliotsmithia*, and *Mesenosaurus* (similar to *Mycterosaurus*). This prediction, in 1940, is all the more incredible when one realizes that Romer & Price had only Broom's (1937) partial description of *Aerosaurus* and a few paragraphs on the fairly scrappy *Mesenosaurus* by Efremov the same year. Romer & Price conceive of the Varanopseids as being cranially like ophiacodonts (i.e., primitive) but post-cranially like sphenacodonts. This perspective caused them to make what appear to be errors in the polarity of certain character states, particularly in their description of *Varanops*. 011227.

Discussion: The varanopseids have been treated here with unusual attention to detail and to intergeneric variation. For the most part, these Notes are concerned with events at the family level and above. There are a number of reasons for this, not the least of which is the expense and effort required to run through the tangled mass of literature with so fine a comb. However, certain taxa are close to high order nodes of unusual interest, and the varanopseids are one of those.

Some time in the middle of the Carboniferous, perhaps 320 Mya or a bit more, the amniotes evolved. Almost immediately, they split into *at least* five important lineages: Eureptilia (lizard, snake, dinosaur, croc & bird ancestors), turtles, the pareiasaur group (which may have included the turtles), bolosaurs, and our own SYNAPSIDA. Three of these groups survive today, of which two are clearly dominant. Almost all other tetrapods were eliminated except for the temnospondyls, who hung on until the late Mesozoic, and the Lissamphibia (frogs, salamanders & caecilians) who survived by radical re-engineering of their body plan. Unfortunately, so poor is the fossil record of the Carboniferous, that we know almost nothing about the early history of these new groups. The best we can normally do is to look closely at their descendants in the Permian and extrapolate backward.

The Varanopseids, as relatively primitive synapsids, can tell us at least a few things about the development of this branch -- an important one to us personally. For example, they clearly show that the development of the slanted occiput was not a result of, nor even coincident with, the curved jaw line of later sphenacodonts and therapsids. The varanopseids had, for the most part, jaws as straight as a ruler. In fact, the slanted occiput came first. As Romer &

Price (1940) observed, the skulls can be derived from the basic amniote pattern "as if one had kept hold of the animal's braincase and violently pushed the rest of the head toward the chest." That is, the top of the skull wasn't angled forward so much as the jaw was pushed back past the end of the skull table, forcing the occiput to slant. In retrospect, this makes good sense. By angling the head over the jaws, the jaw adductors could act more vertically on the jaw, and attach to the jaw at a point further forward, creating a far better mechanical advantage. Of course, the same effect could be achieved by changing the outline of the jaw to curve upwards, and this is what the sphenacodonts achieved. However, the brutally simple solution adopted by the Varanopseids seems to have been the first step.

Like most feats of biological engineering, this solution created its own problems. For example, it made for a very flat skull. The slanting occiput actually reduces the volume available for the jaw muscles as it increases their mechanical advantage. One solution might be to develop a wider skull. However, the basal synapsid skull may depend for its structural integrity on the strong central arch of the skull table bones. See the discussion of Eothyrididae. Broadening the skull would leave the lateral margins without support and extremely vulnerable to lateral impact. Undoubtedly this was already a problem for varanopseids, with their thin, fragile bars of bone under the orbit and temporal fenestra. The eothyrids seem to have attempted a wider skull, but do not seem to have much success with it. If nothing else, the temnospondyls had been at the big-mouth flat-head game for quite a long time and would not be easily muscled out of that territory by bunch of retrofitted amniote newcomers.

Another approach might be to increase the size of the temporal fenestra to accommodate more muscle. Yet another, to get bigger, since muscle volume would increase faster than jaw mass. Both of these trends can be found within the varanopseids. Unfortunately, the slanting occiput also restricts the degree to which the temporal fenestra can be expanded. However, there is no doubt that the more derived varanopseids were both larger and more fenestrated than their ancestors.

With the benefit of hindsight **[1]**, it seems obvious that the curved jaw of the sphenacodonts was the way to survival. However, let us not forget that all this could not have been obvious to a hypothetical young synapsid contemplating a career choice in the Carboniferous. A curved jaw means that one's teeth do not necessarily occlude at the same time, allowing a potential lunch to escape with only a nick. It calls for dental specializations to a degree unheard of in the Carboniferous, as well as a new set of more horizontally-oriented muscles to make the thing really work right, as well as a heavy, almost unwieldy, jaw to carry all the equipment. If we had been asked these questions in the Pennsylvanian, we would quite rightly regard the varanopseids as sensible, progressive folk and the sphenacodonts as hopelessly effete niche players doomed to evolutionary oblivion. **[2]**.

Where all this is going, in case the reader wondered, is Reisz (1972). This was Prof. Reisz's very first publication, ambitiously titled *Pelycosaurian reptiles from the Middle Pennsylvanian of North America*. Understand that, at the time, Romer & Price (1940) had intimidated a generation of paleontologists. After one of the greatest paleontologists who has ever lived has written a nearly 600 page treatise on a subject, there is likely to be a pause, hiatus or, if you will, a diastema, before any major revision is undertaken. When it does happen, it is likely to be because someone is young, bright and inexperienced enough to mention that the emperor has forgotten a few items of clothing. At the time, Reisz was not only just starting out, but was a student of Robert Carroll -- in some ways Romer's successor -- who was not that much older (at least from the geriatric perspective of this writer).

The reason the reader has been subjected to all this fulsome sycophancy is that I disagree with a great deal of Reisz's analysis and many of his conclusions. Having *absolutely* no business doing so, there is a certain amount of preparatory apologetic bootlicking and groveling one is forced to do while working up the nerve to explain. With that unpleasantness out of the way, we can proceed. However, the reader is strongly cautioned that (a) the following commentary is probably dead wrong and (b) we are also viewing this paper with the benefit of hindsight and, in particular, Reisz's own extensive studies over the last 30 years.

Reisz begins his analysis with two observations which are dubious. First, he states that skull sizes increased as a proportion of body size over time. Even if stratigraphic time were an adequate proxy for evolution, which it isn't, the trend wouldn't hold true in light of the fossil record known today. Second, he speculates that increasing absolute size requires a disproportionate increase in jaw size. The reason is that mouth area increases only as the square of linear dimension, while body volume increases as the third power; and this increase in area "is necessary in order that the larger animal may obtain an equivalent amount of food." How then does he explain the notably microcephalic herbivorous forms? How about mouth *volume*? Jaw speed and strength? Changes in prey, in metabolism, digestive and reproductive efficiencies? Any of these characteristics can and have been more important to permitting large size than oral surface area.

Reisz follows this up by concluding that head size not only increased but that "the antorbital region of the skull becomes relatively longer." This is an artifact of the fact that so many of the data points are ophiacodonts, which are so notably longirostrine that Romer believed them to be aquatic piscivores. Varanopsids, on the one hand, and sphenacodonts, on the other, are both much shorter in the antorbital jaw than ophiacodonts. *Archaeothyris*, a very early synapsid form, has a short rostrum for an ophiacodont, but a long face for an eothyrid or varanopseid -- about the relative length of a sphenacodont, in fact.

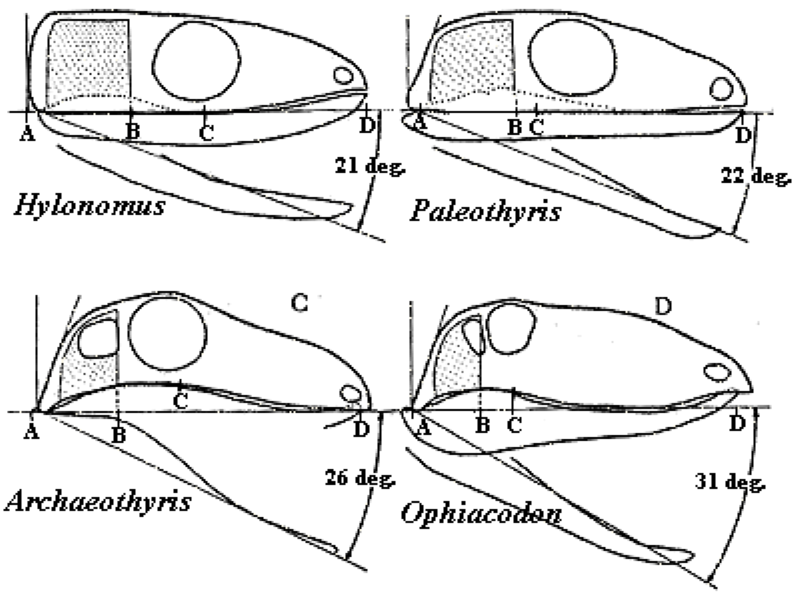


Figure 20 Comparison of the jaw mechanisms in romeriids and primitive ophiacodontids.
A: fulcrum of lever.
B: furthest point from fulcrum on which the jaw muscle can act
AB/AD: mechanical advantage of jaw mechanism.
CD: length of tooth row.
Angle shown is the angle of the jaw when jaw muscles extend by 50% of their original length.
Stippled area: location of jaw adductor musculature.

Relabelled from Reisz (1972) with original legend

Reisz completes his jaw analysis with the mechanics in his Figure 20, reproduced at right. This is Reisz's summary figure on jaw mechanics in early synapsids. The figures have been relabelled for legibility. The original legend has been retained except for the omission of specimen identifications. *Hylonomus* and *Paleothyris* are romeriids -- probable primitive amniotes with unfenestrated skulls. *Archaeothyris* is the more complete of the two Carboniferous synapsids described in Reisz's paper **[3]**, and *Ophiacodon uniformis* is a Lower Permian ophiacodontid. Reisz concludes that temporal fenestration developed as a response to the need for more muscle mass because of the decreasing mechanical advantage imposed by lengthening of the preorbital jaw. He analyzes mechanical advantage in the manner set out in the figure, in essence as a third class lever.

Let's look at some of the problems:

1) A jaw cannot be treated as a massless third class lever with a weight at the end. It *can* be treated as a massless third class lever with a weight *at the center of mass*. So, Reisz's point **D** is in the wrong place. We don't know where **D'** should be, but it will depend on the distribution of mass along the jaw.

2) The third class lever model only works for forces normal (i.e. at 90°) to the lever arm, which is modeled as a straight line between the jaw articulation (**A**) and the center of mass (**D'**). This will decrease the actual force applied to moving the jaw by a factor of cos(**ø**), where **ø** is the number of degrees by which the force angle differs from the normal. We may omit the math, but this is precisely equivalent to moving point **B** to a new point (**B'**) towards **A** resulting in a loss of mechanical advantage by the same factor, *i.e.* cos(**ø**). Thus **B** is also in the wrong place.

3) Because the angle of the jaw is constantly changing, while the muscles pull from the same place (an unrealistic assumption, but remember, this is just a model!), the mechanical advantage of those muscles is a moving target, depending on the jaw angle (also **ø**).

4) Just for amusement, remember also that we are opposing the force of gravity. The extent to which gravity reduces the net applied force depends on both the angle of the jaw and the position of the head. So, as with adolescents, we not only need to be concerned with the synapsid's big mouth, but with its attitude. One can see, for example, that the angle of the neck could readily have as decisive an effect as any of the factors mentioned above, even in the ideal model used by Reisz.

Ultimately, it seems doubtful that Reisz's model can tell us much about fenestration. Properly considered, perhaps it *can* tell us something more about jaw design and the division between varanopseids and sphenacodonts discussed above. Except for the dramatically slanted occiput, varanopseids are constructed somewhat along the lines of the various beasts in the model. One might suspect that there were additional mechanical bells and whistles not well represented by the fossil record. For example, examine the braincase of *Aerosaurus*. Perhaps, for example, some musculature was placed *behind* the occiput and used some of those great wings on the opisthotic as pulleys to improve both the position (**B'**) and perhaps the angle at which force was directed on the jaw. This would be helpful, but would not dramatically change the basic design parameters discussed above, which also increased **B'** by moving the jaw musculature further out over the jaw, while keeping a very posterior jaw articulation (**A**), thus improving the mechanical advantage (**AB' / AD'**).

Sphenacodonts, by contrast, seem to have manipulated **D'** and **ø**. The curved jaw, with its massive coronoid and very low articular would have had two interesting effects. First, by counterweighting the anterior jaw, the coronoid moved the center of mass (**D'**) posteriorly, dramatically improving the mechanical advantage. Second, recall that the lever arm is the line between the jaw articulation and the center of mass. If the articular is below the tooth row, **ø** is actually negative when the mouth is closed. More to the point, the point of maximum advantage (**ø** = 0 and cos(**ø**) = 1), is reached before the jaw closes. Thus a sphenacodont's bite would be strongest when it needed to be strong, not when the jaws had already closed.

Thus, Reisz's 1972 model is very useful in understanding at least one of the major evolutionary splits of the Carboniferous synapsids, one which we discussed in more general terms above. For whatever reason, selective pressures favored a more efficient jaw in Carboniferous synapsids. Given that this has been true in virtually every lineage since the first gnathostomes, we should not be surprised. One lineage, the varanopseids, accomplished this object by manipulating the position of the jaw, "as if one had kept hold of the animal's braincase and violently pushed the rest of the head toward the chest." The other, the sphenacodonts, changed the shape and mass distribution of the jaw without much changing its position. The latter solution turned out to be "correct" by the only measure we have. We sphenacodonts survived. The varanopseids did not. (ATW 020101).

[1] sometimes defined as the last thing one sees before one's head finally disappears up one's cloaca. Back.

[2] A somewhat similar case is touched on in connection with the Heterostraci. Back.

[3] Reisz's characterization of *Archaeothyris* as an ophiacodont might be questioned today. Based largely on later work by Reisz himself, we might now think of it as an early mosaic including many -- perhaps mostly -- varanopseid characters. Back.

References: Dilkes & Reisz (1996) [DR96], Modesto *et al*. (2001) [M+01]; Reisz (1972); Reisz *et al*. (1997) [R+97], Reisz *et al*. (1998) [R+98], Romer & Price (1940) [RP40].

Mycterosaurinae: *Mesenosaurus*. Defined as *Mycterosaurus* > *Varanodon*. [M+01]

Range: Guadalupian to Lopingian of North America, South Africa and Russia.

Phylogeny: Varanopseidae: Varanodontinae + *: *Mycterosaurus* + *Elliotsmithia*.

Characters: **$?** maxilla with broad dorsal process [M+01*]; **$?** maxilla contacts prefrontal [M+01*]; **$** prefrontal expanded ventrally, leaving only narrow lacrimal in preorbital region [M+01*]; **$?** lacrimal duct opens laterally, near posterior edge of lacrimal [M+01*]; **$** squamosal has a narrow occipital shelf contributing to the occipital surface [M+01*]; **$?** supraglenoid foramen absent [M+01*]; **$?** posterodorsal process of squamosal present [M+01*]; **$** serrations on marginal teeth [M+01*].

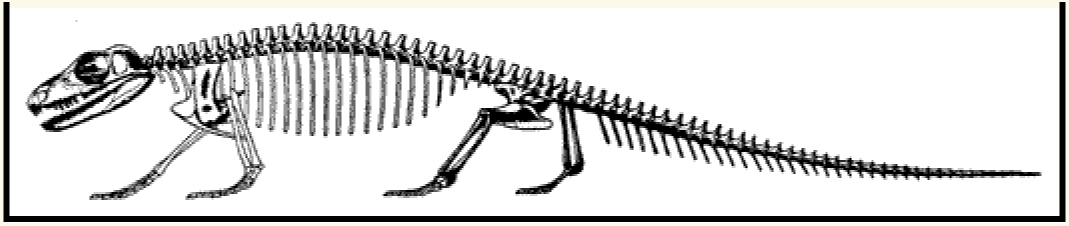
Notes: **[1]** Characters marked as [M+01*] were derived by an independent analysis of the data of [M+01] except that (to suit my own prejudices): *Elliotsmithia* was scored as having a triangular temporal fenestra (char. 9 = 1) as in [R+98]; characters 8 and 24 from [R+98] were used; and characters not applicable to the sauropsid outgroup were treated as gaps, rather than as missing data. The resulting cladogram has the same topology as in [M+01] except that the mycterosaurines are an unresolved trichotomy. **$**, as always, indicates as synapomorphy. **$?** indicates a character shown as a synapomorphy in 2 of the 3 equally most parsimonious trees.

Links: Geography Arena - Journal Details (abstract of [M+01]).

References: Modesto *et al.* (2001) [M+01]; Reisz *et al*. (1998) [R+98]. ATW031123.

Mycterosaurus: *M.*

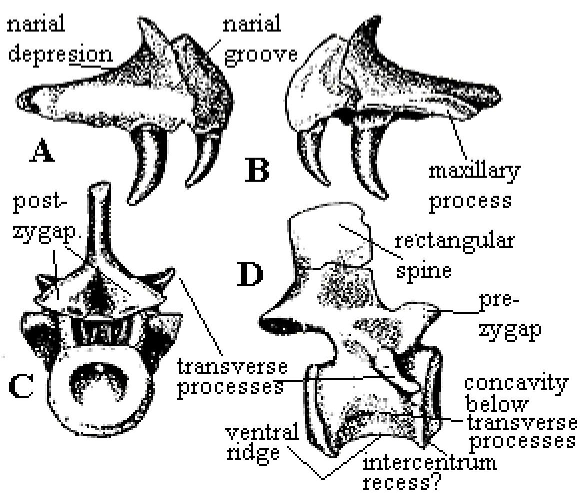
longiceps (= *Basicranodon*). Small, primitive varanopseid.



Range: Middle Permian of North America

Phylogeny: Mycterosaurinae: *Elliotsmithia* + *.

Introduction: *Mycterosaurus longiceps* (right) is the most primitive member of the family. This small pelycosaur has the typical varanopseid features, but lacks several characteristics of the advanced members of this family.



Mycterosaurus, premaxilla in (A) lateral and (B) medial views, dorsal vertebra in (C) posterior and (D) right lateral view. From Reisz et al. (1997).

Characters: lacks massive maxillary buttress above canines (plesiomorphic); postfrontal not reduced (plesiomorphic); anterior supratemporal located in groove in parietal [R+98]; temporal fenestra not expanded anteroposteriorly (plesiomorphic); parasphenoid with dentition on ventral plate, extending to part of cultriform process [R+97]; vertebral roughly square in lateral view & deeply amphicoelous [R+97]; (pleuro)centra with well-defined anteroventral recesses for intercentra (not ossified? not recovered?) [R+97]; longitudinal ridge at base of centrum, widening at both ends into abutments for intercentra [R+97]; transverse processes short and horizontal [R+97]; surface of centrum concave below transverse processes [R+97]; dorsal neural spines rectangular in lateral view, with vertical anterior & posterior edges [R+97]; dorsal neural spines transversely thicker in middle, tapering both anteriorly & posteriorly [R+97]; cervical & dorsal postzygapophyses separated by deep groove [R+97]; postzygapophysis articular facets "tilted slightly medially from the horizontal plane" (??) [R+97]; **$** no *supraglenoid foramen* on scapula [R+97]; posterior coracoid well-ossified in adults and fused to rest of scapulocoracoid [R+97];**$** scapula relatively thin and small, not extending far dorsally; anterior edge of scapular blade slightly S-shaped, thus bent medially above coracoid and laterally above that [R+97]; supinator process is slender and oriented proximo-distally (rather than as a "strongly flared" tubercle -- *compare* figure at *supinator process*) [R+97]; femur with slender, gracile shaft [R+97]; femur with S-shaped flexure [R+97]; *fourth trochanter* absent [R+97]; "internal" (= *lesser?) trochanter* close to femoral condyle [R+97]; femur adductor crest weak or absent [R+97]; femur with *popliteal area* shallow & broad [R+97].

Links: Biology 356; New Page 1; Geography Arena - Journal Details; Geography Arena - Journal Details.

References: Reisz *et al*. (1997) [R+97], Reisz *et al*. (1998) [R+98].

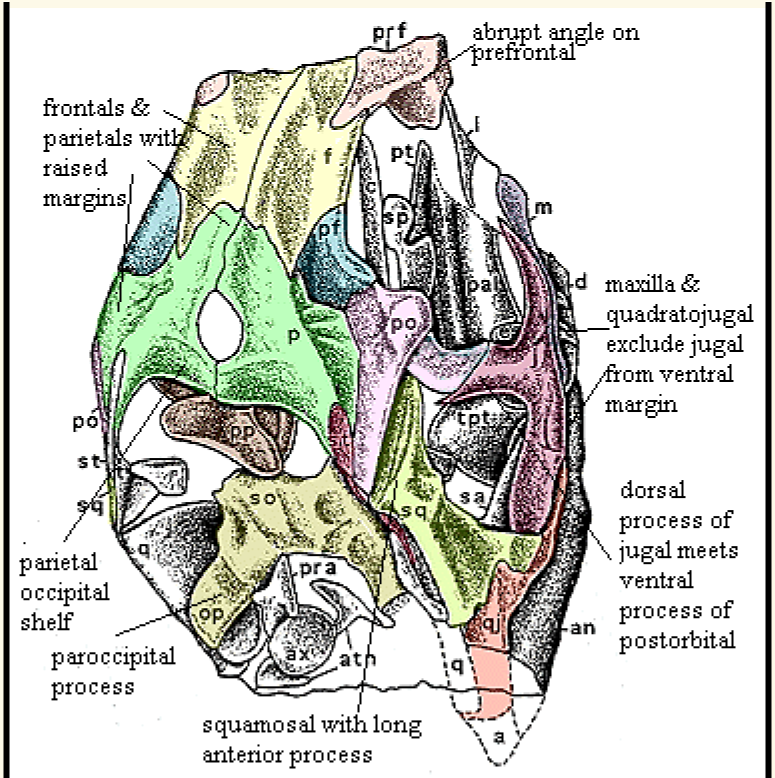
Note: [1] The sigmoid flexure of the femur leaves an S-shaped crest running down the femur which presumably substitutes for both the 4th trochanter and the adductor ridge. **[2]** Reisz [R+97] asserts that in all other varanopseids, the skull has been completely reorganized around an anteroposterior expansion of the temporal fossa. ATW030821.

***Elliotsmithia*:** very late, South African form. *E. longiceps*.

Range: Late Permian of South Africa.

Phylogeny: Mycterosaurinae: *Mycterosaurus* + *.

Characters: prefrontal with abrupt (~80 °!) angle between dorsal & lateral surfaces [R+98]; frontal enters strongly into orbit without distinct flange [R+98]; tapering process of frontal intervenes between anterior parts of parietal & postfrontal [R+98]; pineal opening large [RP40]; pineal foramen raised [R+98];



Elliotsmithia, holotype. From Reisz et al. (1998).

midline suture of parietals raised [R+98]; parietals with posteroventrally directed occipital shelf [R+98]; prefrontal & maxilla only narrowly separated by lacrimal [M+01]; ventral margin of orbit from maxilla & jugal [RP40]; jugal dorsal process stout, others thin [R+98]; quadratojugal & maxilla exclude jugal from ventral skull margin [R+98]; jugal posterior process meets squamosal and excludes quadratojugal from temporal fenestra [R+98]; postfrontal forms gently curved posterodorsal orbital margin [R+98]; postorbital bar projects laterally [RP40]; postorbital large [R+98]; postorbital ventral ramus meets jugal half-way down temporal fenestra & forms posterodorsal orbit [R+98]; temporal fenestra kidney-shaped [M+01] (*contra*, [DR96] [R+98]); quadratojugal long, with slender process below jugal [R+98]; postfrontal "unusually elongated posteriorly" [RP40]; long anterior process of squamosal [DR96] [R+98]; squamosal anterodorsal process does not reach jugal [R+98]; squamosal broadly expanded ventrally [M+01]; squamosal with posterodorsal process [M+01]; supratemporal long contact with postorbital & both contact posterodorsal process of squamosal [R+98]; occiput strongly tilted anteriorly [DR96] [R+98]; occiput strongly concave [RP40]; anterior supratemporal located in groove in parietal [R+98]; postparietals paired? [R+98] (could be crushed left postorbital and/or postfrontal?); **$** long, slender paroccipital process of opisthotic [DR96] [R+98] (but see **[2]**); supraoccipital boad & plate-like [R+98]; supraoccipital lacks lateral process above temporal fenestra [R+98]; sphenethmoid ("presphenoid" of Romer & Price?) present [R+98]; well-developed pterygoid flanges with single row of large teeth [R+98]; pterygoid palatal ramus with denticles [R+98]; jaw articulation even further posterior of occiput than in *Varanops* [RP40]; jaw articulation almost on same level as tooth row [RP40]; dentary very long & probably slender [R+98]; mandibular fenestra absent [R+98]; retroarticular process present [R+98]; hyoid elements extending well back behind skull [R+98]; teeth pointed, compressed & recurved [RP40] [R+98]; cutting edges on distal margins of all teeth [M+01]; 1st maxillary tooth caniniform [M+01]; postcanine teth with se cutting edges [M+01]; **$** anteriorly inclined neural spine on axis [DR96]; **$** dermal ossifications above cervical vertebrae [DR96] [R+98].

Links: Untitled Document; NAPC Abstracts, Ra - Ru.

References: Dilkes & Reisz (1996) [DR96], Modesto *et al.* (2001) [M+01], Reisz *et al*. (1998) [R+98], Romer & Price (1940) [RP40].

Notes: [1] Significance relates to idea that pelycosaurs were restricted to an equatorial belt, a limitation which was not overcome until therapsids evolved. If *Elliotsmithia* coexisted in Gondwana with therapsids, the latitude limitation may be an artifact. However, as [DR96] point out, the upC-lwP glaciation had receded by the upP in which *Elliotsmithia* is found. Thus, the hypothesis of severe temperature restriction remains valid. However, it may be as true for therapsids as for their ancestors. **[2]** This is contained in the diagnosis as an apomorphy; however, the actual description and figure indicate that the process begins at a broad base and tapers slightly ventrolaterally to end at a blunt, unfinished tip *and* that this is intermediate between the rodlike process of *Mycterosaurus* and *Varanops*. 011228.

Varanodontinae: *Varanodon*. defined as *Varanodon* > *Mycterosaurus*.

Range: Late Carboniferous to Upper Permian of North America

Phylogeny: Varanopseidae: Mycterosaurinae + *: *Aerosaurus* + *Varanops*.

Characters: **$** maxilla with dorsal process, but process narrow dorsally [M+01*]; **$** lateral buttress of maxilla present [M+01*]; **$** lacrimal duct opens laterally on concave surface of lacrimal [M+01*]; **$** postorbital posterior process short or absent [M+01*]; **$** postorbital excluded from margin of temporal fenestra by jugal and squamosal [M+01*]; **$** squamosal contacts jugal on postorbital bar [M+01*]; **$** temporal fenestra triangular, not oval [M+01*]; **$** anterodorsal process of squamosal present and forms dorsal border of temporal fenestra [M+01*]; **$** squamosal occipital shelf absent [M+01*]; **$** quadratojugal contributes to margin of temporal fenestra [M+01*]; **$** quadrate occipital margin with strong anterodorsal slope [M+01*]; **$** supraglenoid foramen present [M+01*]; **$** paroccipital process tall, blade-like and attached to tabular [M+01*].

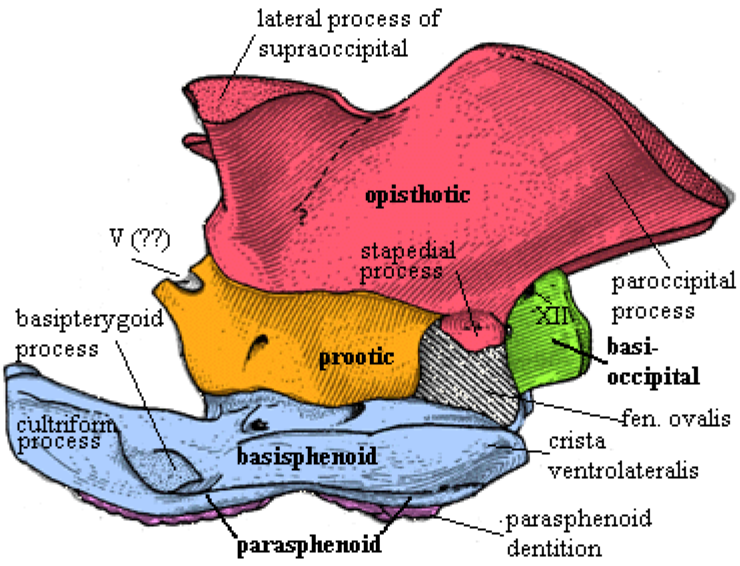
References: Modesto *et al*. (2001) [M+01]; Reisz *et al*. (1998) [R+98].

Notes: [1] Characters marked as [M+01*] were derived by an independent analysis of the data of [M+01] except that (to suit my own prejudices): *Elliotsmithia* was scored as having a triangular temporal fenestra (char. 9 = 1) as in [R+98]; characters 8 and 24 from [R+98] were used; and characters not applicable to the sauropsid outgroup were treated as gaps, rather than as missing data. The resulting cladogram has the same topology as in [M+01] except that the mycterosaurines are an unresolved trichotomy. All three equally parsimonious trees yielded the same synapomorphies for varanodontines. 020219.

Aerosaurus: *A. greenleeorum, A. wellesi*.

Range: Late Carboniferous to Early Permian of North America

Phylogeny: Varanodontinae: *Varanops* + *.



Aerosaurus, braincase in left lateral view. From two figures in Langston & Reisz (1981)

Characters: 1 m & 17 kg [LR81] [RP40]; maxilla long, but not tall [LR81]; lacrimal large and reaches nares [LR81]; "canine buttress" present [LR81]; postorbital posterior process reduced & replaced by expansion of squamosal [DR96]; postfrontal small & restricted to skull table [LR81]; supratemporal included in slot in large parietal [LR81]; anteroposteriorly expanded temporal fenestra [DR96]; lacrimal & jugal exclude maxilla from orbit [LR81]; maxilla & quadratojugal exclude jugal from skull ventral margin [LR81]; quadratojugal included in posteroventral margin of temporal fenestra [DR96]; long anterior process of squamosal [DR96]; squamosal ventral ramus very slender [LR81]; anterodorsal process of squamosal participates in postorbital bar & contacts jugal [DR96]; anteriorly tilted occiput [DR96]; occiput long and gently sloped [LR81]; paroccipital process broad & plate-like [DR96]; supraoccipital with lateral process over temporal fenestrae [R+98]; occipital condyle somewhat flattened [RP40]; braincase not fully fused in mature individual [LR81]; parasphenoid solidly fused to basisphenoid as largest element in braincase [LR81]; parasphenoid overlaps basioccipital & forms ventral margin of fenestra ovalis [LR81]; cristae ventrolaterales large and marked by longitudinal striations [LR81]; **$** dorsum sellae primarily from basisphenoid (as in reptiles and ¿mammals?, but not most pelycosaurs) [LR81]; expanded parasphenoid plate with strong, pointed, recurved teeth (!) [LR81]; long laterally splayed *basipterygoid processes* [LR81]; very long cultriform process [LR81]; pterygoid flanges with single row of large teeth [LR81]; dentary long, overlapping angular & surangular dorsally [LR81]; long splenial extends almost entire tooth row on medial surface (not visible lateraly) [LR81]; internal mandibular fenestra present [R+98]; no reflected lamina [LR81]; only 26 mandibular teeth & 19-22 maxillary [LR81]; teeth longer & flatter than other varanopseids and strongly recurved [LR81]; canines not sharply diffrentiated [LR81]; 5-6 cervical vertebrae & 21-23 dorsals [LR81]; vertebral centra with slight ventral lip, especially cervicals (due to dorsal position of notochordal fossa) [RP40]; sides of cervical centra strongly excavated anteriorly for intercentrum, less strongly excavated in anterior dorsal centra [LR81] [RP40]; crevical vertebrae moderately elongate [RP40]; dorsal centra short [RP40]; neural spines relatively low [LR81]; ribs thin & double-headed [LR81]; gastralia present [LR81]; 70+ caudal vertebrae [LR81]; caudal spines transversely thin [LR81]; supraglenoid foramen "far in advance of the buttress" (??)

[RP40]; humerus & femur only slightly longer than epipodials [LR81]; strongly developed deltopectoral crest [LR81] [RP40]; ectepicondylar notch poorly developed (otherwise humerus like *Varanops*) [LR81]; forearm like *Varanops*, but shafts straighter & more robust [LR81]; manus phalanges 23453 [LR81]; longitidinal dorsal trough of ilium present (primitive?) [LR81]; femur with ends not greatly expanded [LR81]; tarsals block-like [LR81]; metatarsals and phalanges short & robust [LR81]; pes phalanges 23454 [LR81].

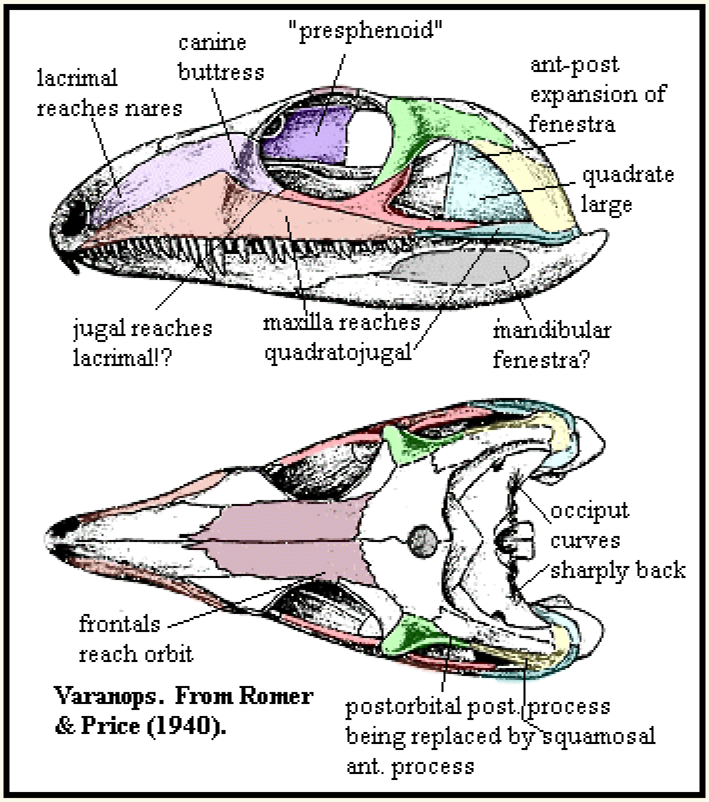
Links: Biology 356; New Page 1; Visuals Unlimited Stock Photography- Early reptile of the Permian ... .

References: Dilkes & Reisz (1996) [DR96], Langston & Reisz (1981) [LR81], Reisz *et al*. (1998) [R+98], Romer & Price (1940) [RP40]. ATW031011.

Varanops: *V. longirostris*.

Range: up(?)P of NAm.

Phylogeny: Varanodontinae: *Aerosaurus* + *.



Varanops. From Romer & Price (1940).

Characters: small (115 cm, 22kg); ***cranial:*** premaxilla short [RP40]; maxilla reaches quadratojugal [RP40]; lacrimals with large orbital exposure and reach nares [RP40]; canine "buttress" present [RP40] (even though canines are poorly developed!); frontals participate in orbit [RP40]; large pineal fenestra well back on parietals [RP40]; unpaired postparietal? [RP40]; orbits strongly frontated [RP40]; jugal with small orbital exposure & does not reach lacrimal [RP40] (contradicted by their own figure!); postorbital posterior process reduced & replaced by expansion of squamosal [DR96] (*contra* [RP40]); anteroposteriorly expanded temporal fenestra [DR96]; quadratojugal included in posteroventral margin of temporal fenestra [DR96]; long anterior process of squamosal [DR96]; anterodorsal process of squamosal participates in postorbital bar & contacts jugal (??!) [DR96]; quadrate very large and extends far anteriorly [RP40]; anteriorly tilted occiput [DR96]; paroccipital process broad & plate-like [DR96] [RP40]; paroccipital process curves sharply backward (occiput strongly concave) [RP40]; presphenoid present [RP40]; lateral pterygoid flanges weak and far posterior [RP40]; interpterygoid vacuities narrow [RP40]; "inwardly turned ventral flange" on quadrate ramus of pterygoid [RP40]; posterior processes of parasphenoid bridged by bone (also in *e.g.*, *Haptodus*) [RP40]; intramandibular fenestra may have been present [RP40] [R+98]; well-developed retroarticular process [RP40]; articular surface horizontal [RP40]; ***dental:*** tooth row extremely long [RP40]; teeth circular in cross-section and *not* compressed (?! could be juvenile feature) [RP40]; ~6 "incisors" (premaxillary teeth?) & 37-38 maxillary teeth [RP40]; possible pair of posteriorly displaced canines [RP40]; but ~11 precanine maxillary teeth [RP40]; ***axial:*** 27 presacral vertebrae, 2 sacrals & 50+ caudals [RP40]; all centra short, with cervicals slightly elongated [RP40]; cervicals with ventral keel [RP40]; anterior centra with slight ventral lip (intercentrum articulation?) [RP40]; centra lateral concavities absent [RP40]; intercentra present [RP40]; 2-headed dorsal ribs [RP40]; gastralia present [RP40]; neural spines "of moderate height" [RP40]; neural arches excavated laterally above transverse processes [RP40]; posterior dorsal spines shorter anteroposteriorly [LR81]; body slender (from shape of ribs) [RP40]; 12 caudals with ribs [RP40]; chevrons strongly developed [RP40]; ***appendicular:*** short interclavicle present [RP40]; scapula short & not expanded dorsally [RP40]; supraglenoid present, but "far forward on the scapular blade" [RP40]; humerus shorter than femur, but more distal limb bones about equal [RP40]; lesser trochanter moderately high [RP40]; 4th trochanter poorly developed [RP40]; all feet are very long, with hind feet being stouter [RP40].

References: Dilkes & Reisz (1996) [DR96], Langston & Reisz (1981) [LR81], Reisz *et al*. (1998) [R+98], Romer & Price (1940) [RP40].

Note: **[1]** [RP40] point out that all of the material known then (and today?) was from a group of juveniles. This may have serious consequences for our understanding of the both the genus and the family of which it is the type & best-known species. **[2]** It becomes obvious, after reading *many* descriptions, that the ventral marginal skull bones of varanopseids are very long, fragile things, easily subject to both breakage and distortion. Descriptions of the posterior maxilla, jugal, quadratojugal, etc. should therefore be taken with a considerable dose of caution. **[3]** The anatomical conclusion of [RP40] is worth noting: "crudely put, the head is essentially that of a primitive pelycosaur [*i.e.*, to Romer, an ophiacodont] the trunk and limbs those of a sphenacodont ... . [*Varanops*' specializations are in the jaw which appears] as if one had kept hold of the animal's braincase and violently pushed the rest of the head toward the chest." **[4]** Note that certain elements in the image from [RP40] are not consistent between the dorsal and lateral views. In particular, the size and position of the lacrimal cannot be reconciled. Equally troubling is the figured squamosal which, according to [DR96] reaches the jugal in the postorbital bar with a long anterodorsal process -- plainly missing in the figure. 011228.

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checked ATW050607

Synapsida

Pelycosauria

Abbreviated Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EURETILIA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

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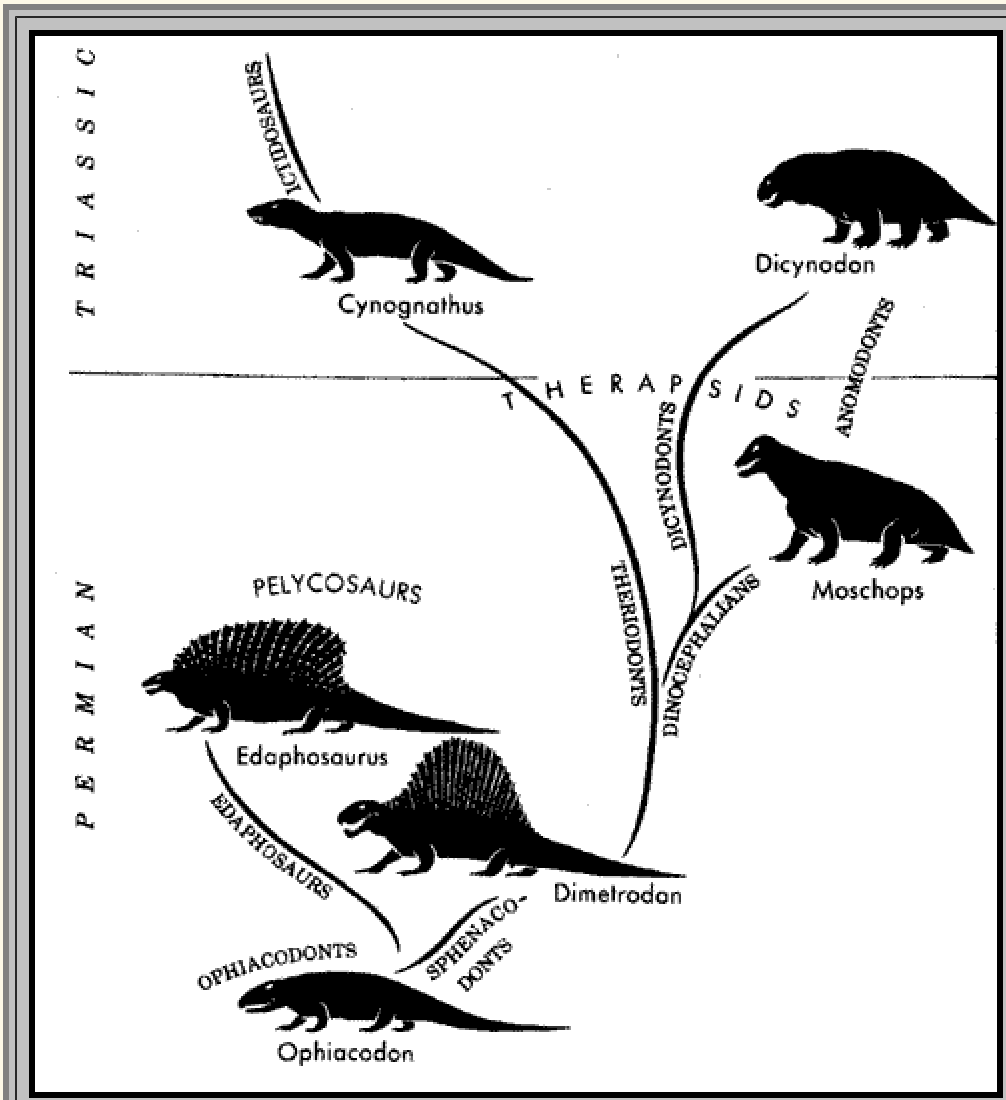
1. Eupelycosauria

The Pelycosaurs

A skeleton of a large carnivorous pelycosaur, *Ctenospondylus casei*, length 3 meters (photo from Fossilnet Gallery)

The "pelycosaurs" are the stem group synapsids who inhabited the Permo-Carboniferous. The pelycosaurs were among the very first groups of amniotes to evolve, early in the Late Carboniferous (Pennsylvanian) Epoch. By the end of that epoch all of the major lines of pelycosaurs, except the caseasaurs had appeared. They remained the dominant life-form (the largest, fiercest, etc) for some 40-odd million years, which is about 3/5ths the length of the age of mammals (Cenozoic). They were supplanted by their descendants, the Therapsids or "mammal-like reptiles", which had a short but glorious reign before being decimated by the terminal Permian extinction events, an opportunity that allowed the Archosauria to take over. In their position on the family tree of life, the pelycosaurs are the earliest and most primitive members of the synapsids, the group that (in the old classification) leads to or (in the new classification) includes mammals. Thus the mammal-line split off quite early from the rest of the reptile line, including turtles, lizards and snakes (squamates), crocodiles, dinosaurs and birds.

The evolutionary development of the pelycosaurs are best known and most completely recorded in the fossil record from the Cisuralian and Guadalupian "Red Bed" sediments of North America, particularly in Texas, Oklahoma, and New Mexico. Elsewhere the remains of pelycosaurs are fragmentary and scattered.



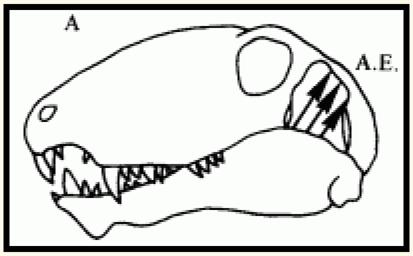
Pelycosaur and Therapsid evolution, showing the main types. Mammals evolve from the ictidosaurs (top left). Illustration by Lois M. Darling, from Colbert (1969).

The pelycosaur skeleton shows the typical generalized primitive features of early amniotes. The skull has a full complement of bones (lacking only the intertemporal bone, which was lost during the transition from labyrinthodonts to early reptiles), there is a pineal opening (common in early tetrapods), there are vertebral intercentra, and the limbs are similar to the limbs of protorothyrid and captorhinid reptiles and diadectomorphs, only somewhat more slender. In many respects the skull of some of the early pelycosaurs was very close to the captorhinid skull, which is one reason for thinking that these reptiles had a protorothyrid / captorhinid ancestry. There is the tendency among cladist systematisers now to deny this, because the captorhinid skull has a few specialized features not found in Pelycosaurs. I argue against this supposition, which is contradicted by the order of appearance in the fossil record, and in any case cladistics is not as infallible a methodology as some of its supporters would like to think. I would suggest instead that the Pelycosaurs were secondarily primitive, evolving from protorothyrids during the late Carboniferous period.

One distinctive feature of many pelycosaurs is a large sail along the back, formed by the great elongation of neural spines of the vertebrae, sometimes up to a meter in length in the larger species. This condition evolved independently at least three times (and quite possibly more) among pelycosaurs. The function of such spines would seem to be a thermoregulatory device for controlling body temperature. A membrane of skin would span the space between the spines, and this was richly equipped with blood vessels, warming the animal in the chilly morning and cooling it during the midday heat. Thus, in the early morning the animal could stand with its sail oriented toward the sun. Like a solar heater, the sail would absorb heat and warm the blood, which circulated through the body, raising the reptile's temperature so it could begin its daily hunt for food earlier than its non-sailback competitors. To prevent overheating after strenuous activity, it could angle its sail away from the sun and into the wind, dissipating heat. The sail and its associated spines could also have served in sexual and intra-species display behavior, and possibly also for camouflage (e.g. if the animal was hiding among the bamboo-like calamite plants, or giant "horsetails"),

An interesting example of convergent evolution is seen between these pelycosaurs and the unrelated dinosaurs. Several genera of dinosaurs, such as *Spinosaurus* and *Ouranosaurus*, both from Gondwanaland during the middle Cretaceous period - developed similar sails on their backs, which may have served a similar purpose.

But the most distinguishing feature of the Pelycosaurs (and a character retained by their Therapsid descendants) were not their famous sail (which not all pelycosaurs had anyway) but the so-called synapsid skull, which features a single, large opening on the side of the skull (the temporal region) behind the orbit (eye socket). This special opening allowed the development of larger and longer jaw muscles, and hence stronger jaws that could be opened wider and closed forcefully, enabling the animal to dispatch struggling or larger prey. It was this simple evolutionary adaptation that gave the pelycosaurs the edge in the struggle for survival. All that was needed was a prolonged period of drought, such as the sudden period of aridity during the Kasimovian Period, to kill off many of the large stem tetrapods that kept the pelycosaurs insignificant, and these creatures were able to emerge as the dominant life-form on Earth during the Permian period, while the captorhinids remained small and relatively insignificant. MAK, minor revisions ATW090307.



More to be added...

Descriptions

Eupelycosauria:

Range: fr upC.

Phylogeny: Synapsida : Caseasauria + * : Varanopseidae + (Ophiacodontidae + (Edaphosauridae + Sphenacodontia)).

Characters: Rostrum depth greater than width (*i.e.* snout width reduced); frontal participates broadly in orbit (at least 1/3 of orbital margin); long, narrow supratemporal; posterior location of the pineal foramen along the interparietal suture; decrease in the length of the skull table and in the length of the parietal relative to the length of the frontal.

Links: Synapsid classification and autapomorphies; Biology 356; PELYCOSAURIA. 010921.

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checked ATW050805

Edaphosauridae

Abbreviated Dendrogram

```
AMNIOTA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         |  |--Ianthasaurus
         |  `--+--Lupeosaurus
         |     `--+--Glaucosaurus
         |        `--Edaphosaurus
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

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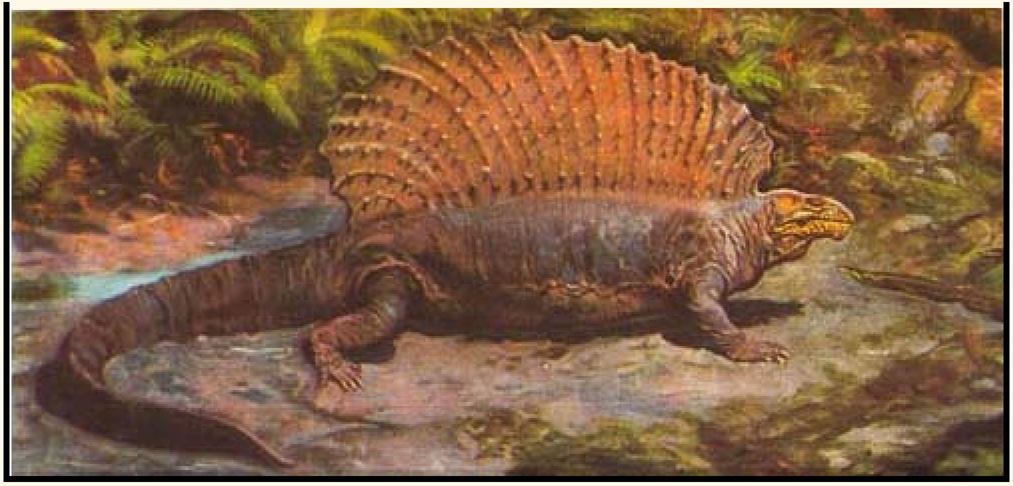
1. Edaphosauridae X
2. ***Ianthasaurus*** X

The Edaphosauridae

Sphenacodont Cousins

An important evolutionary line of early synapsids springing from an ophiacodontid-varanopseid ancestry were the edaphosaurids. Advanced edaphosaurids were ecologically quite different from their contemporaries, the sphenacodontids. Unlike most basal synapsids, some edaphosaurids were herbivores, as is shown by the structure of the skull and teeth. In fact, they were perhaps the first tetrapod animals – certainly the first amniotes --to adopt a herbivorous lifestyle.

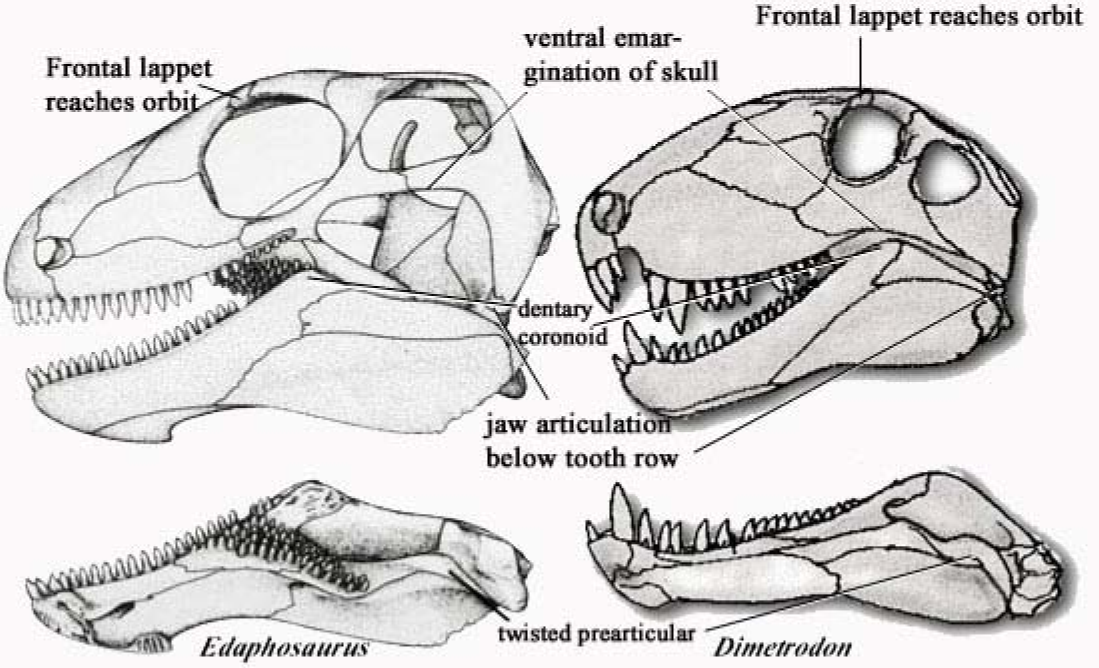
Like many of their carnivorous



sphenacodontid cousins, edaphosaurs were often equipped with a large “sail” along the back, formed by a great elongation of the neural spines of the vertebrae. This striking features, exhibited by several early synapsid lineages, is often said to have functioned as a temperature control device and perhaps also for sexual display. ***See*** discussion below.

Edaphosaurus, ***Ianthasaurus***, and probably ***Glaucosaurus***, can be placed with confidence in this family, but a number of lesser-known forms, like ***Lupeosaurus*** and ***Nitosaurus***, may belong here as well. ***Ianthasaurus***, ***Lupeosaurus***, and ***Edaphosaurus*** are characterized by the presence of greatly elongated neural spines that are rounded in cross-section. ***Glaucosaurus*** is known only from a partial skull. Although it seems probable that ***Glaucosaurus*** had spines like those of ***Edaphosaurus***, we have no proof as yet. The neural spines of ***Edaphosaurus*** and ***Ianthasaurus*** (but not ***Lupeosaurus***) also bear well-developed lateral tubercles or crossbars. On the lower (proximal) part of the spine looks like the mast of a square-rigged sailing ship. Distally, the tubercles on the two sides become less regular and go out of register, so that the right and left tubercles emerge at different vertical levels. The tubercles also become shorter with increasing distance up the "mast". The arrangement of these tubercles along the height of the spines is similar in the two taxa, as is the loss of contact between the postorbital and supratemporal bones of the skull.

Despite their differences, edaphosaurids and sphenacodonts share a large number of cranial features, and are believed to be sister groups. The shared, derived characters of the two groups include the following:



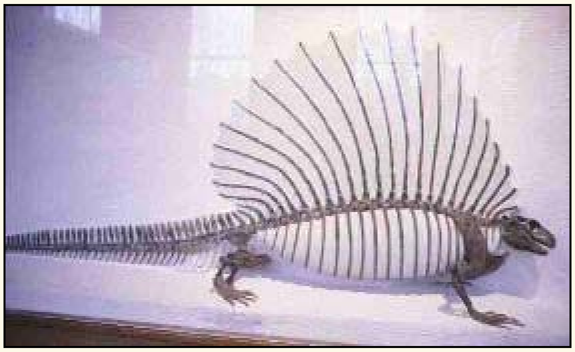
Selected synapomorphies of edaphosaurids and sphenacodontids

1. A lateral projection (lappet) of the frontal usually reaching the orbit;
2. ventral border of skull emarginated [H91];
3. A small quadratojugal which does not participate in the subtemporal bar [H91];
4. Jaw articulation below the tooth row [H91];
5. Rear of dentary with well-developed coronoid eminence [H91];
6. a prearticular twisted posteriorly as to underlie the pterygoideus process of the articular [MR90] [H91];

7. a pterygoideus process formed by the articular alone [MR90]; and

8. excavation of the lateral surfaces of the neural arches [MR90].

Within the edaphosaurids, ***Ianthasaurus*** is notably similar to sphenacodontids. For example, the lateral lappets of the frontal are short, but contact the orbit broadly. In ***Edaphosaurus***, the opposite is true: the lateral tab of the frontal is long and contacts the orbit quite narrowly. The anterior process of the frontal is broad. The sides of the parietals are convex, as in ***Haptodus***, rather than embayed, as in ***Edaphosaurus***. The posterior processes of the parietals are directed straight back to form a median wedge, rather than angling laterally, as they do in ***Edaphosaurus*** [MR90].

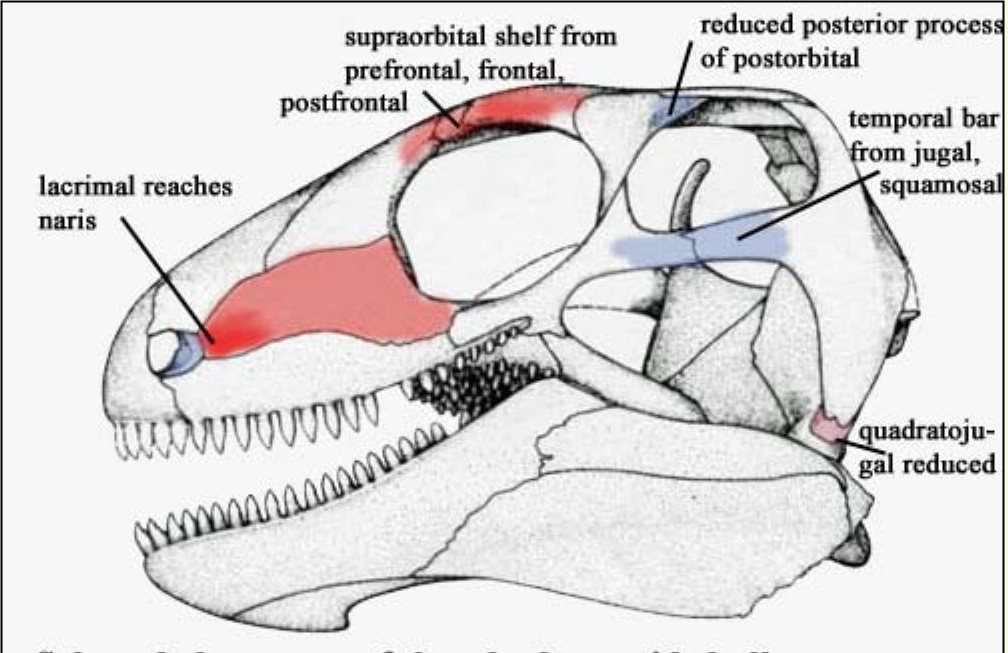


Ianthasaurus was almost certainly an insectivore. In any case it does not seem adapted to live on plants, and its short, blunt conical teeth are typical of bug eaters. As with so many groups of tetrapods of all kinds, the generalized small insectivorous form seems to have been the foundation on which selection built larger and more specialized animals [MR90]. The older literature often speaks of edaphosaurids evolving in the direction of herbivory from insectivory. However, it is unclear whether any of the edaphosaurid genera except ***Edaphosaurus*** ate their vegetables. Plant-eating may have been a late development in this lineage. ***Lupeosaurus*** doesn't seem to be built with the long, fat body of an herbivore -- but we lack the skull. ***Glaucosaurus*** doesn't have quite the dental specializations we might expect for eating plants -- but we lack the body. MAK, ATW081110

Edaphosauridae: Cope, 1882. Type: ***Edaphosaurus*** Cope, 1882. Other genera: ***Glaucosaurus*** Williston, 1915; ***Ianthasaurus*** Reisz & Berman, 1985 [MR90]; ***Lupeosaurus*** Romer, 1936 [S89]. Edaphosauridae ***incertae sedis*** include ***Edaphosaurus credneri*** Jaekel, 1910.

Range: Pennsylvanian to Cisuralian of Central and eastern U.S., central Europe (Germany).

Phylogeny: Eupelycosauria ::: Sphenacodontia + * : ***Ianthasaurus*** + (***Lupeosaurus*** + ***Glaucosaurus*** + ***Edaphosaurus***).



Selected characters of the edaphosaurid skull

Characters:[1]

Rostrum: antorbital region tall [M94]; lacrimal reaches naris [RP40].

Skull table: skull table narrow [RB86].

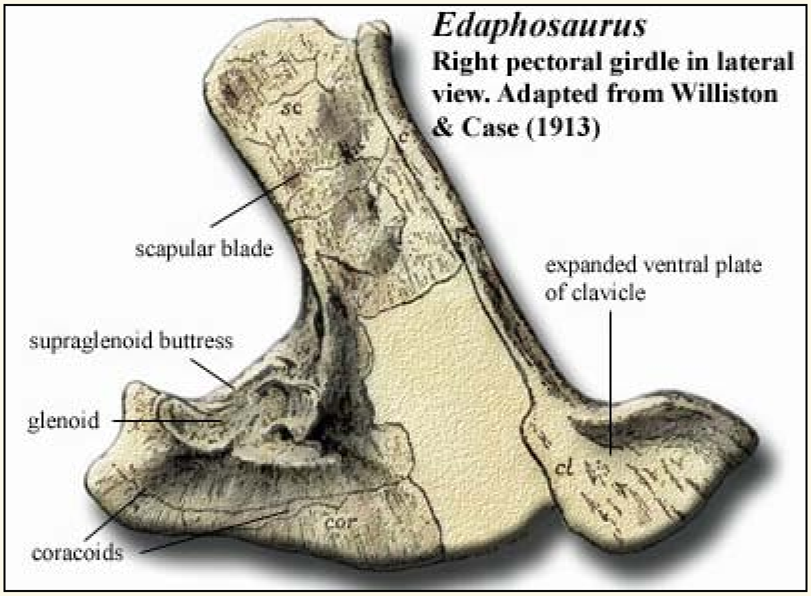
Lateral skull: massive supraorbital shelf (bony “eyebrow”) [RB86]; posterior process of postorbital reduced, with loss of contact between postorbital and supratemporal; temporal bar from jugal & squamosal; skull margin emarginated under temporal fenestra [M94]; anterior process of quadratojugal reduced;

Occiput: supraoccipital smaller than in sphenacodonts [RP40].

Braincase: anterolateral wall of otic capsule formed by prootics [M95];

Mandible: “reflected” lamina of angular (characteristic of sphenacodonts and therapsids) not present;

Axial: body barrel-shaped; “sails” present [MR90]; only cervical centra have ventral keels [S89]; presacrals with elongated neural spines, often bearing multiple short transverse tubercles [S89] [MR90]; distal neural spines lack double-cylinder structure in cross section [HRS07]; neural spines circular in cross section distal to laterally compressed proximal section [BR86] [MR90]; neural spines with thickened cortex and central cavity [HRS07]; cervical neural spines lean anteriorly & posterior spines lean posteriorly [RB86] [S89]; [MR90]; neural spines supported presumed "sails" (independently derived from sphenacodonts?); neural spine tubercles paired proximally (= "crossbars") [MR90];


Edaphosaurus
Right pectoral girdle in lateral view. Adapted from Williston & Case (1913)

Appendicular: limbs short; clavicle expanded ventrally [S89].

Notes:

[1] We have tried to be cautious in using characters from Romer & Price [RP40]. Their “Edaphosauria” is a polyphyletic combination of caseids and ***Edaphosaurus***. Consequently, their diagnosis of the group is a concatenation of plesiomorphic synapsid characters and highly specialized (but homoplastic) adaptations for eating plants. By contrast, their “Edaphosauridae” is limited to the genus ***Edaphosaurus***. However, even with these severe limitations, [RP40] still contains a vast amount of useful information.

Image credits: The edaphosaurid skull is from [M95], the ***Dimetrodon*** skull from [H91].

References: Hopson (1991) [H91]; Huttenlocker ***et al***. (2007) [HRS07]; Modesto (1994) [M94]; Modesto (1995) [M95]; Modesto & Reisz (1990) [MR90]; Reisz & Berman (1986) [RB86]; Romer & Price (1940) [RP40]; Sumida (1989) [S89]; Williston & Case (1913) [WC13]. ATW081110.

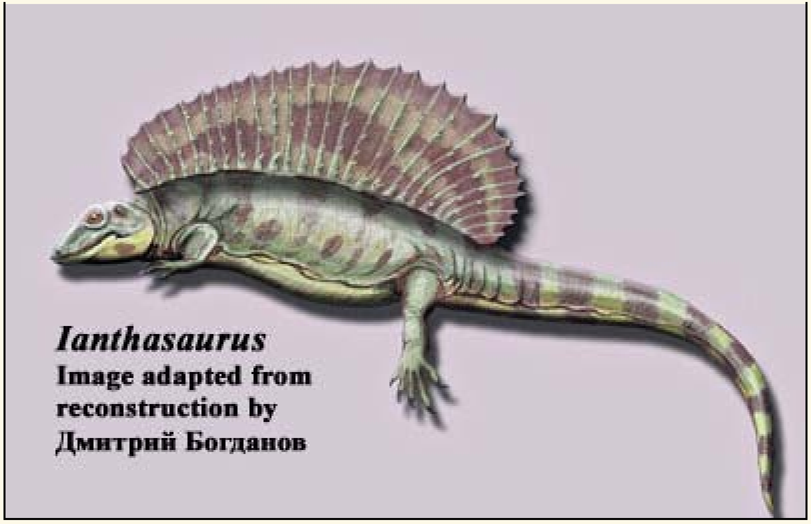
Ianthasaurus

Ianthasaurus: Reisz & Berman, 1986. Type: ***I. hardestii*** [RB86].

Range: Late Pennsylvanian [MR90] of Central U.S. (Kansas) [MR90].

Phylogeny: Edaphosauridae **:** (***Lupeosaurus*** + (***Glaucosaurus* + *Edaphosaurus***)) + *.

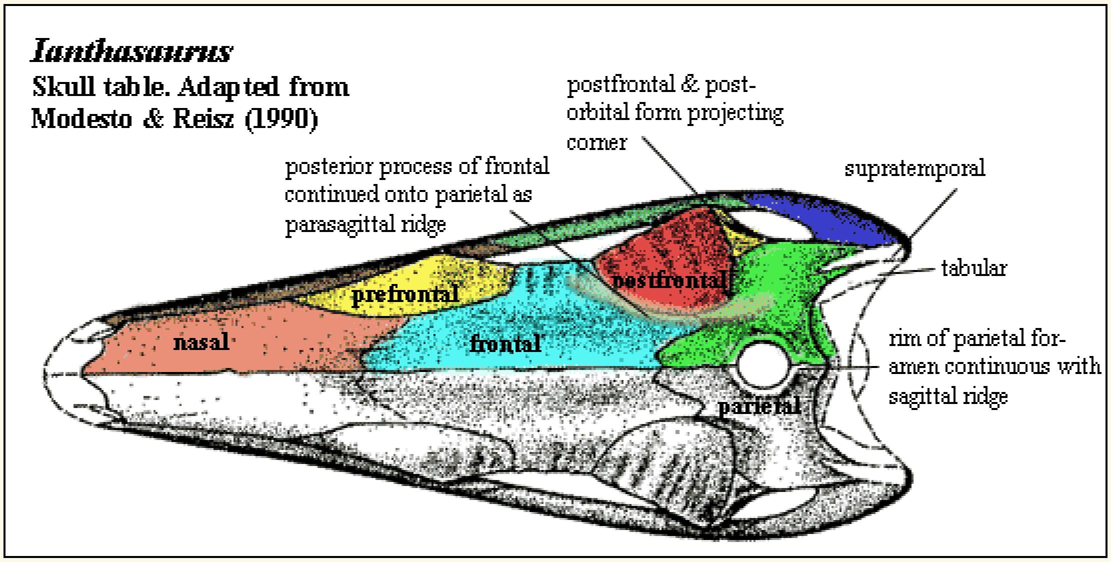
Introduction: ***Ianthasaurus*** is a small edaphosaur from the Late Pennsylvanian that lacks many of the spectacular specializations seen in ***Edaphosaurus***. Put another way, the characters that separate ***Ianthasaurus*** from


Ianthasaurus
Image adapted from reconstruction by Дмитрий Богданов

Edaphosaurus are mostly adaptations for living on plants. [MR90]. For example, the marginal dentition of ***Ianthasaurus*** is similar to that of insectivorous reptiles, with slender conical teeth which are slightly recurved at the tips [BR86], and there is a slight development of a caniniform region. The palatal and mandibular dentition is unspecialized, and there are no batteries of teeth for crushing of plant materials. Also unlike ***Edaphosaurus***, ***Ianthasaurus*** was lightly built and was probably quite agile. ***Ianthasaurus*** also shows many similarities in its cranial morphology to the small, primitive sphenacodont ***Haptodus***. MAK, ATW081017

Characters: skull large [MR90]; skull long [RB86] [MR90]**[2]**.

Rostral skull: nasals long, trapezoidal, covering snout in dorsal view [MR90]**[5]**; nasals with small anterior median process [MR90]; nasals reach nares [MR90]; maxilla long & low [MR90] maxilla participates slightly in naris [RB86]; lacrimal broad, reaching naris [RB86]; lacrimal posterior process stout, forming lower rim of orbit [RB86]; lacrimal posterior process with strong medially-directed shelf resting on tooth-bearing shelf of maxilla [RB86].

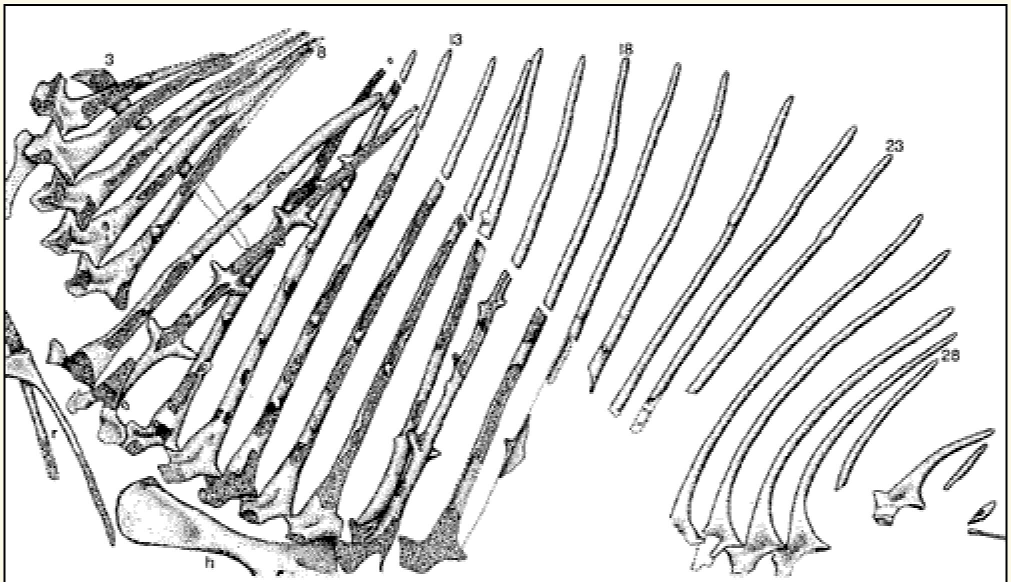

Ianthasaurus
Skull table. Adapted from Modesto & Reisz (1990)

Skull Table: prefrontal triangular, with two sides forming orbital margin and skull table margin, 3rd overlapped by lacrimal [RB86]**[10]**; nasal-frontal suture strongly interdigitating, overlain by anterior process of frontal [MR90]; frontal, prefrontal and postfrontal forming strong ridge above orbit, with all bones scalloped transversely (see figure) [MR90]; prefrontal with strong posterodorsal process participating in supraorbital ridge [MR90]; frontal long and broad anteriorly [MR90]; frontal lateral ***lappet*** strongly developed, located posterior to midpoint [MR90]; frontals with posterior processes participating in ***parasagittal*** ridges [MR90]; frontal-parietal suture interdigitating, overlain by small anterior process of parietal [MR90]; postfrontal expanded posteriorly, joining with postorbital to form distinct projecting “corner” of supraorbital ridge [MR90] **[6]**; parietal 2/3ds length of frontal [MR90]; parietal broadest at circular, rimmed parietal foramen [MR90]; lip on pineal foramen continuous with a short, median sagittal ridge perhaps for attachment of anterior sail [MR90]; parietal with ridge for supratemporal and groove for tabular [MR90]; small median postparietal present [MR90].

lateral skull: dorsal ***ramus*** of jugal thickened & continuous with orbital rim of postorbital [MR90]; jugal anterior ramus meeting posterior process of lacrimal on orbital rim [RB86]; jugal posterior process meeting squamosal to form temporal bar [BR86]; postorbital dorsal process short, not participating in dorsal orbit [RB86]; postorbital with small posterior process joining with parietal to form short posterior continuation of supraorbital ridge [MR90]**[6]**; postorbital-supratemporal contact absent [MR90]; postorbital ventral process meeting jugal to form thin postorbital bar [RB86]; jugal participating broadly in ventral skull margin [BR86]; squamosal formed much (~50%) of oblong ***temporal fenestra*** [RB86]; temporal fenestra small [MR90]; skull margin concave under temporal fenestra [RB86]; posterior flange of squamosal supports supratemporal [MR90]; quadratojugal small, not participating in ***temporal bar*** [MR90]; jaw articulation at about same level as tooth row [RB86].

lower jaw: angular long, moderately deep, with ventral edge straight except gentle upward curvature in posterior 20% [MR90] **[7]**; anterior of angular divided into dorsal & ventral portions by prominent ridge [MR90]; angular not deep [RB86]; angular notch/flange absent [RB86]; ***coronoid process*** low [RB86]; coronoid bones absent [RB86]; prearticular, posterior end underlying pterygoideus process of articular [MR90] **[9]**.

Dentition: small caniniform teeth present [RB86] [MR90] **[8]**; maxilla bearing 27-29 sharply pointed, slightly recurved teeth [BR86] [MR90]; tooth plates absent **[3]** [MR90]; upper and lower teeth of same size [RB86].



Portion of left side of the holotype of *Ianthasaurus hardestii*, anterior to left Note curvature and absence of tubercles on posterior spines, supportive "bracing" below large tubercles. From Reisz & Berman (1986).

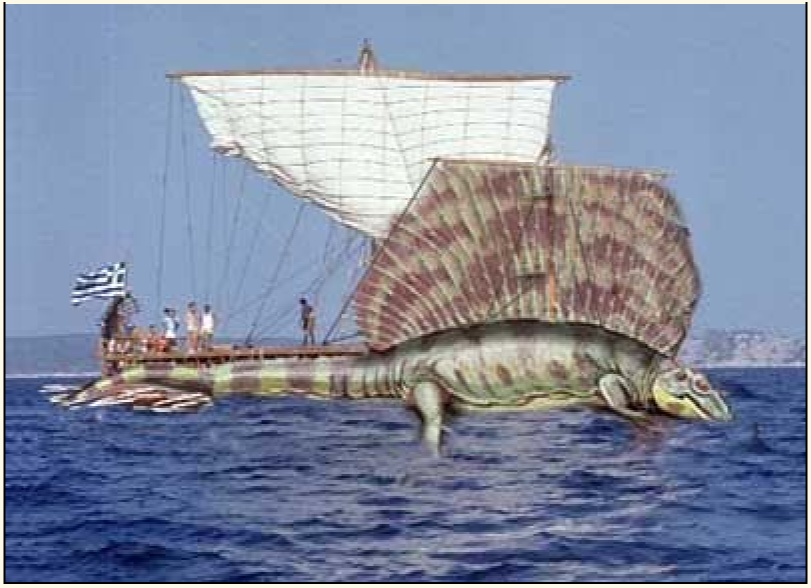
Axial: body small [MR90]; trunk not expanded laterally [MR90]; 29+ ***presacrals*** [RB86**$**] [MR90]; "sail" relatively small [MR90]; presacral neural arches with lateral excavation [RB86] [MR90]; ***transverse processes*** short [RB86]; neural spines laterally compressed below 1st tubercles [RB86]; maximum 5 tubercles on each side of neural spines **[4]** [RB86] [MR90]; neural spines lack longitudinal ridges distal to 1st tubercles [MR90a]; neural spine tubercles angle slightly upward [MR90]; some proximal tubercles supported ventrally by slight webbing [MR90]; some proximal tubercles bearing accessory tubercles [MR90]; elongate cross-barred dorsal process on neural spine of axis [MR90$]; most anterior spines anteroposteriorly extended [RB86]; most anterior spines bent anteriorly, most posterior bent posteriorly [RB86]; tubercles on spines of anterior 2/3ds of presacral vertebrae only [RB86] [MR90]; dorsal centra slightly shorter than cervicals [RB86]; trunk ribs sharply curved proximally and not expanded [RB86] [MR90]; anterior dorsal and cervical ribs ***holocephalic*** [RB86]; sacral ribs very broadly expanded distally [RB86]; probably only 2 sacral ribs [RB86]; caudal ribs with short head, short shaft, and abrupt posterior curve [RB86]; caudal ribs ***dichocephalic*** [RB86].

Appendicular: posterior coracoid absent [RB86]; scapular blade rectangular, with deep notch at base of anterior margin [RB86]; anterior coracoid with broadly expanded convex anteroventral margin [RB86]; anterior coracoid with central anteroposterior ridge [RB86]; humerus long & narrow, with weak ***entepicondyle*** and absent ***supinator process*** [RB86]; humerus not "twisted" [RB86]; ilium, posterior process well developed and blade-like [RB86] [MR90].

Other: insectivorous [MR90] **[1]**. ATW081110 except as noted.

Romer vs. Homer

> **... and when the child of morning, rosy-fingered Dawn, appeared they again set sail for the host of the Achaeans. Apollo sent them a fair wind, so they raised their mast and hoisted their white sails aloft. As the**



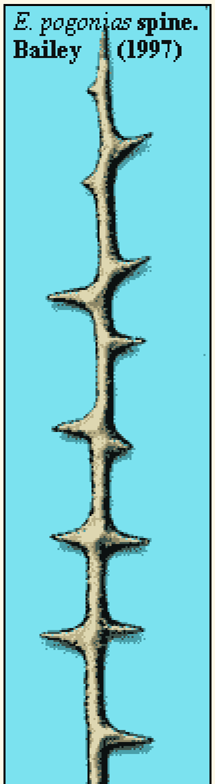
sail bellied with the wind the ship flew through the wine-dark seas, and the foam hissed against her bows as she sped onward. *Iliad I*.

Introduction With the Usual Pretentious Drivel: Romer & Price [RP40] may have been under the impression that ***Edaphosaurus*** meant ***edaphos***) means "base," "bottom," or "foundation" -- perhaps a reference to its presumed phylogenetic position. The Greek root for "ship" is ναος (***naos***), more or less as in Latin (***navis***) or English (***nautical***). Romer may have been referring to ***Naosaurus***, a poorly-known form of dubious affinities. In either case, the turn of phrase is best forgotten. We have serious doubts about ***any*** pelycosaur with foaming prow parting the wine-dark seas, etc.

That said, there is no doubt that the cross-barred "sails" of some edaphosaurids are an interesting and unique feature. The sail is composed of greatly extended neural spines which were presumably joined by a relatively thick membrane. The reasons why we can presume this will become clear shortly. Many sphenacodonts, like ***Dimetrodon***, had a similar structure. But the neural spines of ***Edaphosaurus*** bore

either side of the neural spine, giving the appearance of cross-bars. However, further up on the neural spine, the tubercles of the left and right sides go increasingly out of register. In some of the largest species, the tubercles themselves bear tubercles, or may show traces of a sort of angle brace supporting the tubercle from below. By contrast, other edaphosaurids, such as ***Lupeosaurus***, had no cross-bars of any kind.

Speculations, with More Drivel: Speculations about the purpose(s) of these structures are at least as varied as the sails themselves. Most of the proposed functions for edaphosaur sails sound suspiciously like the same reasons people historically go down to the sea in ships with sails: sex appeal, display, defense, transportation, and energy efficiency. The clear consensus today is in favor of energy efficiency, particularly thermoregulation, with sexual display favored as a secondary function. However, none of these hypotheses is completely consistent with the evidence, and most of the speculations come in at least two, inconsistent forms.



E. pogonias spine. Bailey (1997)

... and Finally, some Actual Data: First, here is what we ***think*** we know. In sphenacodontids, sail area scales with mass. In edaphosaurids, it doesn't. Sail area tends to get smaller relative to mass in the bigger species of ***Edaphosaurus*** [RP40]. However, relative sail area is smallest in the relatively small, generalized insectivore, ***Ianthasaurus*** [MR90]. In short, mass and sail area have no simple relationship in the Edaphosauridae. At the same time, the presence of a sail did mean a significant change in surface area. Hurlbutt [H99] calculates that the presence of a sail increased the total body surface area by about 67% in ***E. boanerges***. The linear dimensions of edaphosaur spines don't scale with anything. Spine length remains roughly constant throughout the clade [RP40].

While the sail may have had a radical effect on body area, it probably contributed very little to body mass. Hurlbutt [H99] calculates that the sail included only 4% of body mass in ***E. boanerges***. We are concerned that his assumptions are too conservative, but the figure is not likely to be all that much higher. There is not much evidence of extensive mechanical support, at least distal to the first crossbar.

At the same time, the sail cannot have been flapping around like pillow case on a laundry line. The evidence consistently points to a rather rigidly bound structure. Taphonomically, the spines are usually found parallel to each other, with extensive long-range order. That is, their order, front to back is often preserved. See, for example, the

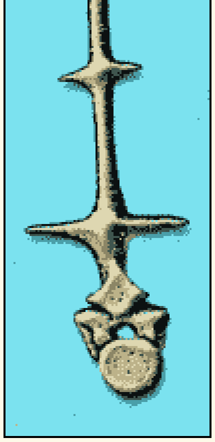


image of the fossil ***Ianthasaurus*** sail in the last section from [RB86]. That is not a reconstruction. That is the pattern on the slab as found. The other known specimen of this species had similar preservation [MR90]. Contrast this with the edaphosaurid skull, which is rarely found in articulation except for elements of the skull table; or the elements of the hand and foot which (so far as we are aware) have never yet been recovered in articulation in any edaphosaurid of any genus. Recovered spines are frequently broken, of course. However, surfaces showing breaks ***during life*** have not been noted -- with one interesting exception. Sumida [S89] notes the presence of a ***healed*** break in his specimen of ***Lupeosaurus***. The implication, as he states, is that the spine was held rigidly enough for the broken ends to anneal.

A rigid material must be under tension, because it must resist gravitational forces. If the material is a vertical structure mounted on the back of a tetrapod, that tension will be significant. The sail must not only resist gravitational force, but the unpredictable forces generated by the movement of the animal. Tetrapods (particularly basal tetrapods) move forward by a process which can be modeled as rotation and counter-rotation about the animal's center of mass. The maximum forces on the sail will thus be at the front and back ends of the sail, and should scale as the moment of inertia. For animals of similar geometry, like edaphosaurs, the moment of inertia turns out to vary approximately as mass to the power 1.6 [WC02]. So, we'd expect to see signs of that strain increase dramatically as we go from ***Ianthasaurus*** to the largest known ***Edaphosaurus***.

We do. Some of the traits we see are compensating adaptations: e.g., smaller heads, thicker spines, and a more even distribution of motive power between arms and legs. But other changes are just the obvious results of a lifetime of stress on bone [B97]. In the large edaphosaur ***E. pogonias***, Romer & Price [RP40] note that the posterior spines are often bent so far that they actually point ventrally and "force their way downward into the area normally occupied by the short spines of the sacrals and proximate caudals" causing the latter to be abnormally formed, twisted or even split. They emphasize that this distortion was not pathological, since it is seen in every reasonably preserved specimen. However, this aberrant behavior is not seen in mid-dorsal spines of any species.

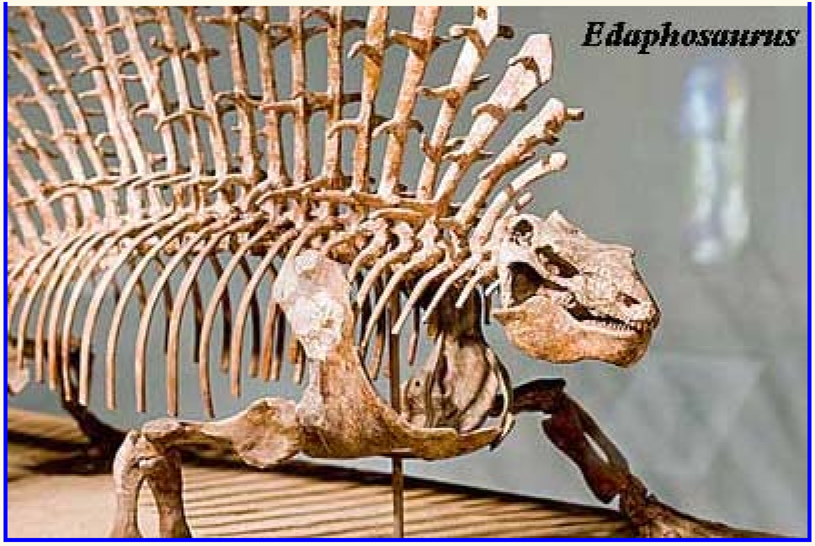
Structurally, edaphosaurid spines are rather different from those of ***Dimetrodon.*** Edaphosaurid spines have a thick cortex, a hollow core, and few vascular channels [H07]. This seems to be a typical biological design for strength and lightness, like the hollow bones of birds.

We should add that none of this explains anything about the crossbars or tubercles. Perhaps the tubercles of adjacent spines were connected by tissue. Perhaps not. There is simply no evidence.

But Enough Evidence. Back to Speculation: Given these more-or-less factual matters, how do the various speculations hold up? Not badly, on the whole -- except, oddly enough, some ideas about thermoregulation and sexual selection.

1) ***Physical protection against predation***. Modesto & Reisz [MR90] offer this as one possible function of sails, adding that the largest tubercles would protect the vital epaxial musculature. The sails were not all that strong; but, then, neither were the predators. The jaws of Permo-Carboniferous carnivores look very different from those of Mesozoic and later predators. It seems very likely that they simply didn't work as efficiently. ***See*** our stunningly dull discussion of this topic at Varanopseidae (or, better yet, don't bother). If the sails were relatively thick and rigid, as we suppose, that may have been enough. This is particularly likely if the sails had evolved to withstand lateral forces. However ferocious they may have been, Permo-Carboniferous predators were not very tall.

2) ***Deterrence***. The first cousin to the protection hypothesis is deterrence. Romer & Price [RP40] conceived this function in terms of intimidation. They were not persuaded, observing "the sail may have been of some slight protective value in that, in side view, the apparent bulk would be enormously increased, and thus perhaps a carnivore might be deterred from attacking. The authors cannot feel sure, however, that a sphenacodont would have been intelligent enough to have been deluded." It's a good point. We have mentioned that Early Permian predators were not all that strong. In addition, they were not all that bright. However, fraud has endless possibilities. The sail may have looked like a Permian palmetto plant. For that matter, perhaps the sail attracted, rather than repelled, attack. An indiscriminate attacker would then get nothing for its trouble but a mouthful of gristle laced with sharp bone fragments, while the edaphosaur would have little injured but its pride.



3) ***Intraspecific Communication***. Several ideas have been proposed based on this general theme, including individual recognition, sexual selection, intimidation of rivals. These kinds of specializations tend to be fairly species-specific. It would be a little odd -- but only a little -- if all members of this numerically important family developed this ***same*** specialization for intraspecific communications. Another discordant note is the absence (thus far) of any sign of sexual dimorphism. This doesn't get us very far. It simply underlines the point that no evidence whatsoever supports these speculations, or even suggests a way to test them.

4) ***Structural support***. No reputable, current literature supports a structural role for the sail (although Romer is said to have favored this idea in the 1920's [B97]). Fortunately, we have no reputation to protect. The deafening silence on this point is based on the presumed insubstantiality of the sail membrane. As Bailey [B97] notes of sphenacodonts, "[t]he nondirectional stiffness imposed by the subcircular cross-section [in ***Dimetrodon***] indicates that the spines were not subjected to the usual anteroposterior stresses of locomotion associated with anchoring points of muscles and ligaments." But those parameters are only partially true in edaphosaurids. As mentioned, edaphosaurid spines are built differently, with a thick cortex, hollow core, and few vascular channels [H07] -- a formula for lightness and strength. They were certainly subject to major stresses toward the anterior and posterior ends. Furthermore, the proximal portions of the edaphosaurids spine are ***not*** "subcircular" in cross section, but show distinct lateral compression [MR90].

5) ***Food Storage.*** This is another one from Romer & Price [RP40]. The biometric work of Bailey [B97] appears to eliminate this possibility. However, Romer & Price were not speaking of the whole sail, but only a layer between the epaxial musculature and the first cross-bar. Just keep this one in mind for a moment while we take on thermoregulation.

6) ***Thermoregulation.*** This the Current Best Guess. Many of the issues have been reviewed by Bennett [B96]. The theory comes in two basic flavors: radiative heating and convective cooling. The radiative heating flavor derives from work on sphenacodonts, which suggested that sails may have been able to speed up morning warming time by a substantial margin. However (a) the math works poorly for more realistic models; (b) heat transfer would be much slower, just when it is needed, because heat flow depends on blood flow (which is slower when the animal is cool); and (c) modern large lizards heat up relatively quickly without sails. In addition, the herbivorous ***Edaphosaurus*** had no obvious need for a quick morning warm-up.

The alternative is convective cooling: using bulk air movement to shed heat. Bennett [B97] tries to show how this works using a wind tunnel and a thin (3mm) aluminum plate welded to insulated pipe containing a heat source. Unfortunately, he measures only the ΔT between arbitrary distal and proximal points on the plate, using constant power to heat the pipe. That only proves that a thin aluminum sheet makes a great radiator with forced convection and a large (unmeasured, but ~25 °K) ΔT between pipe and environment. What we suspect he ought to be measuring is how well the sheet cools the pipe, ***i.e***. the power input needed to maintain a ***constant*** ΔT between pipe and environment. With that said, he does show that the aluminum does a much better job when it has "tubercles" -- even if the tubercles are made of wood. He suggests that the tubercles break up the boundary layer and make it turbulent, which sounds right. However we still don't know whether the stiff, relatively thick, and not particularly well-vascularized sail of edaphosaurids could actually shed heat generated in the body in the same way as a 3mm sheet of aluminum

Conclusion: We don't really have a conclusion. The sexual selection and temperature regulation hypotheses are over-rated, but not necessarily wrong. As several writers have pointed out, the functions of the sail may have been different in different species, or served several functions at once.

Lacking a conclusion, we end with an Interesting Fact. The foundation of "warm-bloodedness" in mammals ("non-shivering thermogenesis") is the ability to burn fat quickly -- particularly a special type of "brown fat." The main depository of brown fat (particularly in small mammals and neonates) lies on the back, between the scapular blades. It is also the usual place for a hump in humped mammals. On an edaphosaurid, that's just under the point where the tubercles, and often the spines, are the most robust. Just as synapsids weren't all that bright, or strong-jawed, or agile, perhaps they had begun to develop non-shivering thermogenesis which wasn't very stable. If so, they would necessarily develop methods of shedding heat in parallel, and possibly in physical proximity, to the heat source. ATW081110.

Notes:

[1] based on dentition, large head, elongate body and small temporal openings [MR90].

[2] most comparative adjectives in the description refer for comparison to the better and earlier-known ***Edaphosaurus***.

[3] The palate is poorly known, but tooth plates are clearly absent from the lower jaw.

[4] As in ***Edaphosaurus***, the tubercles are not strictly paired and go increasingly out of register distally on the spine [MR90].

[5] A large, flattish nasal appears to be primitive for the clade Sphenacodontia + Edaphosauridae. It is reversed in ***Edaphosaurus*** and absent in Varanopseidae and in other more basal synapsids. We are not sure of the status in ***Ophiacodon***.

[6] [MR90] note that [BR86] oriented the postfrontal backward, which had confused the restoration of this area.

[7] Dorsoventral striations on angular “suggest growth was occurring downwards, deepening the keel.” This is significant, since [MR90] note that both the holotype and the one significant referred specimen are probably juveniles.

[8] However, the figures in [MR90] show no obvious canine buttress on the maxilla.

[9] We note the following, so that no reader will have to repeat our wild goose chase on this topic. Modesto & Reisz [MR90] report that Reisz & Berman [RB86] found “a prearticular twisted posteriorly as to underlie the pterygoideus process of the articular.” In fact, Reisz & Berman reported “a prearticular twisted so as to underlie the pterygoideus process of the angular and [the] presence of a pterygoideus process formed by the angular.” This reference to the angular appears to be a replicated typographical error, since the pterygoideus (internal) process is correctly attributed to the articular elsewhere in Reisz & Berman’s paper. See also [H91] (same in ***Dimetrodon***).

[10] The reconstruction by [MR90] is a bit different because the prefrontal is shown to be considerably bent to form a larger part of the strong awning of the skull table over the orbit.

References: Bailey (1997) [B97]; Bennett (1996) [B96]; Hopson (1991) [H91]; Hurlburt (1999) [H99]; Huttenlocker ***et al***. (2007) [HRS07]; Modesto & Reisz (1990) [MR90]; Modesto & Reisz (1990a) [MR90a]; Reisz & Berman (1986) [RB86]; Romer & Price (1940) [RP40]; Ruxton (2001) [R01]; Walter & Carrier (2002) [WC02]. ATW081110.

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checked ATW081111

Edaphosauridae: *Lupeosaurus, Glaucosaurus* & *Edaphosaurus*

Abbreviated Dendrogram

```
AMNIOTA
|
SYNAPSIDA
|--Caseasauria
|   |--Eothyrididae
|   `--Caseidae
`--Eupelycosauria
    |--Varanopseidae
    `--+--Ophiacodontidae
       `--+--Edaphosauridae
          |  |--Ianthasaurus
          |  `--+--Lupeosaurus
          |     `--+--Glaucosaurus
          |        `--Edaphosaurus
          `--Sphenacodontia
             `==Sphenacodontidae
                `--THERAPSIDA
```

Contents

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2. ***Glaucosaurus*** X
3. ***Lupeosaurus*** X

Lupeosaurus

Lupeosaurus*:** Romer, 1937. Type: ***L. kayi Romer, 1937.

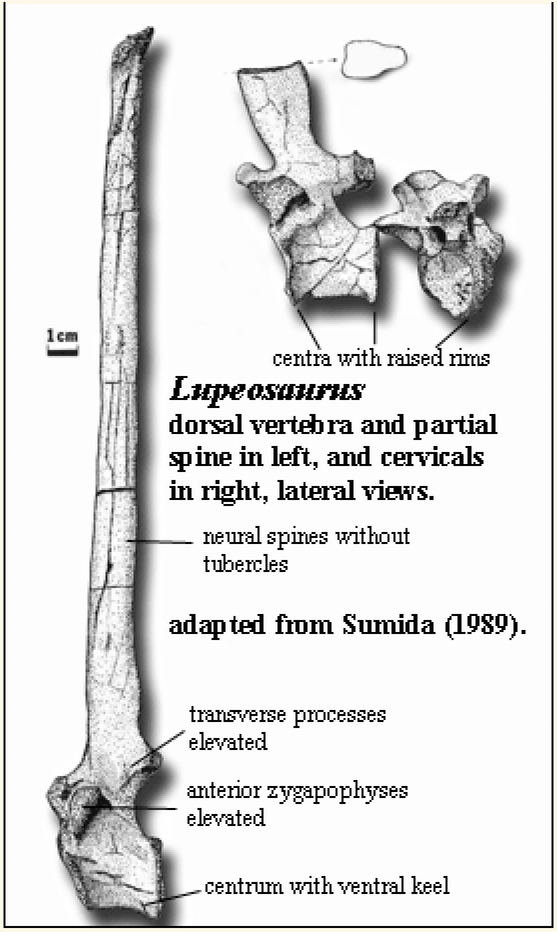
Range: Cisuralian (Asselian or earliest Sakmarian) of Texas [RP40]

Phylogeny: Edaphosauridae :: (***Glaucosaurus*** +

Edaphosaurus) + *.

Introduction: There isn't a hell of a lot to ***Lupeosaurus***. It is known from only two described specimens, both consisting of postcranial bits and pieces. The most significant item is the absence of cross-bars on the neural spines. This left considerable doubt about the affinities of ***Lupeosaurus***. However, the vertebrae and neural spines are otherwise entirely edaphosaurid. See details below. Unfortunately, these, and some pieces of the limb girdles, are about all that exist.

Lupeosaurus was, at a guess, in the neighborhood of 60 cm long and perhaps as much as 20 kg. The ribs suggest, but only suggest, that it was markedly skinnier than ***Edaphosaurus*** and thus not a highly adapted herbivore. On the other hand, it pushes the upper size limit for insectivores in an age when colonial insects had not yet evolved. Everything known about the limbs suggests that they were massive for an edaphosaur. The robust limbs, combined with presumed thinness, point toward a run-of-the-mill carnivore of some kind. Amphicoelous vertebral centra are a little unusual in a (relatively) powerful carnivore, but this was the primitive and usual condition for early synapsids of all types.



Lupeosaurus
dorsal vertebra and partial spine in left, and cervicals in right, lateral views.

adapted from Sumida (1989).

Characters: **[1]**

> ***Axial***: transverse processes located further above centrum than in ***Edaphosaurus*** [S89]; anterior ***zygapophyses*** relatively high above ventral margin of centra [S89]; neural spines elongated, but without tubercles [RP40] [S89]; neural spines with ***anticlinal*** bending [S89]; neural spines circular in cross-section above base [S89]; anterior cervical centra narrower than dorsal centra [S89]; cervical centra with ventral keel [S89] **[2]**; cervical neural spines broadly oval & slightly constricted anteroposteriorly at their triangular base [S89]; cervical neural spines elongate [S89]; dorsal centra deeply ***amphicoelous***, with both ends bearing reinforced rim [S89]; dorsal (but not cervical) neural spines with anterior and posterior furrows [S89]; dorsal rib with distinct heads, does not seem to flare broadly as in ***Edaphosaurus*** [S89]; sacral ribs not fused to pelvis [S89]; anterior caudal neural spines also triangular at base [S89].
>
> ***Appendicular***: dorsal ramus of clavicle stout, with tongue-in-groove articulation with scapula [S89]; clavicle expanded ventrally, with thick, robust ventral plate [S89]; clavicle with broadly overlapping articulation with interclavicle [S89]; ***supraglenoid foramen*** at anterior edge of supraglenoid buttress [RP40]; scapular blade broad distally [RP40]; scapular blade curved back even more sharply than in ***Edaphosaurus*** [RP40] [S89]; scapular blade longer than in other edaphosaurs [RP40] [S89]; scapular blade with long, dorsoventrally oriented fossa on anterior edge of medial face [S89] **[3]**; ***glenoid*** long [RP40]; ilium projects posteriorly more than in ***Edaphosaurus*** [RP40]; dorsal edge of pubis thickened, overhanging lateral surface [RP40]; femur short & massive [O68].

Notes:

> **[1]** The skull is completely unknown.
>
> **[2]** Anteriorly. The posterior face of the centrum is more circular, and wider, than the anterior face. To judge from Sumida's figure [S89: 1344, fig. 1E], the keel

merges with a stout rim surrounding this posterior surface.

[3] An explanation of nomenclature may be useful for the anatomically obsessive. Sumida [S89] identifies this fossa as the subcoracoscapular fossa, an attachment surface for the ***m. subcoracoscapularis***. This muscle is the same as the ***m. subscapularis*** of mammals [LB+01], and the subcoracoscapular fossa is consequently the same as the subscapular fossa. This fossa contains a foramen which emerges on the outside (lateral face) as the supraglenoid foramen [R56].

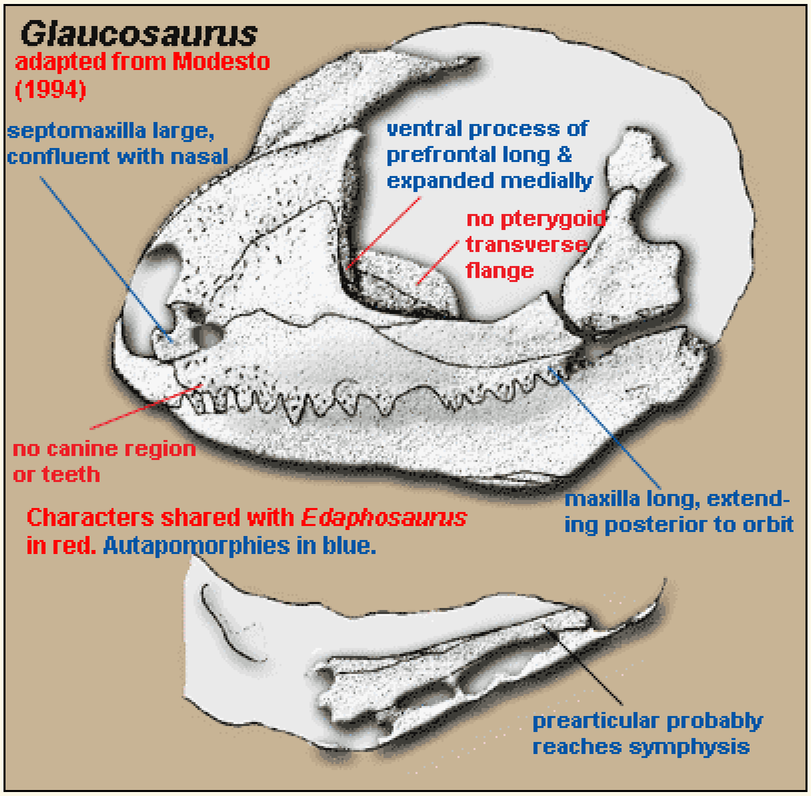
References: Liem ***et al***. (2001) [LB+01]; Olson (1968) [O68]; Romer (1956) [R56]; Romer & Price (1940) [RP40]; Sumida (1989) [S89].

Glaucosaurus

Glaucosaurus: Williston, 1915. Type: ***G. megalops*** Williston, 1915. [M94]

Range: Middle Cisuralian [L06] of Texas

Phylogeny: Edaphosauridae ::: ***Edaphosaurus*** + *.



Introduction: ***Glaucosaurus*** is known only from its holotype, a partial skull and jaw. Almost all of the sutures have been obliterated. Nevertheless, there is broad agreement that ***Glaucosaurus*** is not only an edaphosaurid, but a close relative of ***Edaphosaurus*** itself. Before getting too complacent about this phylogenetic placement, we might recall that the universe of scholars who have felt moved to exercise themselves on this topic is not large. Fortunately, that universe includes Prof. Sean Modesto of Cape Breton Univ., Nova Scotia. Prof. Modesto is merely an excellent describer of things. He also has the much rarer ability to couple description and illustration in such a manner that the reader gets a fair idea of the limitations, uncertainties and judgment calls involved.

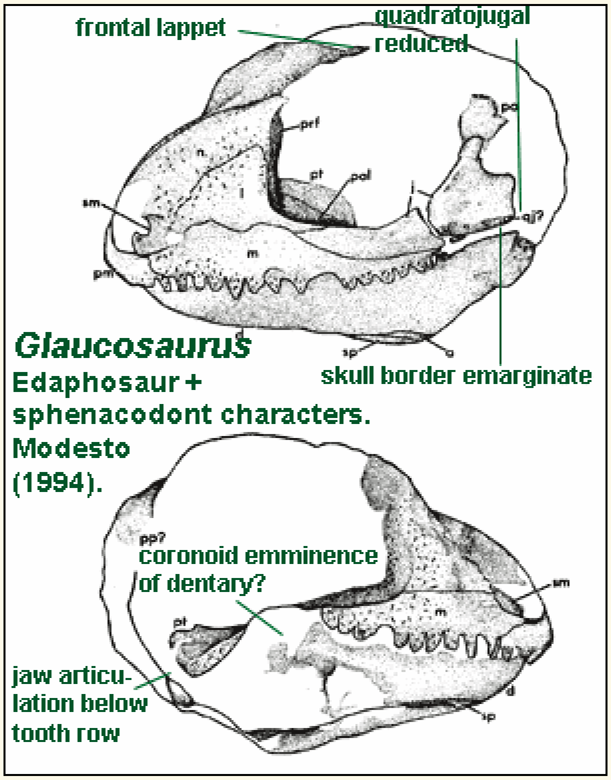
As Modesto [M94] notes, Edaphosauridae is not marked with any cranial synapomorphies. That is, edaphosaurids don't have any unique skull features; and all we have for ***Glaucosaurus*** is a partial skull. However, ***Glaucosaurus*** seems to have two of the unique features of the clade Edaphosauridae + Sphenacodontia: (1) a lateral projection (lappet) of the frontal usually reaching the orbit and (2) ventral border of skull ***emarginated***. Modesto asserts (credibly) that there is some suggestion that three others are also present, although it is not possible to be certain: (3) small quadratojugal which does not participate in the ***subtemporal bar***, (4) jaw articulation below the tooth row, and (5) dentary with pronounced ***coronoid eminence. See*** image below.

All of the known sphenacodonts are carnivores except for certain therapsids (such as us). ***Glaucosaurus*** is plainly not a therapsid, ***e.g***. because the lacrimal reaches the naris, the septomaxilla is large, there are no incisors, etc. And it is just as plainly not a carnivore, since it lacks cutting edges on the teeth or canine-like teeth. So, it is very likely to be an edaphosaur. Assuming that this is the case, it is very close to ***Edaphosaurus***, because only ***Glaucosaurus*** and ***Edaphosaurus*** completely lack both canine teeth and a canine buttress, lack the transverse flange of the pterygoid, and have prefrontal with a ventral (descending) process which is expanded toward the middle of the skull, forming an anterior housing for the eyeball [M94]. However, ***Glaucosaurus*** differs from any of the known sorts of ***Edaphosaurus*** in have an incredibly long maxilla, and in the equally extreme length of the prefrontal 's ventral process. ATW081114.

Characters:

Rostral skull: antorbital region tall [M94]; septomaxilla robust, exposed in lateral view [M94]; septomaxilla confluent with surface of nasal [M94**$**]; caniniform region absent [M94]; maxilla slightly convex in lateral view [M94]; maxilla extends posteriorly to level of postorbital bar [M94**$**].

Skull table: prefrontal ventral process expanded transversely, with extensive lacrimal contact [M94].



Glaucosaurus **Edaphosaur + sphenacodont characters. Modesto (1994).**

Lateral skull: jugal with relatively little participation in ventral skull margin [M94]; jugal lateral surface "lightly sculpted with small, circular dimples" [M94]; subtemporal bar deeper (i.e. taller) than suborbital bar [M94]; subtemporal bar emarginated [M94].

Palate: palatine with prominent dorsal process [M94]; ***transverse flange of pterygoid*** absent [M94] pterygoid dorsal process low [M94] **[1]**.

Mandible: dentary, anterior relatively tall [M94]; splenial exposed laterally only at symphysis, underlying anterior end of angular [M94]; splenial ascends about 50% of medial jaw [M94]; inframeckelian foramen either posterior or absent [M94]; prearticular very long, extending to jaw symphysis [M94**$**]; coronoids toothless [M94] **[2]**.

Dentition: 3 premaxillary teeth [M94**$**]; premaxillary and maxillary teeth of equal size [M94]; canines absent [M94]; 15 teeth on maxilla [M94]; dentary teeth may be smaller than maxillary [M94]; anterior maxillary teeth laterally compressed, slightly recurved, sharply tipped [M94]; posterior maxillary teeth peg-like [M94] palatal process of pterygoid toothless [M94].

Notes:

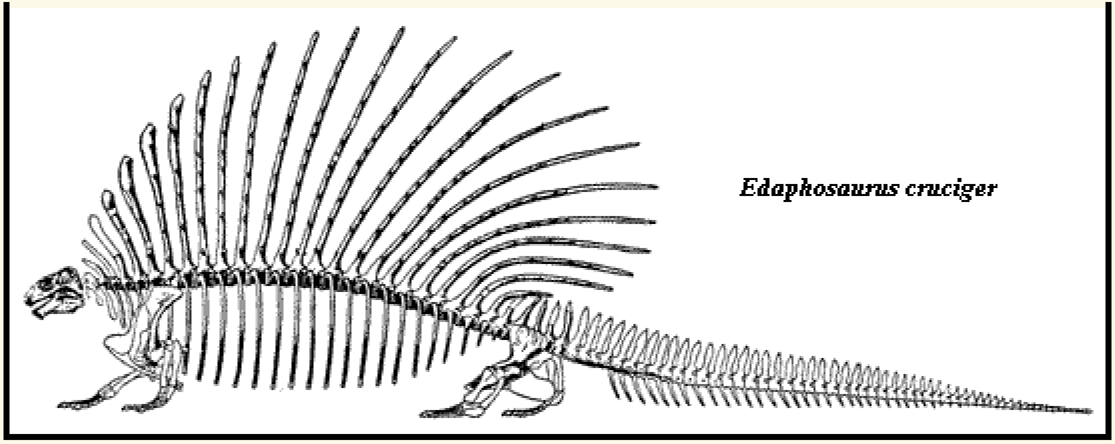
[1] Modesto [M94] states that this condition is the same in ***Edaphosaurus***. We are not quite sure whether Modesto is referring to the dorsal ridge on the anterior ramus or (more likely) the ascending basal part of the quadrate ramus.

[2] Modesto [M94] is uncertain whether the observed structures are in fact coronoids. He notes at a number of points that the specimen has only moderately good preservation and has been seriously compromised by over-preparation. We are sympathetic, having cross-examined many witnesses with the same problems.

References: Lucas (2006) [L06]; Modesto (1994) [M94].

Edaphosaurus

Edaphosaurus: (=



Brachycnemius, ***Naosaurus***)

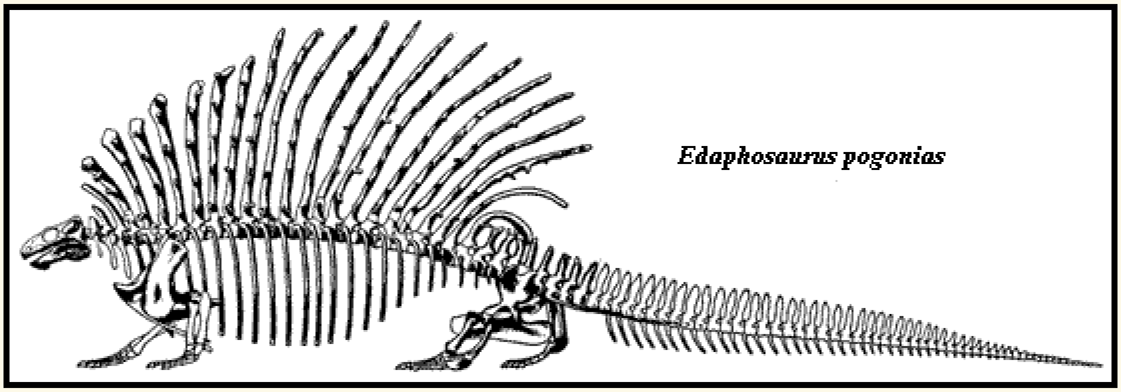
Range: Cisuralian of central, southwestern, and eastern U.S. The range of ***Edaphosaurus*** may extend back to the latest Carboniferous [L06].

Phylogeny: Edaphosauridae ::: ***Glaucosaurus*** + *.

Introduction: ***Edaphosaurus*** possesses a combination of features that clearly indicate that this animal was a heavy, slow herbivore [RP40].

The skull of ***Edaphosaurus*** was remarkably small as compared with the size of the body. It is also short and rather shallow, as contrasted with the elongated skull of the sphenacodonts. Also unlike sphenacodonts and ophaicodonts, the teeth in the edaphosaurs are quite uniform, making an unbroken series around margins of the jaws. In addition to the marginal teeth, there is a massive array of closely packed teeth that ground against a similar set of teeth on the medial surface of the mandible. Clearly these extensive clusters of teeth added to the efficiency in grinding up plant material.

In keeping with the tiny head the cervical (neck) vertebrae are reduced in length, while the dorsal (back) vertebrae are massive, the tail is deep, the limbs are short and robust and the ribs form a wide ribcage. Like most herbivores, ***Edaphosaurus*** would have had a capacious gut and symbiotic bacteria to aid in the breakdown of cellulose and other indigestible plant material

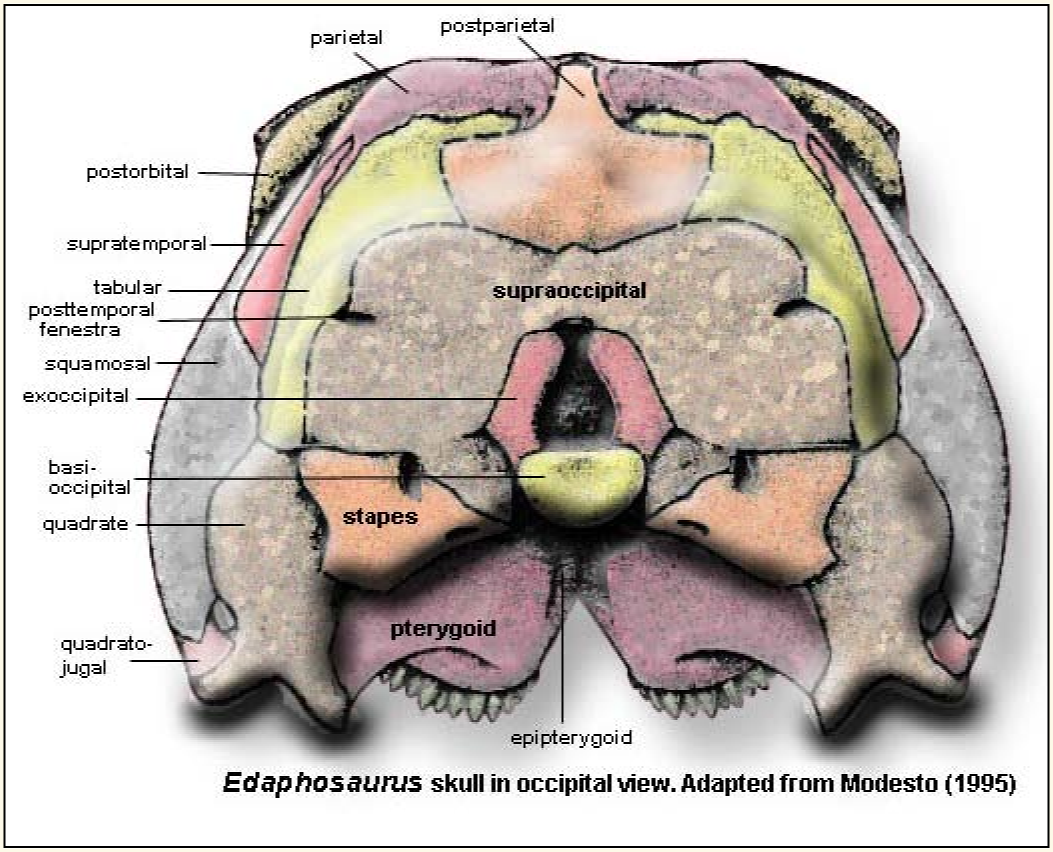


Edaphosaurus was characterized by an elongation of the vertebral spines, but the spines are heavier than they were in other forms like ***Echinerpeton***, ***Lupeosaurus***, and the sphenacodontids like ***Dimetrodon***. Moreover, they were ornamented with numerous short lateral projections, tubercles, or crossbars arranged irregularly along their length, rather like the yardarms on the mast of an old sailing ship. The benefits of such an adaptation are unclear, but inasmuch as ***Edaphosaurus*** was a successful and wide-ranging animal they surely served some purpose. One possibility is that they may have served as protection against predators, by strengthening the neural spines. The front and rear spines are tilted forwards and backwards respectively, perhaps provided protection in the neck and thigh region, respectively.

Nine species of ***Edaphosaurus*** have been described, ranging in size from small (only about half a meter or less) to very large, bulky animals (over three meters long). The largest species, ***Edaphosaurus cruciger*** and ***Edaphosaurus pogonias*** (see above) have modified their cervical and anterior thoracic spines into massive club-like processes. It is quite likely that ***Edaphosaurus*** evolved from a small insectivorous form like ***Ianthasaurus***. MAK

"three consecutively occurring species, ***E. boanerges, E. cruciger***, and ***E. pogonias***, from Lower Permian [Cisuralian] strata of north-central Texas," [RB86] Discussion of herbivory and jaw mechanics [M95]. Propalinal also supposed by [RP40], likewise based on having articular surface >> quadrate condyles. See also jaw of ***Biarmosuchus*** in [S03] with clear divergence between pre- and post-canine teeth.

Characters: head quite small and deep [RP40] [RB86] [M95]; skull short [M95**$**].



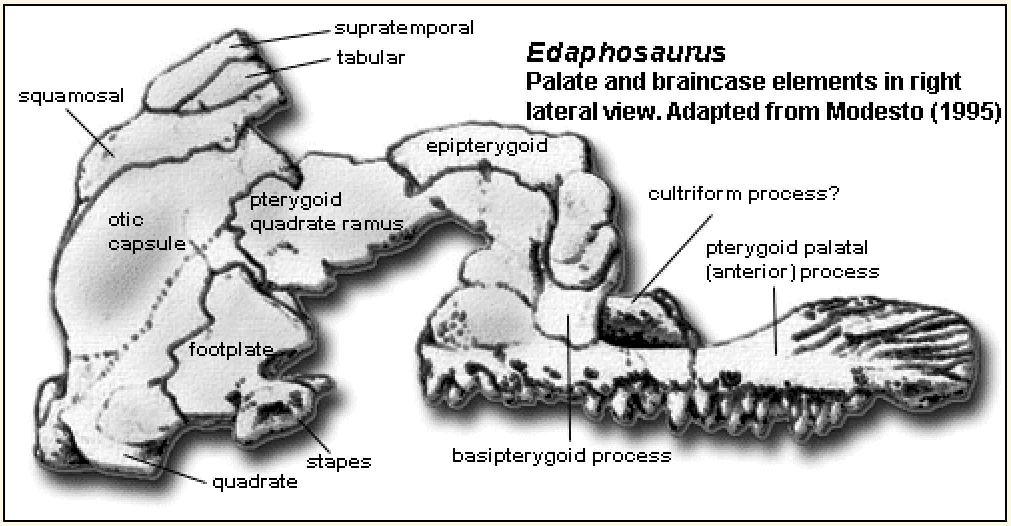
Edaphosaurus skull in occipital view. Adapted from Modesto (1995)

Rostral skull: snout slender [RP40]; premaxilla with dorsal process overlain by, and resting on shelf of nasal [M95]; nares small [RP40]; septomaxilla large, clearly visible in lateral view, with large medially-directed shelf probably contacting nasal septum [M95]; nasal ~75% length of frontal [M95]; nasals with strong medial suture [M95]; maxilla slightly convex in lateral view [RP40] maxilla with “lip” over teeth 10-15 [M95] **[3]**; lacrimal thin, underlies maxilla anteriorly, but thick, overlies maxilla posteriorly [M95]; lacrimal with strong orbital rim and strong contact with prefrontal ventral process [M95].

Skull table: large, well-developed supraorbital shelf formed by prefrontal (***contra*** [RP40]), lateral ***lappet*** of frontal and postfrontal [RB86] [M95**$**]; prefrontal ventral process expanded transversely, with extensive lacrimal contact [M94] [M95]; prefrontal ventral process continued as internal ridge on posterodorsal process [M95]; frontal anterior process reduced [M95]; frontal lateral lappet very slender [M95]; frontal overlies parietal with serrated suture [M95]; ventral ridge from frontal-parietal suture continuous with prefrontal internal ridge [M95] **[2]**; postfrontal with square body forming large portion of supraorbital awning [M95] postfrontal with broad, blunt posterior process not reaching temporal fenestra [M95]; parietal narrow [RP40]; parietal with free, concave lateral margin bordering temporal fenestra [M95**$**]; parietal with 2 pairs of parasagittal ridges on ventral surface [M95]; parietal outer parasagittal ridge continuous with frontal ventral ridge [M95] **[2]**; parietal outer parasagittal ridges continuous with border of parietal foramen, then passing posteriorly to posterior flanges overlying postparietal [M95]; parietal foramen “not greatly enlarged” [RP40].

Lateral skull: jugal narrow [M95]; jugal with short anterior process meeting posterior ends of maxilla and lacrimal below orbit [RP40]; jugal with short palatal flange on anterior process [M95]; jugal with strong, extensive suture with squamosal [M95]; postorbital ventral process extending to about mid-orbit, overlapping jugal to form postorbital bar [M95]; postorbital posterior process short, not reaching squamosal or extending beyond level of parietal foramen [M95]; ventral margin of skull deeply emarginated postorbitally, with temporal bar displaced dorsally [MR95]; temporal fenestra extended (wider than tall) [M95]; temporal fenestra also tall, narrowing postorbital skull table [RP40]; squamosal with horizontal anterior process meeting jugal [M95]; ventral margin of skull (temporal bar) flares widely below temporal fenestra [RP40]; squamosal with short, rectangular occipital flange anchoring supratemporal and paroccipital process [M95]; quadratojugal small, not participating in temporal bar [M95] (***contra*** [RP40]).

Occiput: skull table curves smoothly onto occipital surface [RP40]; parietal with occipital flange contacting tabular & postparietal [M95] postparietal with anteroventral processes fitting in slots of supraoccipital [M95]; postparietal with anterior wedge separating parietals posteriorly [RP40]; supratemporal slim, primarily occipital element [M95] **[4]**; tabular articulates with slot in posterior parietal & sutured to supraoccipital and paroccipital process [M95]; paroccipital process wide, extending posterolaterally & slightly ventrally, terminating with blunt, downturned tip [M95]; paroccipital process dorsal margin suturing to squamosal [RP40] **[8]**; exoccipitals and basioccipital fused [M95]; basioccipital forms most of semicircular occipital condyle [M95]; supraoccipital fused to (fused) otic capsule [M95]; supraoccipital with lateral processes, but poorly developed dorsal process [RP40]; ***posttemporal fenestra*** low [RP40].



Edaphosaurus
Palate and braincase elements in right lateral view. Adapted from Modesto (1995)

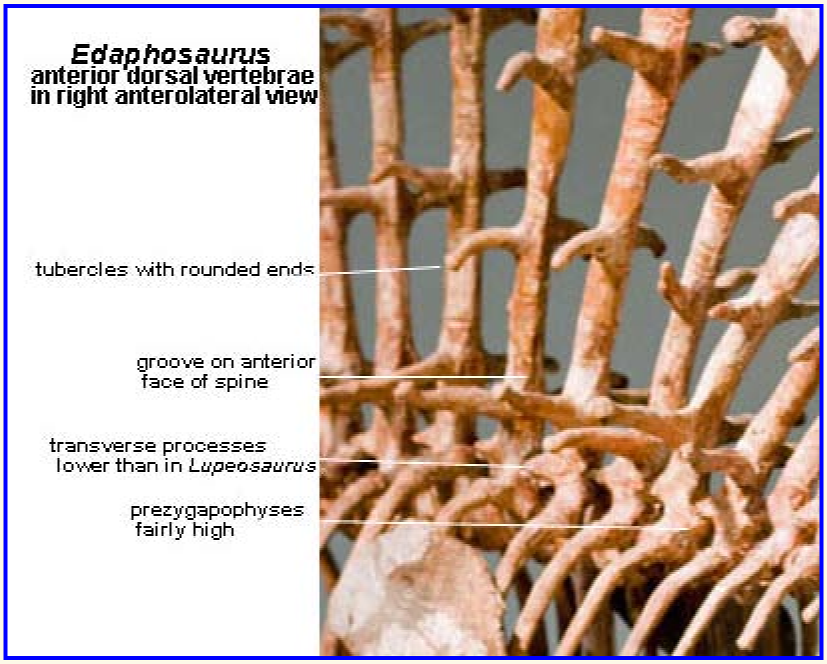
Braincase: otic capsule fused [M95]; stapes with strong dorsal process above footplate [M95]; stapedial foramen large [M95]; stapes with head small, neck distinct, & dorsal process broad [RP40]; prootics form thin, posteriorly-arching dorsum sellae [M95]; basisphenoid and parasphenoid fused [M95]; basipterygoid processes with “hour glass-shaped” double articulations [M95]; sphenethmoid (partially?) ossified, forming trough open dorsally [M95].

Palate: palatal surface of vomer with denticles posteriorly [M95]; ***choanae*** shorter and wider than in sphenacodonts [M95]; large tooth plate formed by palatine, pterygoid and ectopterygoid [M95] **[5]**; tooth plate slightly concave, tilted ventrolaterally [M95]; dorsal process briefly contacts lacrimal and prefrontal, forming lateral wall of (large!) lateral orbitonasal foramen [M95]; ectopterygoid small, contacts jugal briefly [M95]; pterygoid with low, deeply scarred dorsal ridge on anterior process [M95]; pterygoid transverse flange absent, modified to form semicircular posterior border of tooth plate [RP40] [M94]; pterygoid ***quadrate ramus*** thin, but with strongly elaborated proximal region rising vertically from body and wrapping around base of epipterygoid [RP40] [M95]; epipterygoid body overlies pterygoid quadrate ramus [M95]; epipterygoid with ventromedially-directed basal process forming screw-shaped receptacle for ***basipterygoid process*** of basisphenoid (***i.e***. the basal articulation) [M95]; epipterygoid columella (vertical process) slender with slight posterior arch [M95]; jaw suspension offset ventrally [RP40] [M95**$**]; quadrate condyles arranged parasagitally, separated by deep notch [M95**$**].

Lower jaw: lower jaw contracted and tall [RB86] [M95]; dentary and splenial with symphysial surfaces [M95]; dentary not as tall as in sphenacodonts [RP40]; dentary twisted posteriorly so that tooth row faces medially [M95]; splenial likewise twisted through almost right angle [M95]; dentary with strong suture overlapping angular and surangular [M95]; dentary forming lateral part of coronoid eminence [M95];

tooth plates formed by coronoids & prearticular [RB86]; posterior coronoid dorsal surface deeply scarred for adductor muscles [M95]; prearticular forms floor of ***adductor fossa*** [M95]; prearticular overlies medial shelf of angular, then twists ventrally to cover pterygoideus process of articular [M95]; angular large, with deep, thickened vertical keel [M95]; posterior of angular keel roughened [M95] **[3]**; articular surfaces of articular 50% longer than quadrate ***condyles*** [M95] **[6]**.

Teeth: maxillary and premaxillary teeth of equal size [M94]; caniniform region absent [M94]; 21-24 isodont marginal teeth on each jaw ramus [RP40]; marginal teeth slightly bulbous [M95**$**]; marginal teeth small, isodont, slightly recurved, with fine, serrated tips [RB86] [M95]; cutting edges of cheek teeth inclined obliquely with respect to axis of tooth row. [M95]; marginal tooth implantation ***subthecodont*** [M95]; maxillary teeth become increasingly laterally directed posteriorly [M95**$**]; densely packed teeth cover tooth plates [RB86]; dentary teeth become increasingly medially directed posteriorly [M95**$**] **[1]**.



Edaphosaurus
anterior dorsal vertebrae in right anterolateral view

Axial: intercentra not ossified except in some posterior dorsals [RP40]; anterior ***zygapophyses*** relatively high above ventral margin of centra [S89]; neural arches not excavated [M95**$**]; transverse processes close to centra compared to ***Lupeosaurus*** [S89]; sail of greatly extended neural spines present [RP40]; multiple lateral tubercles, when present, usually project horizontally [M95]; lateral tubercles with rounded, unfinished tip (skin-covered), becoming smaller and less regularly paired distally [RP40]; tubercles up to 4 cm long, depending on species [H99]; neural spines extended axially at base, tapering to circular and acquiring anterior and posterior grooves (blood vessels) around first pair of tubercles [RP40]; neural spines with longitudinal grooves & ridges of variable length, originating proximally [MR90a]; anticlinal bending of neural spines, with most posterior actually curved downward distally [RP40] **[9]** [RB86]; 24-29 presacrals [RP40]; cervical centra short [M95**$**]; cervical & posterior dorsal spines slimmer [RP40]; dorsal centra longer than cervicals, relatively longer than in ophiacodonts [RP40] [RB86]; dorsal centra without ventral ridge, more or less circular in cross-section [RP40]; dorsal arches with long transverse processes [RP40] [M95**$**]; dorsal ribs dichocephalous [RP40]; dorsal ribs strongly curved [M95**$**]; dorsal rib tubercula greatly reduced [M95**$**]; last ~7 dorsal centra with raised tubercle for rib capitulum [RP40]; neural spines of sacrals & anterior caudals tall and pointed, with longitudinal ridges running along lateral surfaces [M95**$**]; 2-3 sacrals [RP40]; sacral and caudal neural spines with rugose tips [M95**$**]; sacral ribs not fused to pelvis [RP40]; tail probably long [RP40]; caudal neural spines tall and pointed, with tips expanded sagittally [M95**$**].

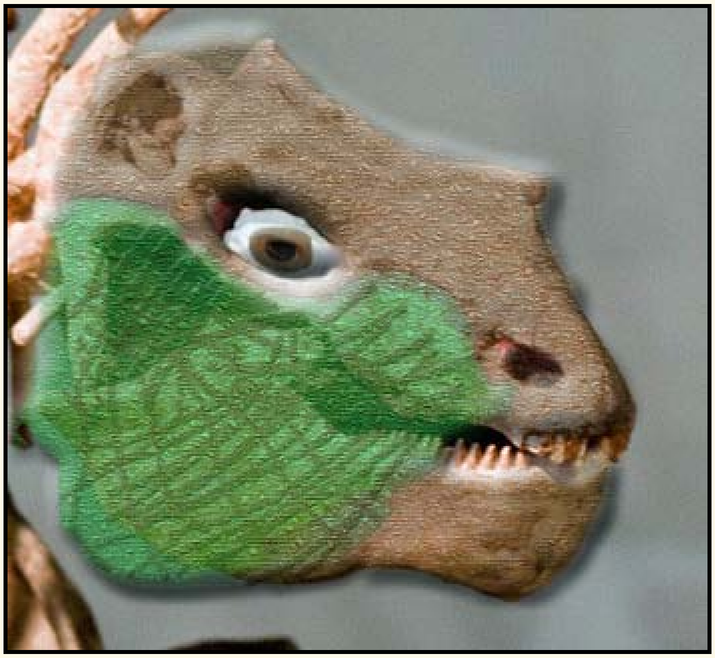
Appendicular: supraglenoid foramen above supraglenoid buttress [RP40]; scapular blade curves sharply back and is narrow distally [RP40]; cleithrum present [RP40]; clavicle broadly expanded [RP40]; “[t]he proximal limb segments are long, the distal segments short” [RP40]; ***ectepicondylar foramen*** present [RP40]; ilium very tall [RP40]; iliac blade expanded slightly [RP40]; pubis relatively short [RP40]; dorsal edge of pubis not thickened & does not overhang lateral surface [RP40]; femur short & massive [O68]; tibia head very broad [RP40]; tibia proximal lateral margin developed into sharp ridge [RP40]; tibia distal head twisted laterally “to an unusual degree" [RP40] ***carpals*** & ***tarsals*** never found in association [RP40].

Other: a 2.5 m ***E. boanerges*** estimated to be about 50% tail and a total mass of 93 kg [H99]; sail was <4% of mass but 40% of area [H99].

Notes:

[1] That is, in the back of the jaw, the teeth are not simply oriented up or down. The lower teeth tend to point inward and the upper teeth outward, with the angle increasing distally. Wear is present on the inner surfaces of the outwardly bent maxillary teeth [M95]. No one seems to know how this would actually work, especially in combination with the tooth plates. Note that the edaphosaur jaw was very deep, massive, and had a long, double symphysis (the left and right jaw were stapled together in two places). It would have virtually no ability to flex laterally. Wear on the inner surfaces of outwardly-bent maxillary teeth therefore supports Modesto's [M95] argument that ***Edaphosaurus*** was capable of ***propalinal*** (forward and back) movement of the lower jaw. However, since at least some of the marginal teeth were not fused to the jaw (ankylosed) [M95: 221, fig. 9], the posterior teeth themselves would have flexed slightly at right angles to the jaw line.

[2] Thus, there is a continuous reinforcing arc from the orbital margin of the lacrimal, through the internal ridge of the prefrontal and onto the frontal (along the frontal-postfrontal suture?), and merging with the lateral parasagittal under the parietal. Modesto [M95: 220] states that, at least posteriorly, the ridge "presumably marks the former contact of the orbital-plate cartilage."



[3] One possible interpretation is attachment for a fleshy cheek, a common – in fact almost universal – feature of large herbivores. Modesto [M95] notes an attachment for an unusual muscle on the posterior third of the vertical keel of the angular. He believes that this muscle was posteriorly-directed and related to propalinal jaw movements (but where could it insert?). However, an anterior origin on the maxillary lip would have made an good, if novel, arrangement for a muscular cheek. The structure of the tooth plates almost preclude a large tongue. Consequently, it is difficult to see how serious chewing could be coordinated without strong cheeks.

[4] ***Contra*** [RP40]. Note that the supratemporal is not above the temporal region. Indeed, it does not contact the temporal fenestra at any point (being separated by the squamosal), and is barely even exposed on the temporal surface of the skull. This is an awkward, but necessary incident to the preference for homology over etymology.

[5] "tooth plates present" is given as a synapomorphy by Modesto [M95**$**].

[6] Romer & Price [RP40: 371] note "A further point of similarity between sphenacodontids and edaphosaurs is that the articular surface of the articular consists of two concave areas which are both elongated antero-posteriorly; [in ***Edaphosaurus***] the inner area is much the shorter. In sphenacodontids this was associated with a corresponding elongation of the articular surfaces on the quadrate. Here, however, we have noted this was not so. Apparently the elongation in edaphosaurs was an adaptation permitting the antero-posterior movement of the lower jaw, a useful function in a herbivore." But, if that were the case, why would the inner articulation be "much the shorter"?

[7] Romer & Price [RP40] report the type species as being ***E. cruciger***. This seems to be incorrect. See [C06] and the discussion at [RP40: 379].

[8] This part of the skull does not seem to be well preserved in any specimen. The interpretation given by [RP40] seems reasonable, but [M95] is notably silent on the exact relations of squamosal, paroccipital process, and stapes.

[9] Romer & Price [RP40] note that the posterior dorsal spines tend to "force their way downward into the area normally occupied by the short spines of the sacrals and proximate caudals" causing the latter to be abnormally formed, twisted or even split. They emphasize that this was not pathological, since it is seen in every reasonably preserved specimen.

References: Case (1906) [C06]; Hurlburt (1999) [H99]; Lucas (2006) [L06]; Modesto (1994) [M94]; Modesto (1995) [M95]; Modesto & Reisz (1990) [MR90]; Modesto & Reisz (1990a) [MR90a]; Olson (1968) [O68]; Reisz & Berman (1986) [RB86]; Romer & Price (1940) [RP40]; Sidor (2003) [S03]; Sumida (1989) [S89].

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Synapsida: Sphenacodontia

Abbreviated Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EUREPTILIA
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            |--Haptodus
            `--+--Sphenacodontidae
               |  |--Sphenacodon
               |  `--+--Dimetrodon
               |     `--Secodontosaurus
               |
               THERAPSIDA
```

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2. *Haptodus* X
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5. Sphenacodontia
6. Sphenacodontidae X

Sphenacodontia: (= Sphenacodontoidea = Sphenacodontida) *Haptodus*. Definition: *Dimetrodon* + Marilyn Monroe.

Range: from the Pennsylvanian

Phylogeny: Eupelycosauria **:::** Edaphosauridae + * **:** *Haptodus* + (Sphenacodontidae + Therapsida).

Characters: maxillary supracanine buttress (thickening of the maxilla on internal surface, above caniniforms); **$** maxilla enlarged, separating lacrimal from narial rim; [BS00]; zygomatic process of quadratojugal lost & replaced by process of squamosal [BS00**$**]

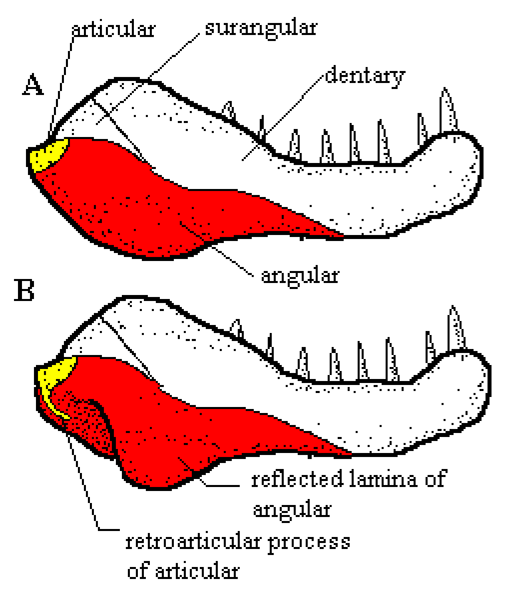


Fig. 1. Synapsid right mandible in right lateral view, with and without reflected lamina of angular and retroarticular process of articular

[HB86]; supraoccipital larger than in edaphosaurids [RP40]; paroccipital process elongated & directed ventrolaterally [BS00**$**] [HB86]; prootic forms anterolateral wall of otic capsule [M95]; dorsum sellae thick and plate-like [M95]; dentary deeper than in *Edaphosaurus* [RP40]; reflected lamina of angular present [BS00**$**] [HB86]; retroarticular process of articular oriented ventrally [BS00**$**] [HB86] [the combination of reflected lamina and ventral retroarticular process suggests early evolution of the mammalian middle ear; that is, that the angular (= tympanic), articular (= malleus), and stapes were used for hearing. For details, see Jaws and Ears]; Premaxillary teeth in deep sockets; enlarged caniniform maxillary teeth, transversely compressed, with anterior & posterior cutting edges [BS00**$**] [HB86]; dorsal centra relatively longer than in ophiacodonts [RP40]; iliac blade expanded [RP40].

Links: Synapsid classification and autapomorphies; Dimetrodon - Suite101.com (very basic, with some errors, but good elementary introduction); Synapsid Reptiles (transcript of intro college lecture).

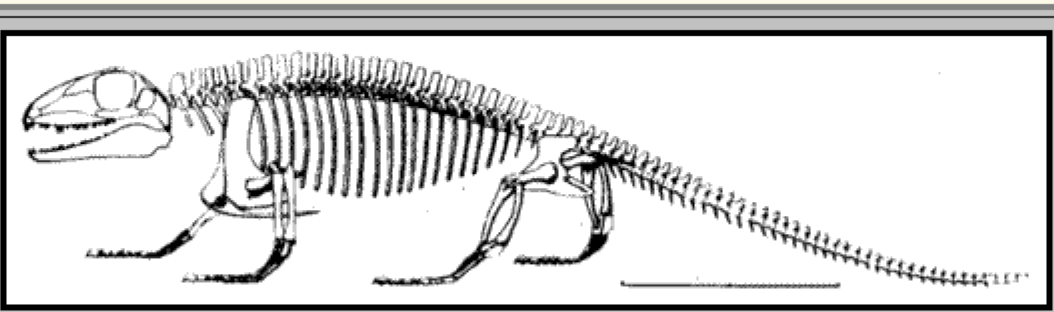
References: Battail & Surkov (2000) [BS00]; Hopson & Barghusen (1986) [HB86]; Modesto (1995) [M95]; Romer & Price (1940) [RP40]. ATW081024.

***Haptodus*:**

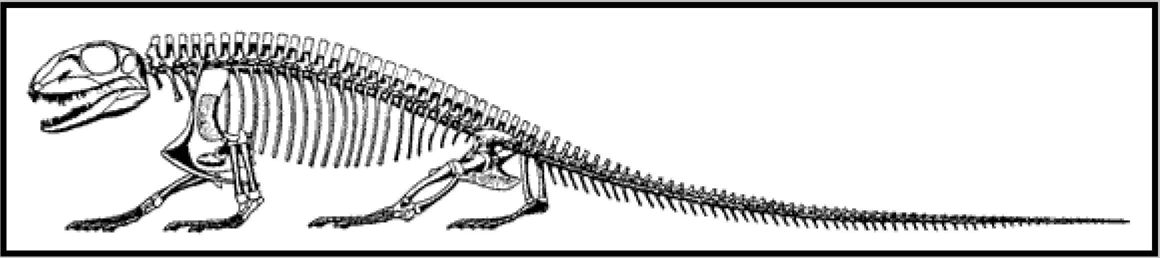
Range: Late Carboniferous and Early Permian of North America & Europe

Phylogeny: Sphenacodontia : (Sphenacodontidae + Therapsida) + *.

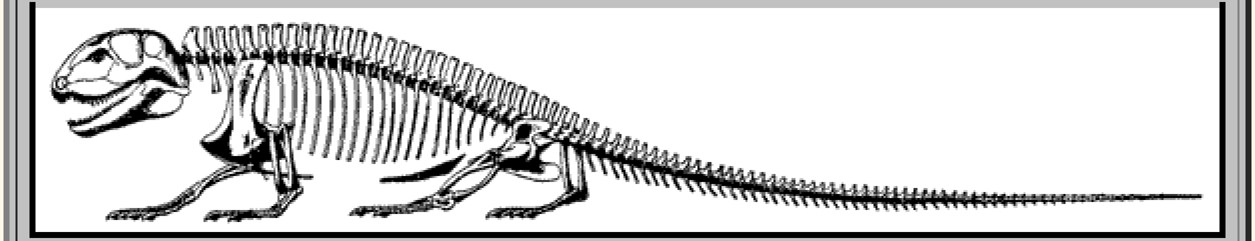
Introduction: *Haptodus* is a relatively small pelycosaur (60-150 cm and perhaps 3-30 kg) which lived in equatorial Pangea, within the "Edaphosaurid-Nectridean Empire." It was a medium-sized terrestrial predator which probably



***Haptodus garnettensis* Currie 1977. Length: about 60 cm. Mass: about 3 kg. Duration Kasimovian (Late Carboniferous). Fossil remains: skeleton and skull elements. Notes The most primitive known member of the Sphenacodontian lineage.**



Haptodus longicaudatus (Credner 1888) (= *Palaeohatteria*). Length: about 60 cm (juveniles). Mass: about 3 kg. Duration: Sakmarian (Early Permian). Fossil remains: numerous remains, mostly of juveniles, from Niederhässlich, near Dresden, Germany.



Haptodus saxonicus (vonHuene 1925) (= *Pantelosaurus*). Adult Length: upto 140 cm. Adult Mass: about 30 kg. Duration: Asselian (Early Permian) Fossil remains: six nearly complete remains, from the Döhlen Basin, near Dresden, Germany (Cuseler Stufe, lower Rotliegende).

constiututed the basal or primitive ancestral type of the Sphenacodontia. It shares many structural features of the skull and skeleton with the more specialised sphenacodontids, indicating they are closely related. *Haptodus* is known from the Late Pennsylvanian (Latest Carboniferous) and Early Permian of North America and Europe. Both small and medium sized individuals are known. These animals were clearly effective predators, like contemporary large tropical lizards, feeding on both arthropods and small vertebrates. *Haptodus* lacked the spectacular sail that characterised the bigger Sphenacodontids like *Dimetrodon*, *Ctenospondylus*, and *Secodontosaurus*. It is also more common in Europe (central equatorial Pangea), whilst the other forms are primarily American (west equatorial Pangea). (MAK 000718).

Sphenacodontidae: *Ctenospondylus*, *Dimetrodon*, *Secodontosaurus*, *Sphenacodon*. Big sail-back carnivorous pelycosaurs and relatives. The dominant carnivores of the Early Permian.

Range: Late Carboniferous and Early Permian.

Phylogeny: Sphenacodontia **::** Therapsida + * **:** *Sphenacodon* + (*Dimetrodon* + *Secodontosaurus*).

Introduction: The sphenacodontids include the large carnivores *Dimetrodon*, *Sphenacodon*, *Ctenospondylus*, and *Secodontosaurus*. Reisz *et al*. (1992). These animals were the dominant predators of their time, and their fossil record extends from the Latest Carboniferous through to the early Middle Permian.

All the sphenacodonts had a deep, narrow skull with massive jaws and a formidable array of teeth – long canines, daggerlike incisors and small, cutting cheek teeth. The name of the most well-known sphenacodontid, *Dimetrodon*, actually refers to this adaptation, it means "two measure teeth". The sphenacodonts were the first animals to develop such a specialized set of teeth, and were the first large terrestrial carnivores to evolve (all earlier large carnivores were either fully or semi- aquatic).

Many of these forms (*Dimetrodon*, *Sphenacodon*, *Secodontosaurus*, and *Ctenospondylus*) are all large to very large predators that have tall neural spines. These, in life, doubtless supported a large "sail" or fin on the animal's back. This strange structure most certainly served as a thermoregulatory device. In the cool morning the creature would turn side on to the morning rays, thus soaking up heat and becoming more active before its rivals or prey did. During the middle of the day, or whenever the creature was in danger of overheating, it could turn head on to the sun, thus shading the fin and allowing excess heat to dissipate.

These animals had long limbs, making them relatively agile, fast moving animals, especially when compared to their slower, bulkier herbivorous relatives. The later and larger types like *Dimetrodon*, *Sphenacodon*, and *Ctenospondylus* all have similarly constructed, massive skulls with extremely large anterior incisors and canines.

Not only were these animals of great ecological significance during their long reign, but they also have an important position on the evolutionary tree, being close to the ancestry of the primitive therapsids, and ultimately to mammlas and man. (MAK 000718)

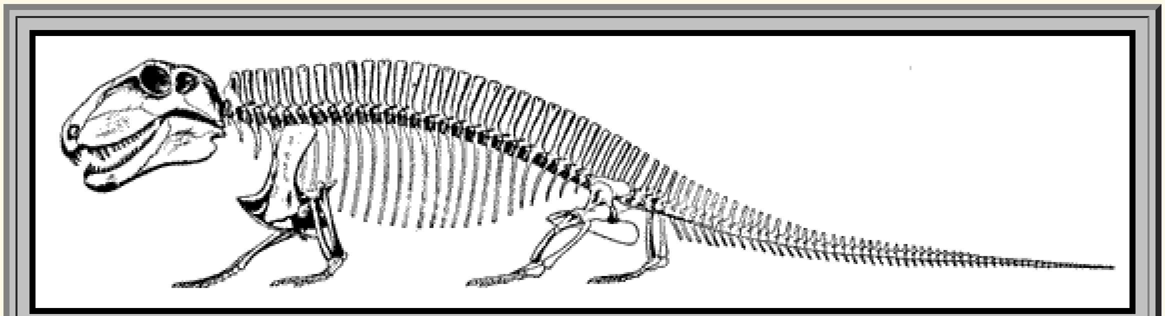
Characters: Deep, massive skull; premaxilla slopes anteroventrally ("hook-nose"); maxilla dorsoventrally broad to support fangs & excludes lacrimals from nares; **$** ventral narial process of nasal forming posterior margin of nares; **$** anterior process of frontal longer than posterior process; pineal foramen on parietal with distinct ridge;

extensive postorbital - squamosal contact; paroccipital process having only terminal contact with squamosal [RP40];paroccipital process dorsal border is sharp ridge [RP40]; jaw articulation well below level of tooth row [shape and position of jaw articulation allowed mandibular adductors attached to back of skull to pull more efficiently, i.e. edge of surangular and coronoid almost perpendicular to muscle fibers]; articular enlarged; angular with "reflected lamina;" teeth with cutting edges formed from ridges extending only half-way tip towards base [R+97]; teeth robust & almost square in cross-section at base [R+97]; enlarged maxillary caniniform teeth which bulge into choana; specialized "incisors;" dorsal centra markedly taller than wide [RP40]; neural spines elongated into sail (probably thermoregulatory device, suggesting * were ectothermic); spines smooth, without crossbars; no sign of sexual dimorphism in sail; sail area heavily vascularized; relatively long, gracile limbs; supraglenoid foramen on scapular blade [RP40]; possibly first terrestrial animals to prey on similar-sized prey [RS01].

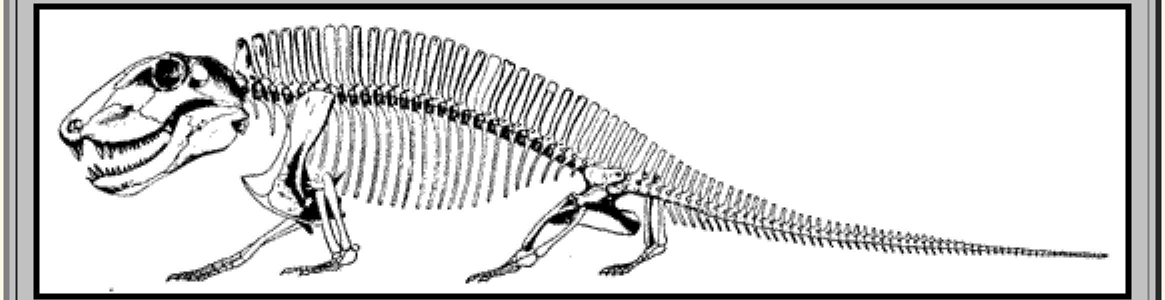
Links: Dimetrodon - Enchanted Learning Software; Synapsida; Synapsid classification and autapomorphies; Biology 356; Introduction to the Pelycosaurs.

References: Reisz *et al*. (1992); Reisz *et al*. (1997) [R+97]; Romer & Price (1940) [RP40]; Rubidge & Sidor (2001) [RS01]. 011227.

***Sphenacodon*:**



Sphenacodon ferox. 177 cm and 52 kg. From the Sakmarian of the Abo/Cutler Formation, New Mexico, USA. Distinguished from the contemporary *S. ferocior* by smaller size, more slender build, and less neural spine development.



Sphenacodon ferocior. 225 cm and 129 kg. From the Sakmarian of the Abo/Cutler Formation, New Mexico, USA. A larger and less common contemporary of S. ferox, distinguished by more robust proportions and greater neural spine development.

Range: Early Permian of North America.

Phylogeny: Sphenacodontidae : (*Dimetrodon* + *Secodontosaurus*) + *.

Introduction: *Sphenacodon* has been recovered from the Early Permian of Euramerica. Like most Sphenacodontids, it was a large predator, 150-250 cm in total length. The vertebral spines of *Sphenacodon*'s backbone were long, and probably acted as attachment points for massive back muscles, allowing the animal to lunge powerfully at its prey. *Sphenacodon* did not have the extremely elongate spines and distinctive "sail" of more derived sphenacodontids. Two species are known. The more common *S. ferox* is smaller, more slender, and less development of the neural spines. The aptly named *S. ferocior* is a contemporary, but shows the greater size and greater spine development typical of the more derived Sphenacodontids. (adapted from MAK 000718)

Characters: head deep & narrow; massive jaws; regional specialization of teeth, with some differentiation of premaxillary incisor-like, canine and smaller maxillary dentition; elongate neural spines.

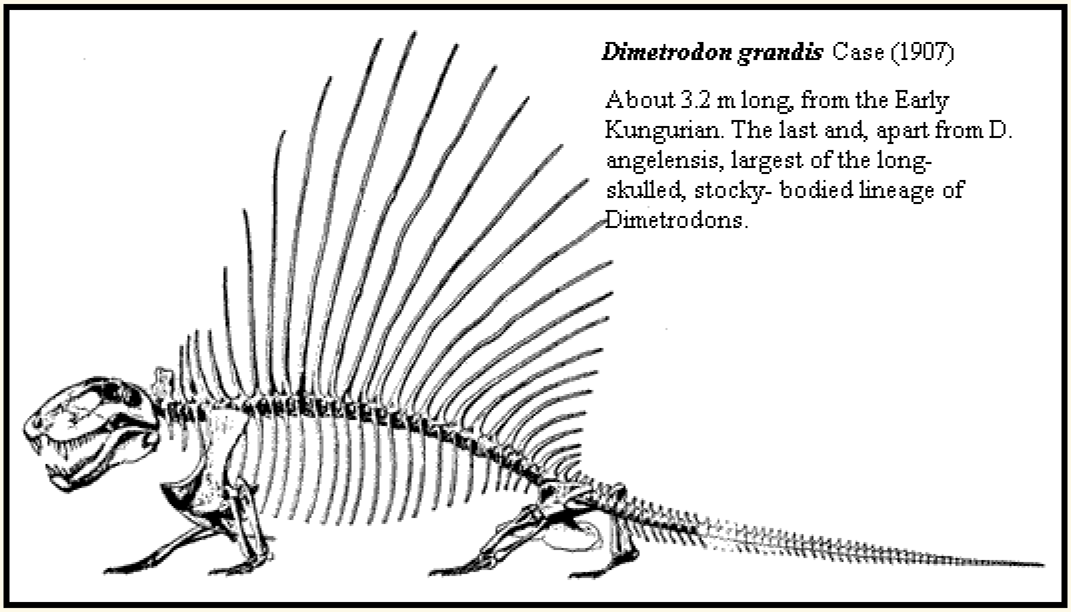
스페나코돈

Links: [(Sphenacodon)] (Korean: another reconstruction, with basic information); Sphenacodon (German: with good short discussion -- one error: *S. ferocior* war die *größere* Sorte, nicht das kleinere); Cuffey 2 - Mammal - Like Reptiles (as part of an evolutionary sequence); Pelycosaurs- ancestors of therapsids (an interesting ecological speculation). ATW040117.

Dimetrodon:

Range: Early Permian to Middle Permian of North America.

Phylogeny: Sphenacodontidae :: *Secodontosaurus* + *.



Dimetrodon grandis Case (1907)

About 3.2 m long, from the Early Kungurian. The last and, apart from D. angelensis, largest of the long-skulled, stocky- bodied lineage of Dimetrodons.

Introduction: *Dimetrodon* means "two-measures tooth," referring to the fact that unlike reptiles, the teeth differ in size. This was an enormous animal for its time, with an adult length of up to three metres or more and perhaps 150 kg, depending on the species. *Dimetrodon* is found in Early to Middle Permian deposits of a localised area in western equatorial Euramerica, now Oklahoma and Texas, in a part of the "West Edaphosaurid- Nectridean Empire" which we may call the "*Dimetrodon* sub-province." *Dimetrodon* is an advanced member of the Sphenacodontid family, and may have evolved from an early *Sphenacodon*-like form (e.g. *Sphenacodon ferox*) during the latest Carboniferous or earliest Permian (Gzhelian-Asselian) time.

Perhaps the most well-known prehistoric non-dinosaur, *Dimetrodon* was a common large carnivorous pelycosaur of the early Permian of North America, immediately recognisable by the "fin" or "sail" of elongate vertebral spines running along its back, upto a metre in length, and in life covered with a layer of skin and blood vessels and serving as a heat-exchange mechanism. In size and build it is comparable to a modern-day alligator, except that it was a fully terrestrial (land-living) creature. *Dimetrodon* was the dominant predator in its environment for some twenty-five million years, during which time it evolved through about a dozen species, become steadily larger as time progressed (an example of "Cope's Law"). *Dimetrodon* legs, although strong, were short, so it may have hunted through ambushing its prey, the sail on the back also no doubt serving to help camoflague the creature when it hid among stands of bamboo-like *Calamite* plants.

The largest, most specialised and most spectacular of the pelycosaur carnivores, *Dimetrodon* remained the dominant carnivore in its environment for some twenty-five million years, before being ousted by the up and coming eotitanosuchian and dinocephalian theraspids during the Ufimian age. Curiously, despite its obvious adaptions, *Dimetrodon* remained confined to a limited geographical region (fossils are known only from the Witchita, Clear Fork and San Angelo beds of the Texas-Oklahoma region, and some fragments of a small early species from New Mexico). This limited area (the actual extent being unknown due to the fact that only in a few places are there fossil deposits) is here termed the "Dimetrodon sub-province".

In skull and general body form, *Dimetrodon* was very similar to contemporary types like *Sphenacodon* and *Ctenospondylus*. However, these latter two have blade-like (narrow or flattened in cross- section) neural spines supporting the sail, whereas *Dimetrodon* has greatly elongated spines that are rounded in cross- section section.

Dimetrodon is such a well-known creature it's even featured in most popular books on dinosaurs (even though it is not a dinosaur, and not even related). There are also several webpages dedicated to it. (MAK 000718)

Links: Dimetrodon Plaque; Dimetrodon - Enchanted Learning Software; Dimetrodon grandis - Permian period -

Dinosaur art picture; Dimetrodon - Suite101.com; Dimetrodon; Dimetrodon; Dimetrodon; American Museum of Natural History: Dimetrodon; Dimetrodon sp.; Dimetrodon; Dimetrodon: A Pelycosaur With Character. ATW021001.

***Secodontosaurus*:**

Range:

Phylogeny: Sphenacodontidae **::** *Dimetrodon* + *.

Introduction: *Secodontosaurus* is an unusual form that, although similiar in body, differs in the shape of the head from other sphenacodonts. The skull is low and narrow, although the neural spine morphology (of the "sail" backbone) is similiar to that of *Dimetrodon*. The cranial modifications of *Secodontosaurus* indicate an adaptation to some specialized feeding strategy, perhaps preying upon burrowing animals, or perhaps aquatic feeding habits. (MAK 000718)

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Synapsida: Dendrogram

Abbreviated Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EUREPTILIA
|
SYNAPSIDA
|--Caseasauria
|  |--Eothyrididae
|  `--Caseidae
`--Eupelycosauria
   |--Varanopseidae
   `--+--Ophiacodontidae
      `--+--Edaphosauridae
         `--Sphenacodontia
            `==Sphenacodontidae
               `--THERAPSIDA
```

Contents

Dendrogram

```
AMNIOTA
|--+--ANAPSIDA
|  `--EUREPTILIA
|
SYNAPSIDA ToL, MH, Tax
|--Caseasauria X
|  |--Eothyrididae •X
|  `--Caseidae •X MH, Tax
`--Eupelycosauria
   |--Varanopseidae X MH, Tax
   |  |--Mycterosaurinae X
   |  |  |--Mycterosaurus •X
   |  |  `--Elliotsmithia •X
   |  `--Varanodontinae X
   |     |--Aerosaurus •X
   |     `--Varanops •X
   `--+--Ophiacodontidae X MH, Tax
      |  |--Archaeothyris •X
      |  `--Ophiacodon •X
      `--+--Edaphosauridae X MH, Tax
         |  |--Ianthasaurus •X
         |  `--+--Lupeosaurus •X
         |     `--+--Glaucosaurus •X
         |        `--Edaphosaurus •X
         `--Sphenacodontia
            |--Haptodus •X
            `--+--Sphenacodontidae X MH, Tax
               |  |--Sphenacodon •X
               |  `--+--Dimetrodon •X
               |     `--Secodontosaurus •X
               `--THERAPSIDA
```

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Synapsida: References

Abbreviated Dendrogram

```
AMNIOTA
|
SYNAPSIDA
|--Caseasauria X
|  |--Eothyrididae X
|  `--Caseidae X
`--Eupelycosauria
   |--Varanopseidae X
   `--+--Ophiacodontidae X
      `--+--Edaphosauridae X
         `--Sphenacodontia
            |--Sphenacodontidae X
            `--THERAPSIDA
```

Contents

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Therapsida

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|-Raranimus
`+-Biarmosuchia
 `-+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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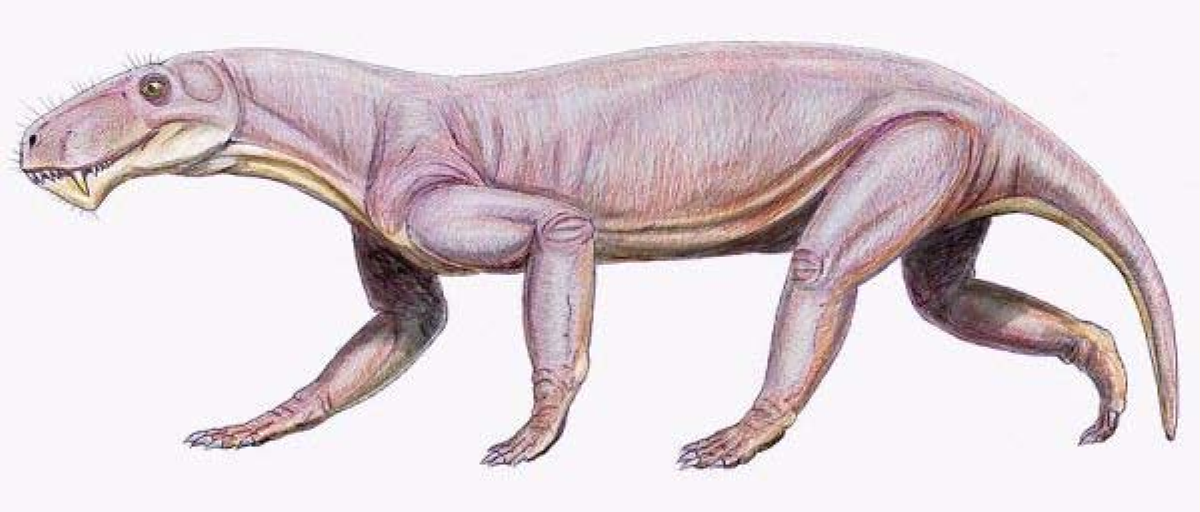

The late Permian therapsid *Lycaenops*, a typical gorgonopsid. This animal was about the size of, and a large dog. It may have been covered in fur, and hence at least partially warm-blooded.
Artwork by Dmitry Bogdanov, GNU Free Documentation/Creative Commons Attribution license, Wikipedia

The Therapsids were one of the great success stories of the Permo-Triassic. First appearing in the middle or even the early (if *Tetraceratops* is a member of this group) Permian, they very quickly dominated terrestrial and semi-aquatic environments, filling a number of ecological niches and guilds, including felid, canid, bear, otter, ungulate, and even mole analogues, as well as many forms with no contemporary counterparts. In keeping with the episodic nature of synapsid evolution, there seem to have been at least two distinct dynasties, a middle Permian fauna dominated by dinocephalians and other primitive forms, and a late Permian fauna characterised by a wide range of more advanced carnivorous and herbivorous groups. These animals were so abundant (especially the herbivorous yet bizaarely specialised dicynodonts with their toothless beaks) that one could easily refer to this period as the age of therapsids, with both anapsid reptiles and relict pelycosaurs playing second fiddle. Their evolutionary success was unfortunately cut short by the end Permian extinction event, and although a number of lineages made it through to the Triassic, their protomammalian metabolism put them at a disadvantage in a hot dry Triassic world far more suited to sauropsid reptiles, and increasingly dominated by thecodontian archosaurs. They survived by becoming progressively smaller and more mammal-like, except for the dicynodonts which if anything became larger. By the time the dinosaurs had appeared, the therapsids had given rise to the first mammals, although one lineage of rodent-like, non-mammalian therapsids, the tritylodonts, would continue to the Middle Cretaceous. MAK120127

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Therapsida

Abbreviated Dendrogram

```
SYNAPSIDA
|
Therapsida
|--Tetraceratops
|--Raranimus
`--+-?Phthinosuchidae
   |--Biarmosuchia
   `--+--Dinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
```

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2. *Tetraceratops* X
3. Therapsida

Tetraceratops - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

Tetraceratops: misnomer & miscellaneous

Mathew (1908)

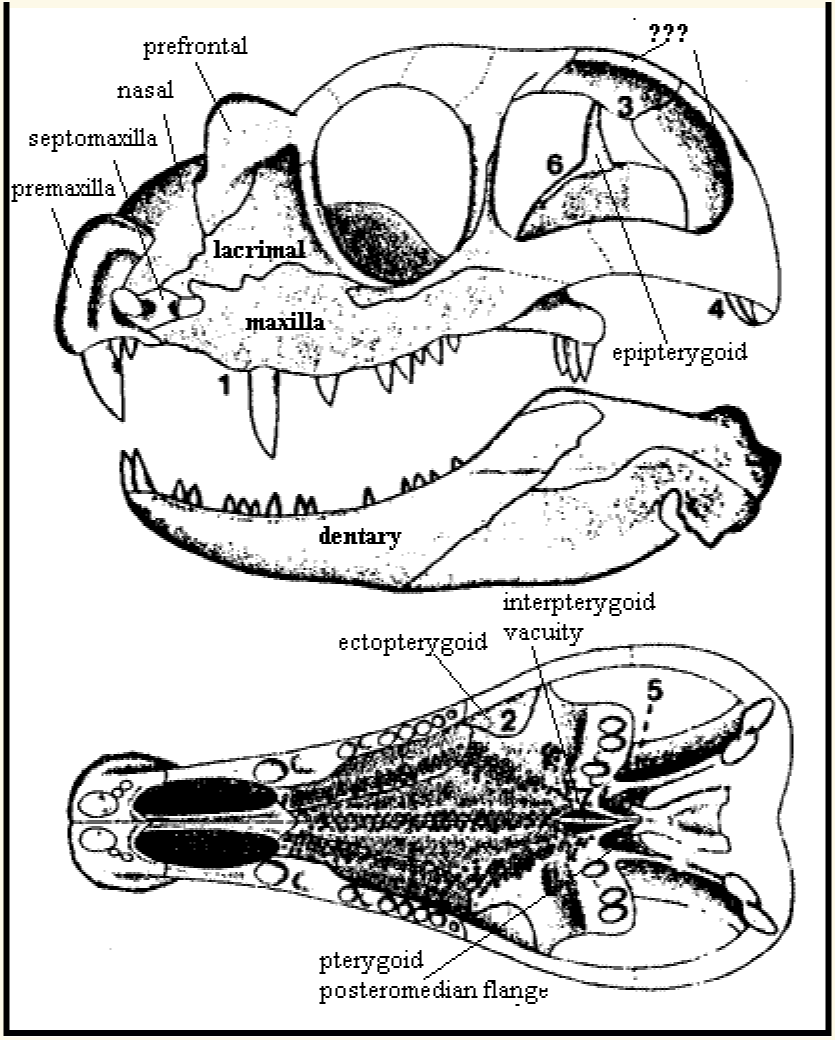
The generic name of ***Tetraceratops*** *insignis* Matthew 1908 means "four-horned face," although it has at least six protruberances, none of which are horns. That original misnomer is symptomatic of the confusion surrounding this animal. The fossil, a 95 mm unque skull, was originally recovered from the Early Permian Arroyo Formation (Clear Fork Group) of Baylor County, Texas. It was initially identified as an eothyrid pelycosaur of uncertain relationships. The only known specimen was embeded in a particularly recalcitrant rock matrix and was very difficult to prepare.

Laurin & Reisz (1996)

In 1996, Michel Lauren and Robert Reisz published an important paper on *Tetraceratops*, based on additional preparation. Laurin & Reisz (1996). Many of their general anatomical findings are discussed on theprevious page. These workers argued that this strange little animal was actually a connecting link between the basal syanapsid "pelycosaurs" and the therapsids.

At least three pairs of horns are present on this animal, one on each premaxilla, prefrontal, and angular bones of the skull. These give the animal a superficial similarity to the primitive therapsid *Burnetia mirabilis*, a biarmosuchian. However, this does not necessarily indicate close relationships, because the horns are not located on the same bones. It is interesting to coinsder that similiar hornlets are found on a number of different (and only distantly related) theropod dinosaurs - *Dilophosaurus*, *Cryolophosaurus*, *Allosaurus*, *Carnotaurus*, *Tyrannosaurus*, etc). It is not unlikely that in all these instances the horns may have been brightly coloured and served as instruments of intra-specific display.

Laurin & Reisz determined that *Tetraceratops* and the therapsids form a monophyletic group because they share the following seven derived features (synapomorphies) which appear in the primitive condition in sphenacodontines (see diagram at left):



(1) the precanine teeth are lost;
(2) the ectopterygoid teeth are lost;
(3) the upper margin of the lateral temporal fenestra is broadened and forms a new concave, ventro-laterally facing surface from which the jaw adductor musculature originated;
(4) the quadrate, the upper element of the jaw suspension, is reduced in size;
(5) a posteromedian flange of the pterygoid is present behind the interpterygoid vacuity;
(6) the ventral plate of the epipterygoid is much reduced in size;
(7) the interpterygoid vacuity is reduced in length.

The presence of a number of diagnostic therapsid features cannot be tested in *Tetraceratops* because of the fragmentary nature of the specimen. However, all other therapsids would seem to form a monophyletic group excluding *Tetraceratops* because they share the following derived characters that are **not** present in *Tetraceratops* and pelycosaurs:

(A) the septomaxilla is small, lacking a facial process;
(B) the maxilla contacts the prefrontal;
(C) the maxilla contacts the nasal and excludes the lacrimal from the naris;
(D) a distinct incisiform region is present; and
(E) all the incisors are equal in size.

This combination of primitive and advanced features showed that *Tetraceratops* is intermediate between pelycosaurs and all previously known therapsids, an could serve as pretty good ancestral type (or "sister taxon" in cladistic jargon) to the later Therapsida.

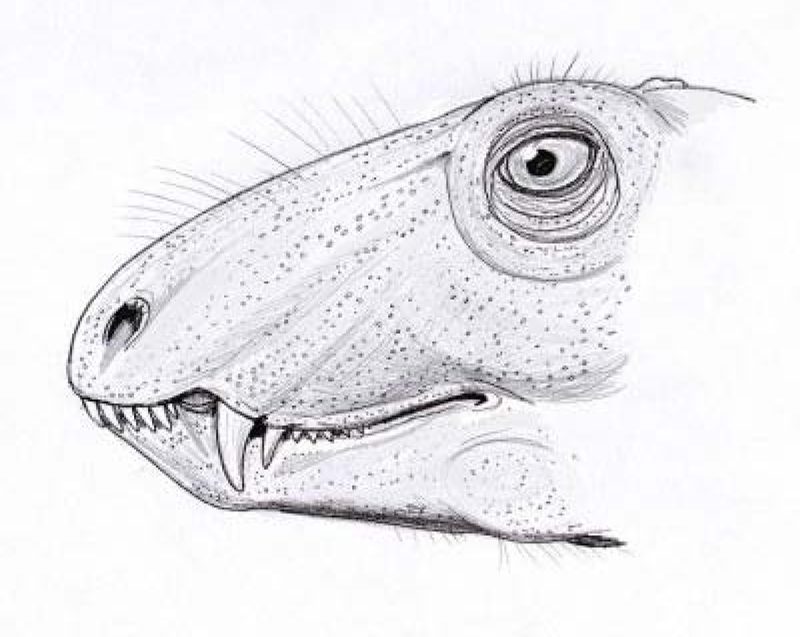
Conrad & Sidor (2001)

More recently, however, Conrad & Sidor (2001) again reviewed this specimen and concluded that *Tetraceratops* was neither an eothyrid nor a therapsid. Rather, it was a sphenacodontid. Their detailed findings are mentioned on the previous page. In essence, they assert that the skull had been sheared over time. as a result, the entire arch of the posterior jaw was displaced upwards. As a result, what appeared to be the skull roof above the temporal fenestra was actually bits and pieces of the zygomatic (jaw) arch. This actually affects only character #3 above. However, this was enough to change the shape of the cladogram in a subtle, but significant way, shifting *Tetraceratops* onto a dead-end side track, the Sphenacodontidae (like *Dimetrodon*), rather than being on the main line to the Therapsida. However, whether *Tetraceratops* is a therapsid or just a close cousin, it is plainly a reasonably good guide to the sorts of forms which connect the "pelycosaurs" with the Therapsida.

Evolution & Ecology

It is quite likely that proto-therapsids such as *Tetraceratops* (and many others which never became fossilised) evolved in an upland environment where they were not easily fossilised, away from the swamps and deltas frequented by the Pelycosaurs (the only upland Pelycosaur lineages were the Caeseidae and, most certainly, their eothyrid ancestors). This early Permian upland evolution proceeded parallel to the Permocarboniferous lowland fauna, and probably originally derived from reptiles that adapted to dry habitats during the long Kazimovian arid period. It was from this upland evolution, via intermediate forms like *Tetraceratops*, that the great therapsid evolutionary radiation emerged. MAK000802, ATW020518.

Raranimus



Raranimus - artwork by Dmitry Bogdanov - Wikipedia

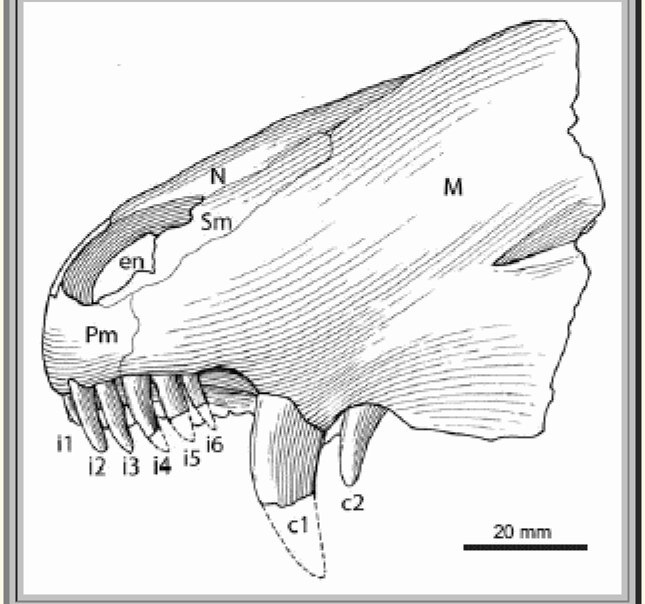
Overworked author's note: the following is from Wikipedia (quoted here in toto because it is so well-written and there are so many pages to get through...) - content mostly by Smokeybjb. MAK091113

Raranimus is an extinct genus of therapsid of the Middle Permian. It was described in 2009 from a partial skull found in 1998 from the Dashankou locality of the Xidagou Formation, outcropping in the Qilian Mountains of Gansu, China. The genus is the most basal known member of the paraphyletic order Therapsida, from which the class Mammalia is a descendant taxon. (Liu, Rubidge, & Li 2009)

Description

Raranimus shares a number of features with later therapsids and ancestral sphenacodontids. The skull consists of a well preserved rostrum. The teeth suggest a carnivorous lifestyle for *Raranimus*, as the incisors are recurved and the second canines are serrated on their posterior edges. The incisors are morphologically similar to those seen in more derived theriodonts. The presence of two linguo-labially compressed canines is a diagnostic feature of *Raranimus*. The presence of two functional canines is characteristic of sphenacodontids, and this condition is seen in no other therapsid other than *Rananimus*. However, the slender, compressed shape of these canines is a derived characteristic of therapsids, with the canines of similarly sized sphenacodontids being more massively built. The precanines are small and anteriorly serrated, similar to what is seen in the synapsids *Dimetrodon* and *Tetraceratops*.(Romer & Price 1940, Laurin & Reisz 1996]

In the palate region of the skull, the anterior process of the vomer ventrally overlies the premaxilla at the anterior margin of the choana. This overlap is also seen in dinocephalians. However, unlike any other therapsid, the choanae are short and extend only from the level of the fourth incisor back to the first canineLiu, Rubidge, & Li 2009



Partial skull of *Raranimus dashankouensis* (drawing of holotype) left lateral view. Abbreviations: c1–2, canine 1–2; ch, choana; en, external naris; i1–6, incisor 1–6; M, maxilla; N, nasal; p1–3, postcanine 1–3; Pf, prefrontal; Pl, palatine; Pm, premaxilla; Pt, pterygoid; rc, replacement canine; ri, replacement incisor; Sm, septomaxilla; sp, small precanine maxillary tooth; V, vomer. From Liu, Rubidge, & Li 2009 p.395.

Phylogenetics

According to a phylogenetic analysis conducted along with its initial description, Raranimus is considered to be the basalmost therapsid. Liu, Rubidge, & Li 2009 There has been some controversy as to whether or not *Tetraceratops* is a therapsid or a more basal pelycosaur. If *Tetraceratops* is a therapsid, as has recently been proposed, it would be the oldest and most basal one known, surpassing Raranimus in age by several million yearsLaurin & Reisz 1996. However, later studies have questioned the placement of *Tetraceratops* within Therapsida, and the 2009 phylogenetic analysis using *Raranimus* places the genus outside of the clade. (Liu, Rubidge, & Li 2009, Sidor & Hopson 1998, Conrad & Sidor 2001]

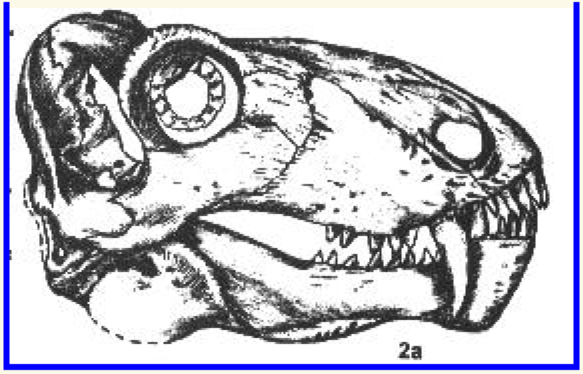
Raranimus occurs in strata that were deposited during the early Roadian stage of the Middle Permian.[The hypothesized age for this locality is supported by the presence of the dissorophoid temnospondyl Anakamacops, the bolosaurid *Belebey*, and the basal therapsids *Biseridens*, *Sinophoneus*, and *Stenocybus*.] The sphenacodontids were most diverse before the Roadian in the Early Permian, yet therapsids did not appear as a diverse group until near the Roadian-Wordian boundary. This has left a morphological and temporal gap in the fossil record during which the origin of therapsids must have occurred. (Abdala et al 2008) This gap has been called "Olson's Gap".[Lucas 2004, Ivakhnenko 2005

With the general absence of therapsid remains found from strata deposited during Olson's Gap, different hypotheses have developed in order to explain the group's origins and initial diversification. One theory suggests that therapsids diversified quickly through rapid apomorphy accumulation sometime during the gap, while the other proposes that therapsids evolved gradually over the course of up to 35 Ma. (Abdala et al 2008, Kemp 2006] Only recently have remains of basal therapsids such as *Raranimus* been found from China that occur during Olson's Gap. Other therapsids that are known to have existed during the gap include *Sinophoneus* and *Stenocybus*.[Cheng & Li 1997]

Descriptions

Therapsida: mammals > sphenacodontids [LR96].

Range: From the Early? Permian [RS01].



Phylogeny: Sphenacodontia **:** Sphenacodontidae + * **:** *Tetraceratops* + (*Raranimus* + (Phthinosuchidae + (Biarmosuchia + (Eotitanosuchia + Eutherapsida)))).

Characters: Large head with relatively rigid skull; **$** long dorsal process of premaxilla [B&S, H&P] [RS01]; **$** septomaxilla with posterodorsal facial process separating nasal & maxilla [B&S, H&P, *contra* LR96]; **$** maxilla enlarged, separating nasal & lacrimal [B&S, H&P]; **$** maxilla contacts prefrontal (except *Tetraceratops*) [LR96] [RS01]; **$** enlarged temporal fenestra [B&S, H&B] [RS01]; **$** upper margin of fenestra forms concave, ventrolaterally facing surface (for origin of jaw adductors?) [LR96]; **$** pineal foramen raised on prominent boss [B&S, H&P] [RS01]; **$** supratemporal absent [B&S, H&P] [RS01]; **$** squamosal with groove on posterior [B&S, H&P]; **$** quadrate reduced [LR96]; **$** braincase firmly sutured to back of dermal skull roof [LR96]; dentary anteriorly expanded [RS01]; anterior coronoid absent [RS01]; **$** posterior coronoid ventrally shifted & fails to form dorsal margin of jaw in medial view [RS01]; **$** reflected lamina of angular bone notched dorsally [B&S, H&P] [RS01]; **$** reflected lamina with pattern of ridges on lateral surface; **$** vomer expanded transversely between choanae [B&S, H&P]; vomer with concave ventral surface; at least partial secondary palate; **$** posteromedian flange of pterygoid present behind the interpterygoid vacuity [LR96]; **$** pterygoid short & palatines meet at midline (except *Tetraceratops*) [LR96]; **$** interpterygoid vacuity shortened [B&S, H&P, LR96]; basicranial articulation fused [RS01]; **$** parasphenoid ventral plate ridged & lacks central groove (except *Tetraceratops*) [LR96]; **$** precanine teeth absent; **$** premaxillary teeth of equal size (except *Tetraceratops*) [LR96]; enlarged canine dentition [RS01]; **$** upper canine length increased [B&S] **$** no more than twelve upper postcanine teeth [LR96]; **$** teeth absent from ectopterygoid [LR96]; **$** palatal teeth restricted to raised denticle fields (except *Tetraceratops*) [LR96]; heavy body; **$** intercentra absent from trunk [RS01]; more than 3 sacral vertebrae; tail reduced; limb girdles reduced and more mobile; limbs more slender, but fairly short; limbs held more vertically; **$** scapular blade slender [RS01]; **$** pectoral glenoid deepened & rounded [RS01]; **$** humeral head rounded, not screw-shaped [RS01]; expanded iliac blade; **$** acetabulum deepened & rounded [RS01]; **$** inturned head of femur [RS01]; general reduction of ventral components (e.g. clavicle -- indicative of more upright posture); inflected femoral head [RS01]; development of greater trochanter on femur (with iliac blade, indicates gluteal hindlimb musculature); phalanges shorter (used as lever, rather than holdfast); possibly had hair; increased metabolic rate probable; found in terrestrial habitats with nearly world-wide distribution.

Links: There are a remarkable number of good sites: Thrinaxodon; Paleontology and Geology Glossary: T; Therapsida; Therapsida; Untitled7; Mammal-like reptiles.

References: Battail & Surkov (2000) [B&S]; Hopson & Barghusen (1986) [H&B]; Laurin & Reisz (1996) [LR96]; Rubidge & Sidor (2001) [RS01].

Image: *Titanophoneus potens* courtesy mathematical.com. ATW020206.

Tetraceratops: *T. insignis* Mathew, 1908. [CS01] argue convincingly that this is not a therapsid.

Range: Early Permian of North America.

Phylogeny: Therapsida **:** + (*Raranimus* + (Phthinosuchidae + (Biarmosuchia + (Eotitanosuchia + Eutherapsida)))) + *.

Characters: Skull high & short; **$** first premaxillary tooth much larger than others [LR96]; upper tooth row slightly convex; 1 small precaniniform; **$** long diastema on maxilla anterior to caniniform [LR96]; maxilla with broad alveolar shelf; postcaniniform teeth with sharp, curved crowns; **$** very large teeth on transverse flange of pterygoid [LR96]; ectopterygoid teeth absent; dentary largest jaw element; **$** dentary ends ventral to coronoid process [LR96]; angular with reflected lamina (*contra*, [CS01]); posteroventral flange of angular may have had additional horn; surangular forms coronoid; surangular with prominent knob for articular; choana long, narrow, bordered medially by vomers; palatines ling & narrow with medial denticle field; ectopterygoid small & triangular; posteromedian flange of pterygoid present; pterygoids with medial and lateromedial denticle rows; ventral plate of epipterygoid (?) reduced; ventral plate of epipterygoid excluded from basicranial articulation; interpterygoid vacuity shortened; pterygoids meet medially anterior & posteriorly to vacuities; basipterygoid articulation present (not fused); **$** parasphenoid ventral plate narrow [LR96], with large medial depression; parasphenoid fused with basisphenoid; premaxilla very deep; septomaxilla small (!? also described as "massive" in same paper) with no facial process; maxilla contributes to narial margin; **$** bony, possibly horn-bearing, tuberosities on premaxilla, prefrontal and angular [LR96]; tuberosities covered with fine ridges laterally & small foramina dorsally (=distally); maxilla does not contact nasal; lacrimal contacts nares briefly; nasal small, with (probable) median ridge; large orbital contribution of the lacrimal [LR96]; prefrontal with large tuberosity (horn); deep posteroventral excavation of prefrontal; long thin ventral process on orbital rim under lacrimal; **$** suborbital process of jugal very narrow [LR96], terminating in blunt wedge in maxilla; postorbital ramus of jugal overlaps postorbital extensively (but not "twisted" as in later forms); postorbital overlaps & firmly sutured to squamosal, excluding parietal from temporal fenestra (questioned by [CS01]); broad, concave shelf of squamosal on upper, *internal* margin of temporal fenestra (origin of jaw adductors); wide tabular overlapping occipital portion of squamosal ([CS01] assert that [LR96]'s tabular is actually a fragment of the squamosal); braincase attached firmly to cheek; **$** paroccipital process (?) narrow [LR96] & cylindrical, attached to tabular and squamosal; quadrate reduced; quadrate with two clearly separated condyles of equal size.

Links: New Page 1; The osteology and relationships of Tetraceratops insignis, the ..; The First Therapsids; Artist-Brad McFeeters [The Dinosauricon]

References: Conrad & Sidor (2001) [CS01]; Laurin & Reisz (1996) [LR96].

Notes: **[1]** Despite the name, *Tetraceratops* had at least 6 horns. Only 4 were exposed at the time it was named. **[2]** LR96 is a paradigm of what a descriptive paper should be. If everyone wrote like this, the professional literature would be half as long and twice as useful. Highly recommended. **[3]** [CS01] argue that much of the skull roof area is actually the zygomatic arch. Based on a revised parsimony analysis, they assert that *Tetraceratops* is a garden-variety sphenacodontid. ATW031019.

Raranimus: *R. dashankouensis* Liu, Rubidge, & Li 2009.

Range: Roadian (Early Middle Permian) of China. (Xidagou Formation, Dashankou, Gansu, China)

Phylogeny: Therapsida **:** + (Biarmosuchia + (Eotitanosuchia + Eutherapsida)))) + *.

Characters: Plesiomorphic, short choana; long facial process of septomaxilla; one precanine and two functional linguo-labially compressed canines on maxilla; six incisors.

Size: complete skull estimated to exceed 16 cm.

Reference: Liu, Rubidge, & Li 2009

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checked ATW040305; last modified MAK091114, 120127

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Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

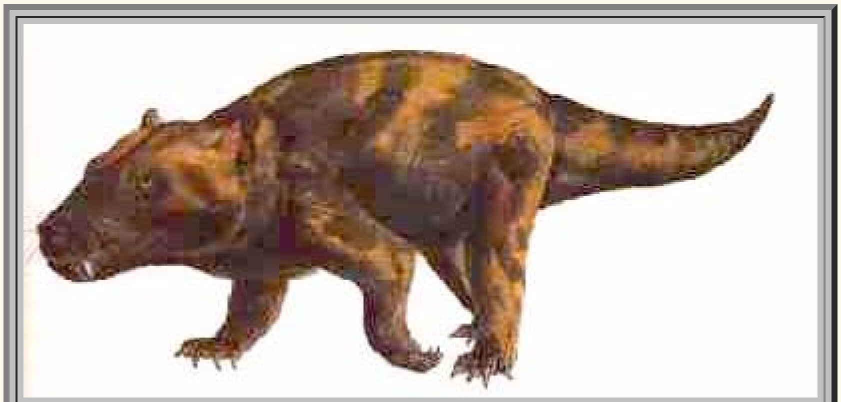
Therapsida: Overview

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|-Raranimus
`+-Biarmosuchia
 `-+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

Contents

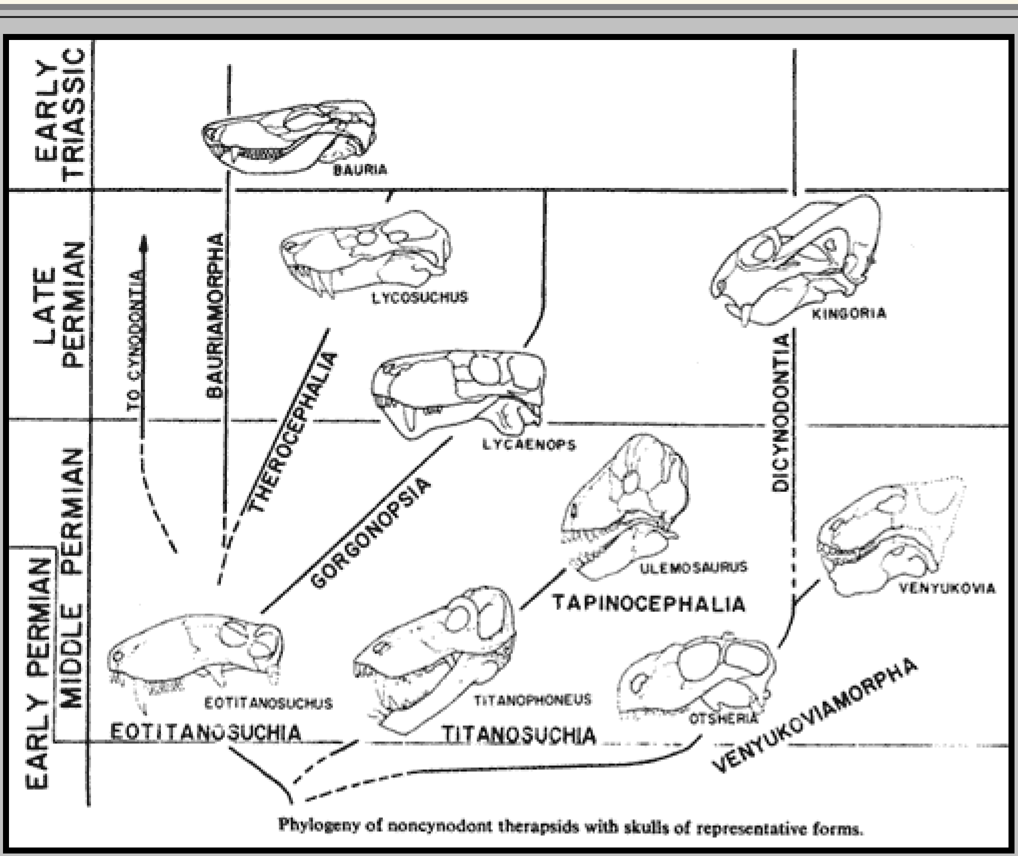
A Quick Introduction



Cynognathus. Early Triassic of South Africa. From Cox *et al*. (1988).

The Therapsida, the basal members of which were traditionally called "mammal-like reptiles" are the advanced synapsids, and include the mammals. The evolutionary Linnaean classification groups the therapsids into several suborders - usually Phthinosuchia/Biarmosuchia, Dinocephalia, Anomodontia, and Theriodontia, this last often subdivided. *See* the unit Dendrogram.

Overall, the story is as follows. Evolving from mid-Permian ancestors similar to *Tetraceratops* (a small synapsid completely unrelated to the well-known dinosaur *Triceratops*), these creatures evolved progressively more mammalian features, first in the disorderly branching of poorly known basal forms like the Biarmosuchia, Phthinosuchia, and Eotitanosuchia. From this basal group the tree developed a threefold branching. The earliest to develop were the somewhat more derived ungainly carnivores, omnivores and herbivores of the Dinocephalian lineages. Following them came two very distinct lines of adaptive evolution, the diverse and successful dicynodonts (Anomodontia), and the very mammal-like theriodonts. Mammals evolved from the later group through the various intermediate stages covered here and in the next two units.



Phylogeny of noncynodont therapsids with skulls of representative forms.

Therapsida. Stratigraphic phylogeny (somewhat different from that discussed here) from Hopson (1969).

The early members of these groups, Dinocephalia, Anomodontia, and Theriodontia are the subject of this Unit. As with so much in nature, it seems to all be about food, at least getting enough food, and processing it better. Quite simply, the three principal radiations within the Therapsida appear to be based on three solutions to the problem of bringing the food-processing surfaces of the upper and lower jaws into closer contact to achieve a more efficient system for subdividing both plant and animal foodstuffs.

The pelycosaurs (basal Synapsida) are known mainly from the Early Permian of North America (with a smattering of European forms); but this is due to accidents of preservation in the fossil record, and possibly also to restriction to the equatorial belt during the Permo-Carboniferous ice ages. Our knowledge of the therapsids is more geographically extensive. Members of all the basic therapsid lineages, apart from the Theriodonta, occur in the earliest therapsid faunas of Russia, *i.e.*, the early Middle Permian Ocher fauna (Wordian Age). It used to be thought that even more primitive fragmentary remains from the slightly earlier San Angelo formation of Texas were also therapsids (Olson, 1962), but it is now known that these remains were misidentified -- these were actually caseids, not therapsids at all.

The fossil remains of the therapsids animals are also represented in the middle and upper Permian deposits of Africa, especially the spectacular Karoo formation of South Africa, from other formations in Russia, the uppermost Permian sediments of China, and from the Triassic of all of these regions. In addition, therapsids have been recovered from Europe, North America, Australia, and Antarctica. Of all the therapsids, only our own lineage, the Cynodontia, survived into the Jurassic. This group is covered in the next Unit. MAK, slightly revised ATW051108.

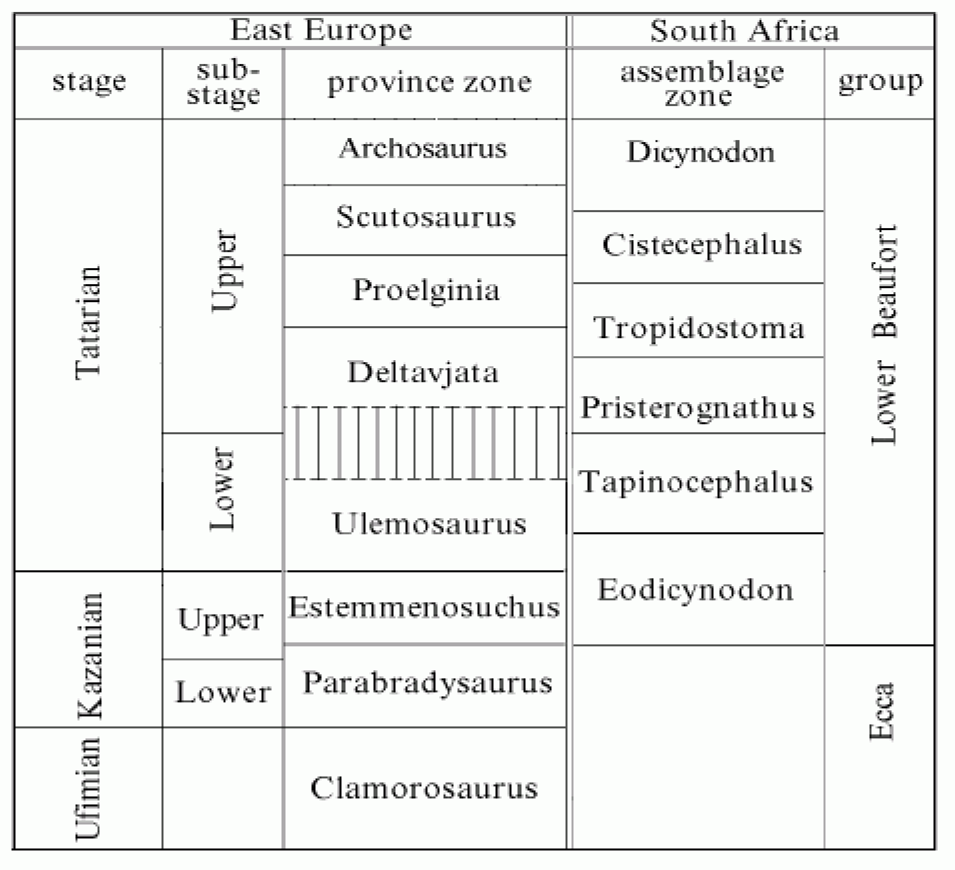
Time: Perm, Praetoria, and the Permian

As any Russian will be happy to tell you, Russia is quite different from the rest of the world; and this is especially true of the Cisuralian region. Here, waves of Indo-Europeans and Ugriks and Slavs and Tatars and Mongols and Germans and others whose very names have been forgotten have thundered like surf across the plains and forests and splintered against the base of the ancient Urals. Here, about 400 km east of Kirov, in the foothills of the Urals, is the city of Perm, which gave its name to the Permian Period. Economically, Perm has been a mining and metals town since the Sixteenth Century. Paleontologically, it is the capital of the northern Therapsida, most famous for its anteosaurs, who, like the various nations of mankind, left their remains scattered from Archangelsk to Orenburg in waves of evolutionary development during the Late Permian.

Historically, South Africa has been rather similar, with successive waves of San, !Kung, Bantu, Zulus, Dutch, English, Indians This is the capital of the southern Therapsida, who likewise left successive ecological assemblage zones in the incomparable deposits of the Karoo.

Unfortunately, Russian and South African idiosyncrasies also extend to matters of Late Permian stratigraphy. The ICS nomenclature adopts the Russian Ages for the earlier parts of the Permian, but things are more confused in later, Zechstein Time. The Russian Tatarian Age, in particular, has been synonymized with everything from the Changhsingian to the entire Zechstein. In South Africa the *Lystrosaurus* Assemblage Zone, starts late in in the Changhsingian and lacks the decency to stop at the Permo-Triassic boundary, as everything else in the world seems to have done. By contrast, the Capitanian, a rather bland time elsewhere, was a time of great faunal turnover in South Africa.

Accordingly, it is necessary to supplement the standard nomenclature as shown below. The ICS has not adopted dates for most of the later Permian Ages, and the literature is remarkably divergent on the equivalences between Russian, South African, and ICS time periods. Therefore, we have adopted the following, somewhat arbitrary equivalences for the terms which are emphasized in the table below (replaced pervious table with this one modified from Ochev 2001 MAK091115). We have generally also followed the lead of Modesto & Rybczynski (2000) for Russia, and Hancox & Rubidge (1997) for South Africa. ATW



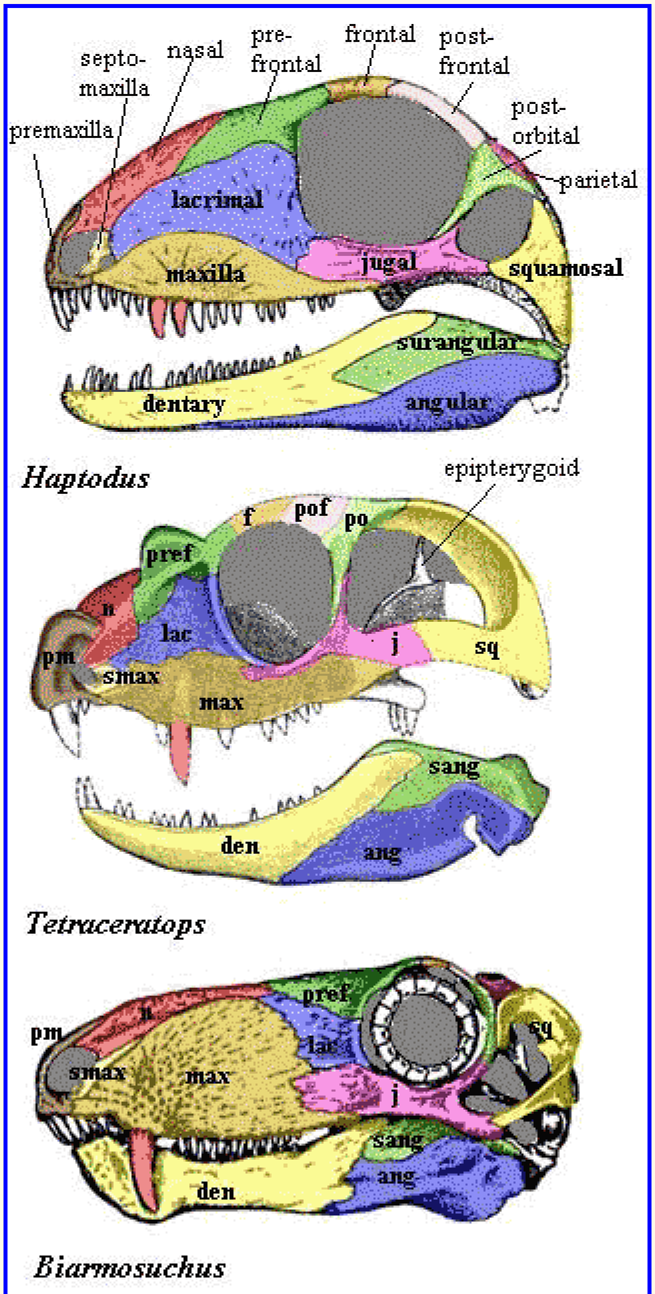
East Europe			South Africa	
stage	sub-stage	province zone	assemblage zone	group
Tatarian	Upper	Archosaurus	Dicynodon	Lower Beaufort
		Scutosaurus	Cistecephalus	
		Proelginia	Tropidostoma	
		Deltavjata	Pristerognathus	
	Lower	Ulemosaurus	Tapinocephalus	
			Eodicynodon	
Kazanian	Upper	Estemmenosuchus		
	Lower	Parabradysaurus		Ecca
Ufimian		Clamorosaurus		

A Profusely Illustrated Guide with Moral Exegesis

Therapsids are difficult stuff. Evidently, some remarkably strange and interesting evolution occurred in the Late Carboniferous or Earliest Permian. At this point we have little or no idea why, but in the relatively brief period of 20 My we go from Bob the Basal Amniote (~300 Mya) to *Tetraceratops* (~280 Mya). We may judge how quick and uneven things were from a few basic facts of time and place. *Oedalops*, the most basal **[1]** synapsid known from more than scraps, was contemporaneous with *Tetraceratops*, the most basal Therapsid known from more than scraps. Not only did they live at about the same time, but they lived within a few hundred kilometers of each other.

A glance at the main entry for Therapsida will quickly demonstrate how much had changed from even advanced pelycosaurs. For many years, in fact, the gap seemed inexplicably large. Then, in the late 1980's, Robert Reisz and his graduate student, Michel Laurin, began re-examining *Tetraceratops* -- a fossil which had been discovered and described as an aberrant eothyrid almost a century ago. The eventual result was Laurin & Reisz (1996). This paper is a real joy to read, like hearing two professional musicians work through a piece they know and understand. The result is smooth, compelling and complete, yet economical and understated. It is solely in an effort to avoid sounding too much like a review of Château Fombrauge, 1995 (a classic Grand Cru Bordeaux from St.-Emilion) that we will reluctantly move on from aesthetics to anatomy.

Although the skull of *Tetraceratops* is not quite complete, it does allow us to compare a series of fairly well known skulls: (1) *Haptodus*, a basal sphenacodontid pelycosaur from the Upper Carboniferous and Lower Permian **[2]**; (2) *Tetraceratops*; and (3) *Biarmosuchus*, as reconstructed by Ivakhnenko (1999). The last requires some explanation. Ivakhnenko synonymizes *Biarmosuchus tener* and *Eotitanosuchus olsoni*. Whether or not his reconstruction corresponds to an actual creature, it at least represents a good morphotype for slightly more derived, but still primitive, therapsids from the Late Permian. Thus, these three reconstructions bracket the critical divide marking the Therapsida from other synapsids.



Skulls of Haptodus, Tetraceratops and Biarmosuchus in left lateral view from Carroll (1988), Lauren & Reisz (1996), and Ivakhnenko (1999), respectively.

1. Marginal Dentition

We can orient ourselves with the canine teeth (in **red**) -- actually caniniforms, since canines are regarded as a specialized tooth form of mammals. In *Haptodus* the canines are not sharply set off from the other dentition. *Haptodus* has several precaniniform teeth on the maxilla, and the postcaniniform teeth form a graded series of decreasing size. *Tetraceratops* may have the therapsid condition of a single canine, although Laurin & Reisz identified a possible replacement pit for a second canine. In any event, there is only a single precaniniform tooth on the maxilla, and the canines are preceded by a marked diastema and succeeded by a series of post-canine teeth which are curved, pointed, but of much smaller size. In *Biarmosuchus*, there is clearly a single canine, very much larger than any other tooth. The post-canine teeth are smaller, uniform, and not markedly recurved. There are *no* pre-canines on the maxilla.

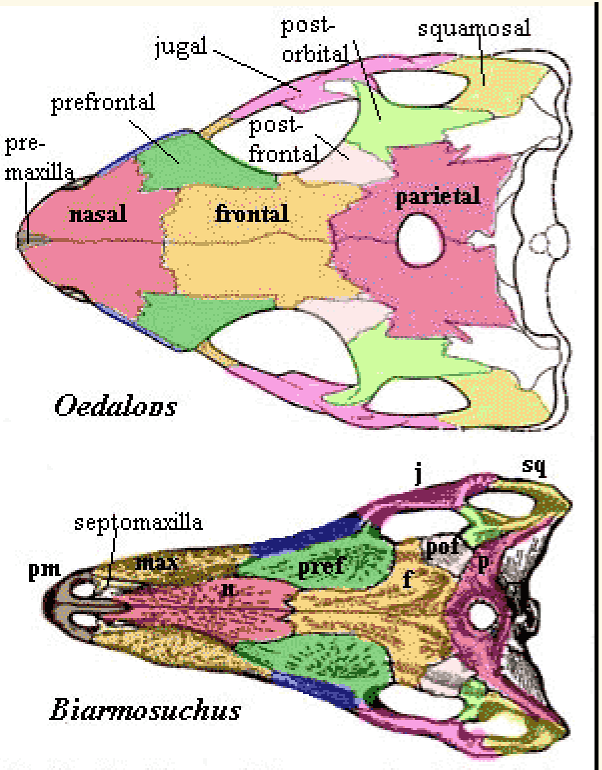
The premaxillary teeth show the same trend toward specialization. In *Haptodus*, the premaxillary teeth are unspecialized and form a graded series in size, increasing anteriorly. *Tetraceratops* has one large pair of premaxillary teeth, but the remainder are small and relatively uniform. *Biarmosuchus* has the mammal-like condition with small, uniform incisor-like teeth. Thus the basic 3-part regionalization of the marginal dentition was complete by the Middle Permian, long before the development of molariform teeth, precise occlusions, or diphyodonty.

2. Lower Jaw

In *Haptodus*, the dentary is already a very large -- perhaps the largest -- element in the lower jaw. Although the dentary does become progressively larger over the course of the Mesozoic, the Permian evolution of the therapsid condition does not seem to involve growth of the dentary so much as a progressive restriction of the angular to the posterior portion of the jaw. Note that the dentaries of *Haptodus*, and even *Oedalops* (Langston [1965]), actually extend *further* onto the dorsal surface of the coronoid process than do the dentaries of the therapsids *Tetraceratops* and *Biarmosuchus*. Similarly, the reflected lamina of the angular is certainly more obvious in *Biarmosuchus* than in *Haptodus*, but does not seem to be an evolutionary novelty of Therapsids.

3. Dermal skull

Just as the dentary comes to dominate the anterior jaw, the maxilla



Skulls of Oedalops and Biarmosuchus in dorsal view, from Langston (1965) and Ivakhnenko (1997).

seems to push other rostral bones to marginal positions. The lacrimal is the most obvious bone on the preorbital skull of *Haptodus*, extending from the orbit to the nares. In *Biarmosuchus*, it is reduced to a peri-orbital element, with the maxilla taking up the space formerly occupied by the anterior portion of the lacrimal.

The dorsal skull of pelycosaurs is made up of a series of blocks forming an arch, as discussed in connection with the Eothyridae. This still seems to be the basic design in *Tetraceratops*, and even *Biarmosuchus*. However, in *Biarmosuchus* and therapsids generally, the premaxilla is added on to the anterior end of the series, somewhat reinforced by the septomaxilla. **[3]**. Perhaps this is related to the development of specialized anterior dentition – the canines and incisors.

By contrast, a great deal is going on in the posterior region, although in this case, there is perhaps less than meets the eye. The posterior skull is poorly preserved in *Tetraceratops* and all specimens of *Biarmosuchus*. However, it is possible make out the main outlines as follows:

(a) A number of elements are lost (the tabular, postparietal and supratemporal). This merely continues a trend noticeable from the earliest Synapsids.

(b) The temporal fenestra tends to increase in size and, somewhat more consistently, to develop surface areas for progressively more external attachment of the jaw adductors.

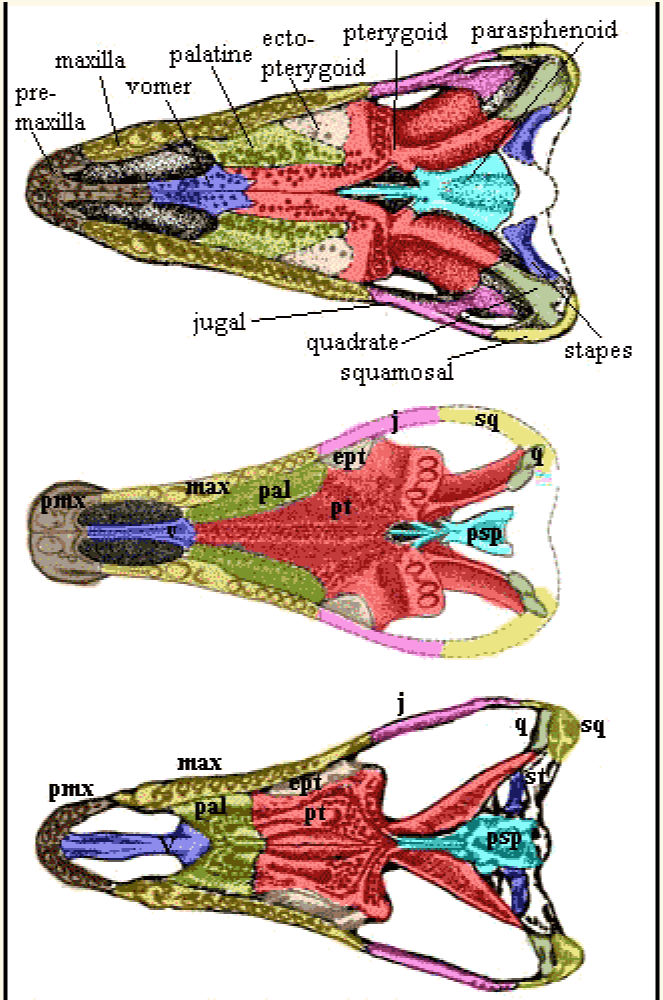
(c) This shift, in turn allowed the braincase (not shown in the figures) to become more firmly attached to the dermal skull.

It is instructive to compare these developments with the evolutionary changes in the diapsid clan. Diapsids generally faced less of an evolutionary bottleneck in solving the fundamental problem of the gnathostomes: how to pack in more and better muscle to drive stronger jaws. Diapsids simply had more room to maneuver, especially since most diapsid taxa have done well with flexible skulls and jaws of relatively light construction. Crocs and sphenadonts are notable exceptions. A high level of skull kinesis seems to be the rule among most other diapsids. By contrast, the synapsids seem, for whatever reason, to have been committed to a rigid skull and jaw. The therapsids solved their mechanical problem by putting an increasing amount of the muscle mass outside the dermal bones, a strategy which absolutely *required* a rigid skull. The transfer of muscle mass outside the skull and the related commitment to a rigid internal framework eventually had the peculiar consequence of allowing the development of larger, better supported brains.

4. The palate

Between *Haptodus* and *Biarmosuchus* the most obvious change is in the dentition. The marginal tooth-bearing surfaces become narrower, the marginal teeth are larger and fewer, and the palatal teeth and denticles gradually disappear. Many other changes appear to be associated with the palate becoming a more vaulted structure with a partial secondary palate. For example, the vomers fuse, broaden slightly, and develop a concave ventral surface. The palatines come to meet medially anterior to a shortened pterygoid. The interpterygoid vacuities disappear. Posteriorly, the palate seems to open up. This is likely an artifact, in part, of the increased space devoted to jaw musculature. However, the difference is so dramatic that one suspects more than that may be involved.

The quadrate and stapes have already begun shrinking at this



Skulls of Haptodus, Tetraceratops and Biarmosuchus in palatal view from Carroll (1988), Lauren & Reisz (1996), and Ivakhnenko (1999), respectively.

point, long before the developments in the jaw bones which would later permit evolution of the mammalian ear. The reduction of the stapes itself is easily explained by the greater integration of the braincase with the dermal bones of the skull. This reduces the importance of the stapes in supporting the braincase ventrally. The reduction of the quadrate is more difficult to understand. One possibility is that the jaw is being supported in part by a sling of soft tissues. Certainly the miniature quadrate of later forms, such as *Probainognathus* (see image), seems hopelessly inadequate to the task of supporting the jaw without some such mechanism.

5. Moral Exegesis

It is important to separate what we see in the evolution *of* the therapsids from what we see of evolution *within* the therapsids. The range considered here -- the smallest bracket we can draw around the origin of the Therapsida -- exhibits some of the long-term trends within the Synapsida, as well some trends continued in the therapsid line. But it does not show all these trends, nor does it show them consistently.

There is, for example, no indication that the size of the temporal fenestra is increasing in any organized way. The dentary is not increasing in size. The dentary *is* changing shape and invading the historic anterior territory of the angular, but note that the dentary actually retreats slightly before the surangular in the passage from *Tetraceratops* to *Biarmosuchus*. Palatal dentition is generally decreasing, but the pterygoid teeth of *Tetraceratops* are bigger than anything that preceded them, and the palatal denticle fields seem denser than in *Haptodus*. The parasphenoid, likewise is proportionately larger in *Biarmosuchus* than in *Tetraceratops*.

Evolutionary trends are an excellent aid to memory. They save tremendous amounts of work in memorizing detail over thousands of species and hundreds of millions of years of time. But evolutionary trends are *post hoc* constructs akin to mnemonics. Like Linnean taxonomy, evolutionary trends are a good means to teach and remember – but ultimately misleading and fundamentally flawed as explanatory tools.

Trends are not, and should never be confused with, teleology, adaptation, or even functionality. For example, within the phylogenetic range of interest, the palatines overgrow the anterior process of the pterygoid, ultimately meeting at the midline and excluding the pterygoid from surface of the anterior palate. But, repeat after me: "This does not mean that the condition of the palatines is (a) moving toward any predetermined mammalian condition, (b) selected for as tending to any optimum condition, or (c) adapting towards a functionally superior state." The first statement is teleological and presumes in advance a master plan or master planner. The second statement makes two assumptions: (1) that mammals (and thus, people) are "optimum" in some moral or functional sense and (2) that later organisms are better adapted than earlier ones. The third statement is perhaps better, but presumes (1) that a condition of the palatines can be determined to be more or less functionally appropriate in a vacuum and (2) that the palatines have a fixed function against which some such judgment can be made. (The interested or unpersuaded reader is referred to **The Palatines** for some counter-examples). Every one of these assumptions *may* represent a true fact. But some of them are beyond the range of science, and the rest are not universal truths and cannot be presumed in any particular case.

Although it is speculative, the better position may be that default presumption ought to be the reverse. That is, absent evidence, we should assume that each character is more or less optimally adapted within the context of (a) the entire assemblage of characters that make up the organism, (b) the ecosystem in which that organism operates and (c) the phylogenetic framework in which that species evolved. That sounds good, but don't we suspect that a single family of modern Texas jackrabbits released into Permian Texas would soon drive every one of these slithering sphenacodonts into phylogenetic oblivion? Maybe. Maybe not. However, that isn't the issue. We study evolution and not science fiction. No *Tetraceratops* could give birth to a rabbit. Evolution moves from x to $x + dx$. The appropriate question is whether, within the range of genetic variation available to *Tetraceratops*, the observed bone structures were at a local optimum for survival.

The high level answers to that question, the "why" or "why not," are probably beyond us at this point. However, it leads us in the right direction, toward issues that can be addressed. What did the palatines do? How do they interact with other elements of the palate? With diet and environment? What does this suggest about the ecology of the animal? What was likely to be the range of genetic variability? By contrast, the comparison of basal therapsids to derived therians leads nowhere. It only tempts us to invoke "trends" under the metaphysical influence of which, like a pantheon of warring godlets, evolution is supposed to take place. ATW010824

6. Important Note Added in Disproof

Conrad & Sidor (2001) have recently re-reanalyzed *Tetraceratops* and argue that it is neither an eothyrid nor a therapsid, but rather a frazzled sphenacodont who happened to get up on the wrong side of its bedding plane. Specifically, they state that "[d]orsal movement of the right side of the skull relative to the left suggests that the previously identified piece of skull roof is actually the zygomatic arc. Elements previously identified as opisthotic, tabular, and postorbital appear to represent the quadratojugal, squamosal, and zygomatic process of the jugal respectively. The supposed reflected lamina is a break in the angular; its orientation is the reverse of the reflected lamina in advanced sphenacodonts." Unfortunately for the discussion above, Conrad & Sidor seem to have a very good point. We are not in a position to (yet again) analyze the mortal remains of *Tetraceratops*. However, as mentioned, *Tetraceratops* lacks several traits we associate with the therapsids. ATW020131

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[1] Most basal, but not earliest. A number of reasonable synapsid specimens are known from the upC. However, *Oedalops* is phylogenetically closest to Bob. The implication is that the transition from Bob to *Tetraceratops* may have taken considerably *less* than 20 My.

[2] Figures from Carroll (1988: 366). The original citation is Currie, PJ (1979), *The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria)*. **Paleontographica, Abt. A** 163: 130-168.

[3] This is the only point at which one might quibble with Laurin & Reisz. The septomaxilla is described as both "small" and "massive." It is said not to have a facial process and figured as having one. This is probably a stylistic, rather than substantive problem. In the nature of things, the septomaxilla is a small bone, although it is perhaps relatively bulky in *Tetraceratops*. The facial process in *Tetraceratops* does not intrude pointedly between the maxilla and nasal in the manner of later therapsids, but rather wanders aimlessly into the face and stops as if confused.

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Therapsida: Phthinosuchidae

Abbreviated Dendrogram

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SYNAPSIDA
|
Therapsida
|--Tetraceratops
|--Raranimus
`--+-?Phthinosuchidae
   |--Biarmosuchia
   `--+--Dinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
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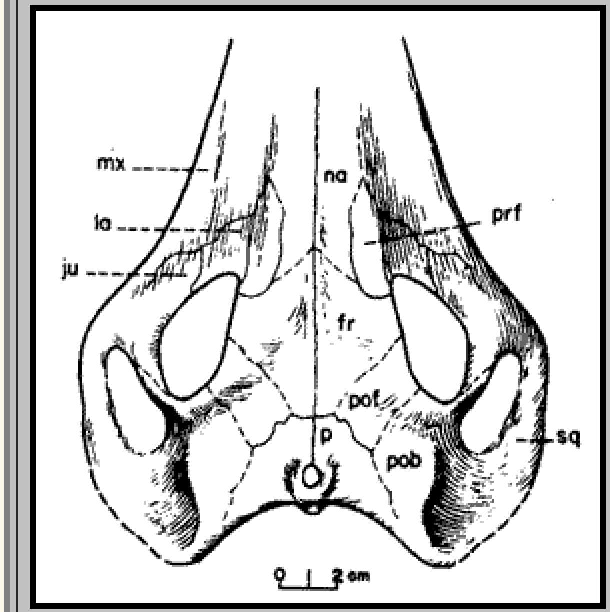
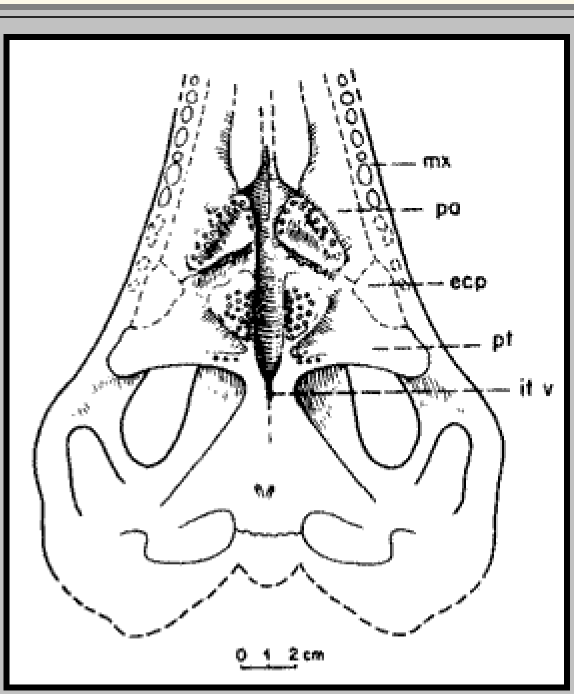
1. Phthinosuchidae X

Phthinosuchus - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

Phthinosuchia: Not Worth Learning to Pronounce!

Under this lugubrious general heading are two very poorly known basal therapsids from the Middle Permian of Russia. They do not seem to be closely related, but in any case are placed (rightly or wrongly) each in their own family. The group





Pthinosuchus discors Efremov 1954. (= *Rhopalodon* sp. Seeley 1894, Watson 1921 and 1942, Nopsca 1928). Uralian Cupric Sandstones, Bashkiry, Western Cisuraly, Russia. Early Tatarian (early Capitanian epoch), Middle Permian.

Skull in dorsal, palatal & left lateral views. Many of the suture lines should not be taken too seriously. Note, *inter alia*, the extreme posterior position of the pineal foramen and absence of any obvious tabular, quadrate, or occipital bones of any kind. The possibility that this scrappy specimen has also undergone very significant deformation should be considered.

"Phthinosuchia" is thus a hodgepodge of a very fragmentary cranium (*Phthinosuchus*), a wastebasket full of dentary fragments, and a few postcrania which may or may not belong to the same animal. All that can be said is that this scrappy material comes for the most part from animals close to the therapsid stem, perhaps related to the Biarmosuchia. It is vanishingly unlikely that these remains represent valid therapsid lineages. Much more material is required if light is to to be shed on the early rich evolutionary radiation of the Middle Permian therapsids.

Of the two taxa, only a single partial skull is known for the **Phthinosuchidae**, and it is the more informative of the two. The front part of the snout is lacking. On the right side, only the imprint of bones remains. Overall it is insufficiently prepared and locally hidden by plaster. It is strikingly similar to that of a sphenacodont, but with larger synapsid openings behind the eyes and more prominent canine teeth. It may be intermediate in structure between the pelycosaurs and the therapsids. No postcranial elements have been attributed to this family. The anterior part of the skull illustrated by Seeley has since been lost. The frequent reproductions of Efremov's reconstruction gives the impression that the skull is a more complete than it really is. The images shown here give a more correct representative than that in many textbooks.

This skull has been described in great detail by Tataranov (1974). Even though it is compressed laterally it must have been high and narrow (dare we say it, phthin?), with a convex dorsal profile and a temporal fossa that is higher than wide. The snout was probably high and short. The skull roof is relatively narrow at the level of the large orbits and wide at the level of the temporal fossae. The pineal foramen is marked by a large protruberance and situated near the posterior limit of the cranial roof. The lacrimal is short. Frontal participates broadly in the orbit. The postorbital and temporal arches are thin; the occiput is high and slightly inclined ventro-anteriorly. The mandible is slender, and the dentary does not seem to extend dorsally beyond the level of the surangular. There exist a large number of postcanine teeth. The occiput, from what little one can tell, was wide and high. The mandible was very slender.

This specimen has been described at length a number of times, e.g. by the Russian palaeontologists Efremov in 1954 and Tatarinov in 1974. It was said to be related to the Anteosauria or carnivorous dinocephalians by earlier researchers, such as Seeley and Watson. Nopcsa in 1928 classified it in the gorgonopsians, and was followed in this by Efremov and by Romer. But no gorgonopsian specializations are found, apart from some shared primitive characteristics. Romer, noting the absence of gorgonopsian specializations, used *Phthinosuchus* to erect the infraorder "Phthinosuchia." Although Carroll (1988) includes the suborder "Phthinosuchia" in his genus list, there is simply no phylogenetic basis for this taxon.

Other *Phthinosuchus* characters are less suggestive of gorgonopsids than of anteosaurs. For example, the proportions of the skull roof are anteosaurian. However, other anteosaur specializations are absent, such as the narrow intertemporal skull found in the contemporary *Archaeosyodon*. There is a median suture on the underside (ventral), rather like in *Eotitanosuchus*. But in all respects, in view of the incomplete state of the specimen and absence of the posteranial skeleton, it is impossible to determine much about its actual relationships with other therapsids.

The other "Phthinosuchian" is *Pthinosaurus*, and is erected on an even less convincing specimen, a partial lower jaw. About this uninformative. vaguely rectangular object, perhaps the less said the better. Two dentary fragments, a scapula, ulna, and an angular, from the same locality have also been referred to this species. However, we have no information about the basis for this referral and respectfully decline to further perpetuate this mythical taxon. MAK000802, ATW020518.

Phthinosuchidae: *Phthinosuchus.*

Range: Late Permian of Russia.

Phylogeny: Therapsida **::** (Biarmosuchia + (Eotitanosuchia + Eutherapsida)) + *.

Characters: 1-2m?; lower jaw slender; coronoid process absent; small temporal fenestra only slightly larger than orbit; slight thickening of dorsal border of orbit; lower jaw articulation displaced anteriorly; occiput saod to be slightly slanted forward dorsally.

Links: Lecture 03 - Cont. Drift (odd taxonomy); paleng2_0p189abs; Notes From Other Vertebrates; therapsid2c; RÉPTEIS SINÁPSIDAS (Spanish).

References: Battail & Surkov (2000).

Note: Not intended to include *Phthinosaurus*. The type and referred fragments called *Phthinosaurus* are sometimes united with Phthinosuchidae in "Phthinosuchia." There is nothing that suggests that this is a clade. In addition, the material of *Phthinosaurus* is below the (admittedly subjective) scrappiness threshold for inclusion in these Notes. ATW011206.

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Therapsida: Biarmosuchia

Abbreviated Dendrogram

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SYNAPSIDA
|
THERAPSIDA
`-Raranimus
  |--Biarmosuchia
  |  |--Biarmosuchidae
  |  `--Ictidorhinidae
  |     `--Burnetiamorpha
  `-+--Eotitanosuchia
    `-Eutherapsida
      |--Dinocephalia
      |  |--Anteosauria
      |  `--Tapinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
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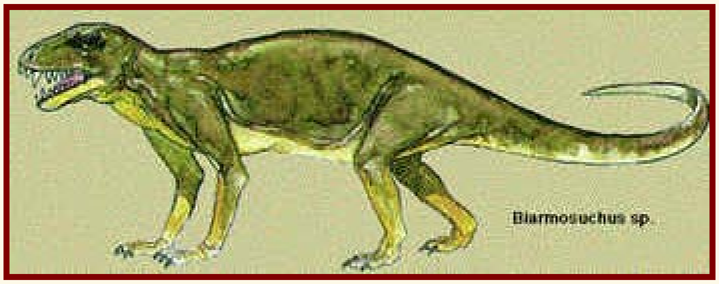
Biarmosuchus - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

Biarmosuchia: Stem Therapsida?



The term "**Biarmosuchia**" is a more or less artificial term used to unite a number of primitive and little-known basal (ancestral) therapsids from the Middle and Late Permian period. These forms are intermediate in both morphological development and geologic age between the Sphenacodontidae (and the proto-therapsid *Tetraceratops*) and more derived therapsids. Biarmosuchia currently contains the Russian forms (Biarmosuchidae) and the South African forms (Ictidorhinidae and Burnetidae), which may or may not form a monophyletic group Accordingly, this is not a clade but an organizational grade (a "horizontal" taxon). Nevertheless, the group has enough similarity -- largely through shared primitive characteristics -- to be a useful paraphyletic group for didactic purposes, if nothing else. This very problematic group is currently being considered for review by South African therapsid specialist Bruce Rubidge. For what relevance it may have, the authors of this site find themselves taking the opposite of their usual views, with ATW suspecting monophyly and MAK asserting paraphyly. The weight of scientific opinion probably favors the view that the Biarmosuchia are probably just the stem line of therapsids, not a clade.

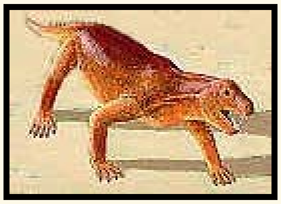
Basically, the Biarmosuchia are moderately sized, lightly built carnivores, appearing somewhat more modern and athletic than sphenacodontids. The skull is very similar to a sphenacodont skull; however, it shows a more derived condition in the large temporal openings, in the depression of the jaw articulation, and in the presence of single large canine teeth in both upper and lower jaws. The larger, more completely differentiated canines are backed by the increased mass (and hence power) of the jaw-closing muscles, as indicated by the flaring of the rear part of the skull where these muscles were attached. The primitively movable braincase was fused to the palate so that the entire skull formed a single sturdy unit.

The post-cranial skeleton also seems to show changes from the "pelycosaur" condition. Although the vertebrae of an animal like *Biarmosuchus* resemble those of sphenacodontids (but absent the long neural spines) the structures of the shoulder and pelvic girdles and the limbs indicate a rather more derived posture. The feet are more symmetrical, indicating that they faced more directly forward throughout the stride, and the number of joints and length of some phalanges (toes) is greatly reduced, indicating a condition more like that of later therapsids, including mammals.

Nevertheless, these were primitive animals, close to the therapsid ancestral stem. Relative to later Therapsida, the temporal (synapsid) opening just behind the eye socket is small. This means there is less room for the attachment of muscle that closes the lower jaw. In more advanced therapsids, the temporal opening is larger, thus enabling a large suite of muscles, and a more powerful and versatile bite. MAK000802.

The best known species is the Russian **biarmosuchid**, *Biarmosuchus tener* Chudinov 1960 from the Late Permian, Zone I (Ocher Faunal Assemblage), Upper Kazanian, Ezhovo, Ocher locality, Fore-Urals, Perm Region.

Biarmosuchus was about the size of a large dog (skull length 15 cm (immature) to 21 cm, with an overall length of about 2 meters. This genus is abundantly represented, but most of the specimens remain inadequately prepared and have not been used for an anatomical and functional analysis. Such details as the configuration of the palatines are unknown, as well as numerous characteristics of the postcranial skeleton. It may be that several taxa are represented, but in the present state of our knowledge, it is not possible to define them. *Biarmosaurus antecessor* is based on a larger (206 mm as opposed to 153 mm) skull than the holotype, representing a mature individual. This animal is similar in size to *Phthinosuchus*, but opinions differ as to how distinct the two forms are. The large size of the orbit (eye socket) constitutes the most notable difference. For a long time *Biarmosuchus* was placed in the same family as *Eotitanosuchus*, but it is now believed the two forms appear to be quite distinct (see however Ivakhnenko (1999) for an opposing opinion). *Biarmosuchus* would seem to represent one of the most primitive of the Biarmosuchia, and could be taken as a good generalized model for the other, mostly later, forms. In 1999, *Biarmosuchus tchudinovi*, a new species, was described by Ivakhnenko from the Sokol locality, Udmurtia, Russia. MAK000801.



Similar, but perhaps more derived forms are known from the Late Permian of South Africa under the family names of **Ictidorhinidae**, Burnetidae and Hipposauridae. An attempted life reconstruction of *Hipposaurus* is shown at right. At the moment, we can draw few conclusions other than that the basal Therapsida were widely dispersed and so similar overall, that their monophyly is unquestionable.

Eotitanosuchia

The **Eotitanosuchia** were large (skull length 45 cm, overall length perhaps 2.5 meters) to very large (possibly up to 6 meters long, weights of up to 500 kg or more, assuming a very large jaw fragment belongs to this group and is proportional) predatory therapsids of the middle Permian (Wordian epoch). Like the Biarmosuchidae they are rather poorly known, although they were probably more common than their few remains indicate. They seem to be more advanced than the Biarmosuchia in that the temporal opening behind the eye socket, although small, is still somewhat larger than the biarmosuchians, being expanded in the upper rear (posterodorsal) margin, allowing the area of attachment of the adductor (jaw closing) muscles to be visible from the dorsal (top) view looking down. The eotitanosuchian bite was stronger and more efficient than the biarmosuchian bite.

For this reason, some paleontologists see the eotitanosuchids as transitional between the biarmosuchians and higher therapsids. They may indeed be so, but it is just as - if not more - likely that features of a larger temporal opening and hence increased muscle mass and biting power evolved simultaneously, among a number of early therapsid groups, due to the obvious advantages this adaptation conferred. One must be wary in applying cladistic methodology to characteristics that are likely to evolve simultaneously among many competing lineages. It is interesting that in other respects the eotitanosuchians are quite primitive -- they were the least modified in their jaw apparatus from their sphenacodont ancestry.

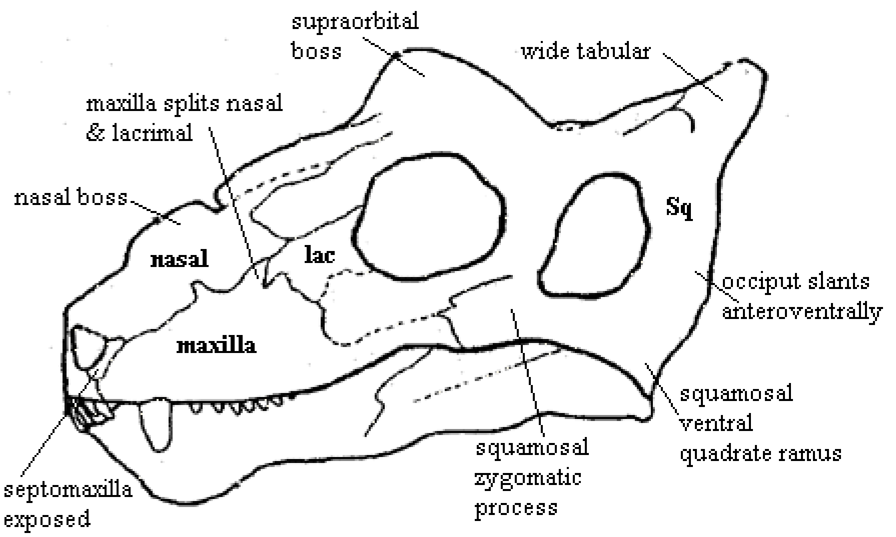
Eotitanosuchus is often grouped with the Phthinosuchidae and the Biarmosuchidae. In fact, Ivakhnenko (1999) argues that *Biarmosuchus tener* and *Eotitanosuchus olsoni* are the same organism, which would eliminate the Eotitanosuchia as a separate taxon This conclusion does not seem to have been widely accepted. Regardless of the eventual outcome of this debate, Ivakhnenko's paper does seem to show that *Eotitanosuchus* is very similar to *Biarmosuchus*. Further, given the rather close similarity between *Eotitanosuchus* and later therapsids, this observation supports the view that Biarmosuchia is paraphyletic. Others view *Eotitanosuchus* as quite distinct from other basal therapsids and perhaps closer to the Gorgonopsia. But gorgonopsian specializations are either not present in Eotitanosuchus or, as is more often the case, the state of the characters is unknown. This genus is characterized by many primitive features of the septomaxilla, the postorbital, the parietal, the interparietal, the basioccipital, the quadrate rami of the pterygoid and the vomers of the skull. The length of the dorsal process of the premaxilla (front jawbone) and the postorbital twisting (rear side of the skull) constitute specializations that indicate it is not a direct gorgonopsian ancestor. These features however are shared by the anteosaur and biarmosuchid lineages. MAK000808. ATW010819.

Biarmosuchia: *Burnetia*, *Hipposaurus*, *Ictidorhinus*, *Niuksenitia*, *Proburnetia*.

Range: Late Permian of Russia & South Africa. Gondwanan origin [RS01].

Phylogeny: Therapsida::: (Eotitanosuchia + Eutherapsida) + *: Biarmosuchidae + Ictidorhinidae.

Characters: Skull similar to sphenacodonts; generally light construction without thickened bones [I99]; skull with numerous protuberances and horn-like outgrowths [RS01]; septomaxilla broadly exposed on surface; maxilla separates lacrimals and nasals; retains parietal foramen with raised edge; wide tabular; **$** orbits greatly enlarged [BS00]; (slightly) enlarged temporal fenestra; broad, concave shelf on the upper margin of the temporal fenestra; supratemporal absent; temporal jaw muscles probably still confined to interior of skull; quadrate reduced; **$** squamosal with elongate zygomatic process extending under orbit [RS01]; **$** squamosal with long ventral quadrate ramus [RS01]; occiput plate-like, slanted so that top of skull overhangs bottom (opposite of pelycosaurs) [RS01]; occiput strongly attached to braincase; braincase attached firmly to cheek; stapes large, transverse; **$** dentary with marked difference in height between canine & postcanine regions [RS01]; reflected lamina of angular with ridges radiating from a common center; epipterygoid excluded from the basicranial articulation; vomers partially fused and extend below palatines; other palatal elements arched; shortened interpterygoid vacuity; pterygoid with postero-median flange; very large canine teeth; **$** postcanine teeth with basal swelling & coarsely serrated margins [BS00]; some teeth retained on transverse flange of pterygoid; ectopterygoid teeth absent; glenoid and acetabulum open ventrally (more erect posture and mobile limb); **$?** cervical vertebrae elongated [RS01]; scapular blade narrow; clavicle & interclavicle retained; **$** distal carpals 4 & 5 fused [BS00]; pelvic girdle otherwise plate-like and primitive; humerus primitive, with both ends widely expanded; femur more slender, sigmoid, with inturned femoral head; **$** distal tarsals 4&5 fused [RS01]; phalanges small and of more equal length (probably faced forward).



Proburnetia skull in anterolateral view. From Barghusen & Sidor (2001).

Links: stars.

References: Battail & Surkov (2000) [BS00]; Ivakhnenko (1999) [I99], Rubidge & Sidor (2001) [RS01].

Image: *Biarmosuchus tener* from Gondwana Studios.

Note: **[1]** It is often asserted that Biarmosuchia is paraphyletic, i.e. synonymous with Therapsida. **[2]** See also note and figure under Eotitanosuchia. ATW010817.

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checked ATW031025; last modified MAK091111

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Therapsida: Biarmosuchia: Biarmosuchidae / Eotitanosuchidae

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
`-Raranimus
  |--Biarmosuchia
  |  |--Biarmosuchidae
  |  `--Ictidorhinidae
  |     `--Burnetiamorpha
  `-+--Eotitanosuchia
    `-Eutherapsida
      |--Dinocephalia
      |  |--Anteosauria
      |  `--Tapinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
```

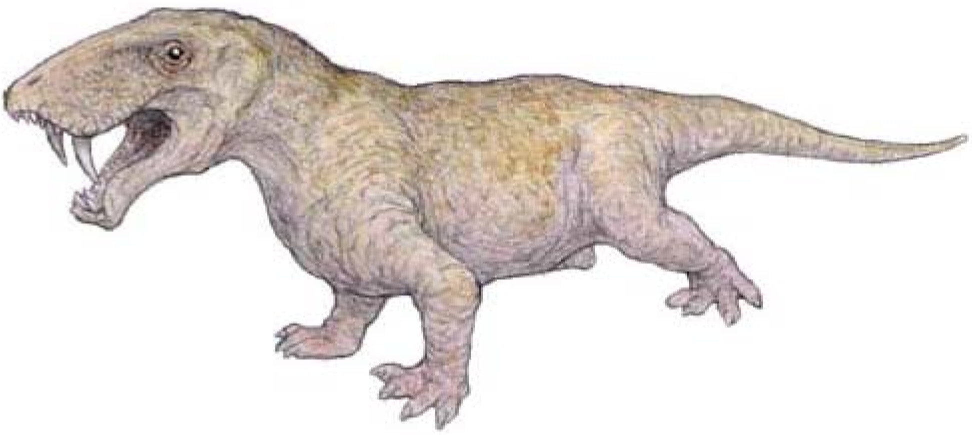
Contents

Taxa on This Page

1. Biarmosuchidae X
2. *Biarmosuchus* X
3. Eotitanosuchia X
4. *Eotitanosuchus* X
5. *Ivantosaurus* X
6. *Kamagorgon* X

Biarmosuchia: Biarmosuchidae / Eotitanosuchidae

Ivantosaurus ensifer - the largest carnivore of the Permian period
life reconstruction artwork by Dmitry Bogdanov - Wikipedia

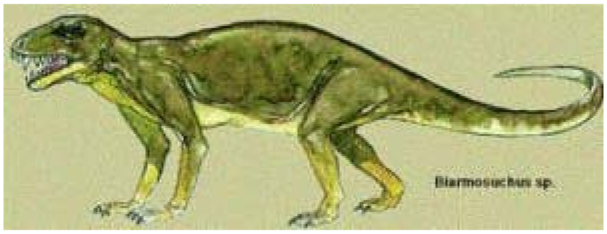


Eotitanosuchus - illustration copyright © Satoshi Kawasaki

Suborder	"Biarmosuchia"		
Family	Eotitanosuchidae (=Biarmosuchidae)		
Species	***Biarmosuchus tener*** *Chudinov 1960*	***Eotitanosuchus olsoni*** *Chudinov 1960*	***Ivantosaurus ensifer*** *Chudinov 1983*
Horizon:	Upper Kazanian or Lower Tartarian		
Locality:	Echovo locality, Ocher Province, Perm Region, Russia		
Possible age:	Late Roadian/early Wordian		
Length (skull):	15 cm (immature) to 21 cm	35 cm	about a meter?
Length (total):	1.5 meters	c. 2.5 meters	over 6 meters?
Size:	large dog		large bull

Diet:	small tetrapods	tetrapods	large tetrapods

Eotitanosuchus attacks *Estemmenosuchus*; illustration © Seiji Yamamoto



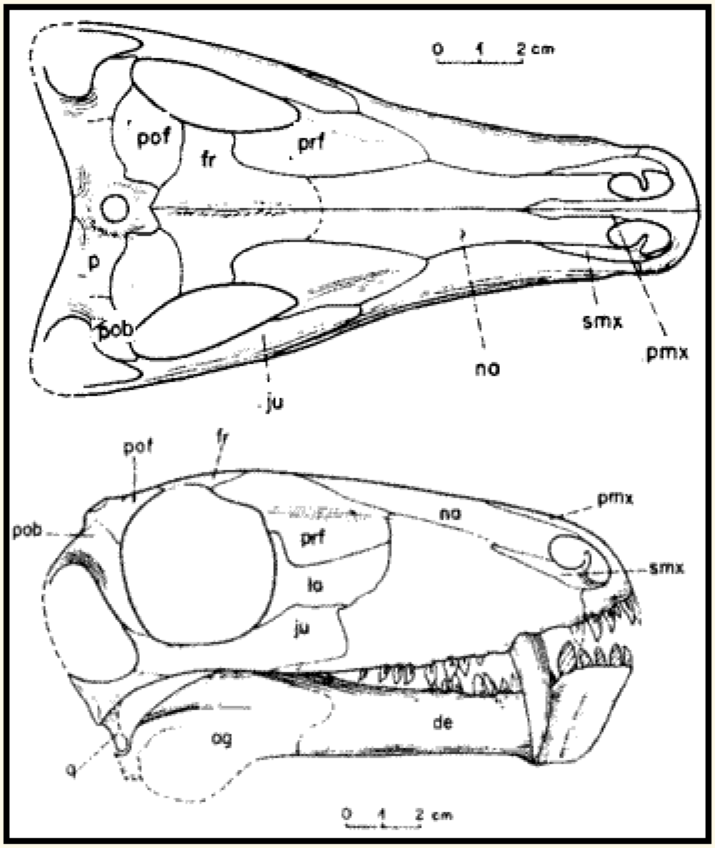
Biarmosuchus; authorship of this illustration unknown

Comments: The Eotitanosuchids constitute an important element of the Kazanian fauna; representing a good ancestral type that other, more advanced, therapsids would have evolved from. They are thought to have been semi-aquatic. Three monospecific genera - *Biarmosuchus*, *Eotitanosuchus*, and *Ivantosaurus* - are known from the Ocher locality, differing dramatically in size. Ivakhnenko 1999 argues that these represent different growth stages of the same animal (Ivakhnenko 1999). Personally I think it is more likely that these represent three different but closely related forms (belonging to the same family, perhaps even the same genus), representing different predator size guilds, with the smallest (*Biarmosuchus*) being the most common, and - in keeping with the nature of trophic webs - the largest, *Ivantosaurus*, being the rarest (it is known only from a fragment of maxilla that includes a very large canine tooth). Regardless of whether these are related but distinct species, or growth stages of the same species, it seems that these two forms are more similar than have usually been acknowledged. Thus the illustrations here can equally apply to all three.

Biarmosuchus, known from two skulls and postcrania, was a medium-sized predator, similar in size to a large dog. It was a lightly built, probably agile animal that would have fed on smaller tetrapods. Their legs are quite long, and the animals were probably quite agile in spite of their size.

Eotitanosuchus known from a single large skull without a lower jaw, was without doubt a dominant animal of its environment. Found preserved in flood deposits (once coastal bogs) containing many skeletons of estemmenosuchids, it has been suggested that this large predator was an excellent swimmer, possibly semi-aquatic or frequenting marshy ground. This however is just speculation. The name means "Dawn giant crocodile", which is a bit misleading because although a large preditor it was not huge. A catalogue of a Russian dinosaur exhibition (Vickers-Rich and Rich, 1993) states that the oft-illustratred skull (about 35 cm long) is from a juvenile, an adult has a skull about 1 meter long. I have not found any other information on this, apart from the reference to the eotitanosuchid *Ivantosaurus ensifer*, known from a jaw fragment from the same locality (Sigogneau-Russell 1989 pp.29-30). So It seems what is being stated here is Ivakhnenko's thesis that this is the adult form of *Eotitanosuchus*/*Biarmosuchus*. It is just as likely that this was a distinct animal, and that these were three related forms of different sizes. In any case, assuming that the rest of the creature was in proportion, *Ivantosaurus* would have been the largest carnivorous therapsid known, exceeding in size even the largest Late Wordian/early Capitanian anteosaurs.
References: Sigogneau-Russell 1989, Ivakhnenko, 1999, Vickers-Rich and Rich, 1993
(revised MAK091114, 120127)

Biarmosuchidae: *Biarmosuchus*



Range: Middle Permian of Russia

Phylogeny: Biarmosuchia: Ictidorhinidae + *.

Characters: Long dorsal process of premaxilla [S89]; very narrow interorbital roof (?!) [S89]; short lateral postorbital bone, not reaching the level of the ventral border of the orbit [S89]; paroccipital process reaches quadrate [S89]; parasphenoid keeled ventrally [S89]; long palatal dentigerous tuberosities [S89]; mandibular symphysis not sloping [S89]; incisors perhaps without a heel(?) [S89]; short cervical vertebrae, but longer than dorsals, and with a ventral keel [S89]; long neural apophyses [S89]; slightly divergent zygapophyses [S89]; interclavicle very wide anteriorly [S89]; humerus with feeble torsion and with entepicondylar foramen [S89]; humerus wide distally [S89]; ilia widen only slightly anteriorly (means ilia diverge slightly? bones transversely broader? or what?) [S89]; pubis very strongly developed [S89]; slender limbs [S89]; phalangeal formula 23454 [S89].

Links: Gondwana Studios; Lecture 03 - Cont. Drift (but where is he getting this information?); synapsurv.PDF; THE FOSSIL RECORD; therapsid3a.

References: Sigogneau-Russell (1989) [S89]. ATW030224.

Eotitanosuchia: *Eotitanosuchus, Ivantosaurus, Kamagorgon*.

Range: Middle Permian ((Late Roadian/early Wordian).) of Russia.

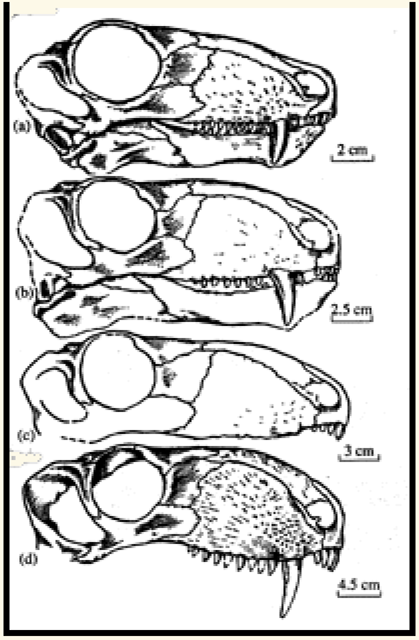
Phylogeny: Therapsida::::: Eutherapsida + *.

Characters: Large (2.5 meters (possibly upto 6m?), carnivorous forms; incisors & postcanines small; canines very large; no precanines; vomers incompletely fused; pterygoid narrow posterior to transverse flanges, with quadrate rami almost parallel; interpterygoid vacuities small; dorsal process of premaxilla elongated; maxilla reaches maximum height in posterior; some pachyostosis of upper orbital rim; postorbital bar slightly twisted; **$** temporal fenestra larger than biarmosuchids, with expanded (& thickened?) posterodorsal margin for origin of jaw adductors visible in dorsal view (H&B); lack moveable quadrate; paroccipital process contacts quadrate.

Until recently only two genera -- each of one species, are recorded -- *Eotitanosuchus* and *Ivantosaurus*. The latter is known from only two jaw fragments, and seem to be very similar to *Eotitanosuchus*. Tatarinov (1999) has recently described a new species and genus of eotitanosuchian.

Genus *Eotitanosuchus* Chudinov 1960
Type species: *E. olsoni* Chudinov 1960
Diagnosis: Snout long and high; orbit large; interorbital roof narrow; occiput high; step in the alveolar border (?); lacrimal high and long; vomers fusing (= partially fused?).

Eotitanosuchus olsoni Chudinov 1960
Locality: Echovo locality, Ocher Province, Perm Region, eastern European Russia
Age: Upper Kazanian, Middle Permian (Late Roadian/early Wordian)..
Size: skull: 35 cm, overall length may have been over 2 meters



The holotype is a crushed and deformed skull. Additional skull and skeletal material is known. There are 8 or 9 small and flattened postcanines in the jaw. *Eotitanosuchus* is found preserved in flood deposits (once coastal bogs) containing many skeletons of estemmenosuchids.

Ivantosaurus ensifer Chudinov 1983 **? = *Eotitanosuchus ensifer*** (Chudinov)
Locality: Echovo locality, Ocher Province, Perm Region, eastern European Russia
Age Upper Kazanian, (Late Roadian/early Wordian).
Holotype and only known material, maxilla and quadrate found in association and in their respective natural positions.

Either a giant individual of *Eotitanosuchus* (if *E. olsoni* is a juvenile this would therefore be a large adult), or, perhaps more likely, a distinct species. This is a very large animal (length would have been around 6 meters). Maxilla short and high. Two upper canines, long, and with their axes inclined forward. It is not clear if one of the canines is a replacement tooth. Sigogneau-Russell (1989) seems to think this is unlikely, which would make this a quite different animal from *Eotitanosuchus*. As with the therocephalian "family" Lycosuchidae, these may simply be replacement canines. There are few known animals, living or extinct, with two sets of canines (it would be a very inefficient chewing mechanism)

Kamagorgon ulanovi Tatarinov 1999
Locality: Sokol locality, Udmurtia, Western part of the Middle Urals, Perm region, Russia
Age Upper Kazanian (Late Roadian/early Wordian)..
material: Based on an incomplete skull

The snout is relatively short, the canines are massive and long, the parietals are thickened, and the mandibular symphysis is extremely high. The palatal teeth cover the pterygoids and palatines and are not concentrated on special bony tubercles.

Links: Eotitanosuchus; Stars of the Show (A to I); therapsid3a; Paleontology and Geology Glossary: E.

References: Battail & Surkov (2000); Hopson & Barghusen (1986); Ivakhnenko (1999); Sigogneau-Russell (1989); Tatarinov (1999).

Image: Three specimens of *Biarmosuchus tener* (a-c) compared to *Eotitanosuchus olsoni* (d) as reconstructed by Ivakhnenko (1999). ATW020727; MAK000808.

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checked ATW031025; last modified MAK120127

Therapsida: Biarmosuchia: Ictidorhinidae / Hipposauridae

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
`-Raranimus
  |--Biarmosuchia
  |  |--Biarmosuchidae
  |  `--Ictidorhinidae
  |     `--Burnetiamorpha
  `-+--Eotitanosuchia
    `-Eutherapsida
      |--Dinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
```

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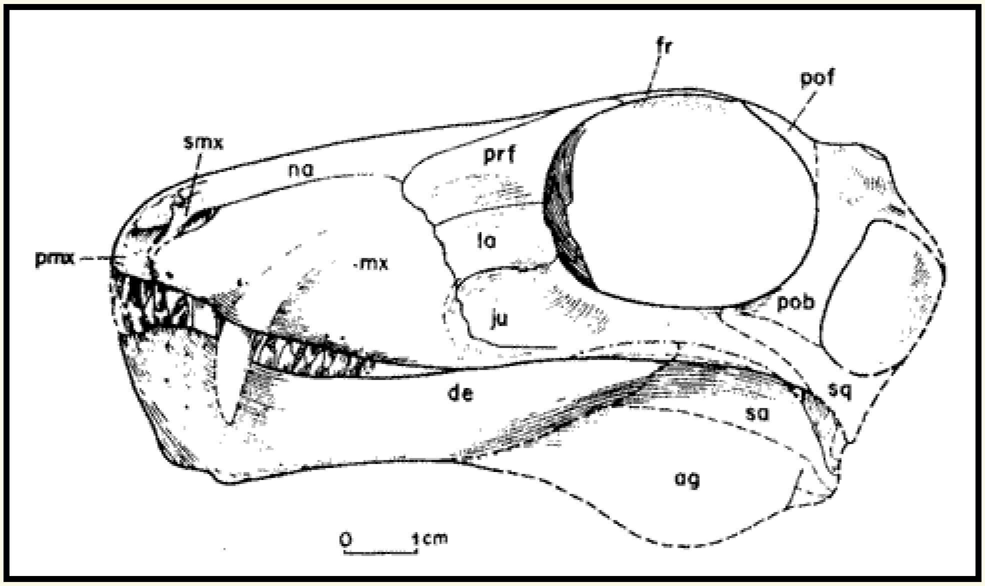
1. Ictidorhinidae X

Biarmosuchia: Ictidorhinidae / Hipposauridae

Ictidorhinus - Dicynodon zone, South Africa. This little animal (skull length about 5 cm) was among the last of the Biarmosuchia. Life reconstruction artwork by Smokeybjb - Wikipedia

Apologies for the paucity of material; more will be added to this page in due course....



Ictidorhinidae: (= Hipposauridae) *Hipposaurus, Ictidorhinus, Lycaenodon, Pseudhipposaurus, Rubidgina.*

Range: Late Permian of South Africa

Phylogeny: Biarmosuchia: Biarmosuchidae + * ::: Burnetiamorpha

Characters: "incipient" heeled incisors?

Comment: a paraphyletic group according to the cladogram given by Sidor & Welman 2003 pp.639

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Therapsida: Biarmosuchia: Burnetiamorpha

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
`-Raranimus
  |--Biarmosuchia
  |  |--Biarmosuchidae
  |  `--Ictidorhinidae
  |     `--Burnetiamorpha
  |     `--Burnetiamorpha
  |        |--Lemurosaurus
  |        `--Burnetiidae
  `-+--Eotitanosuchia
    `-Eutherapsida
      |--Dinocephalia
      |  |--Anteosauria
      |  `--Tapinocephalia
      `--+--Anomodontia
         |  |--Venyukovioidea
         |  `--Dicynodontia
         `--Theriodontia
            |--Gorgonopsia
            `--+--Therocephalia
               `--CYNODONTIA
```

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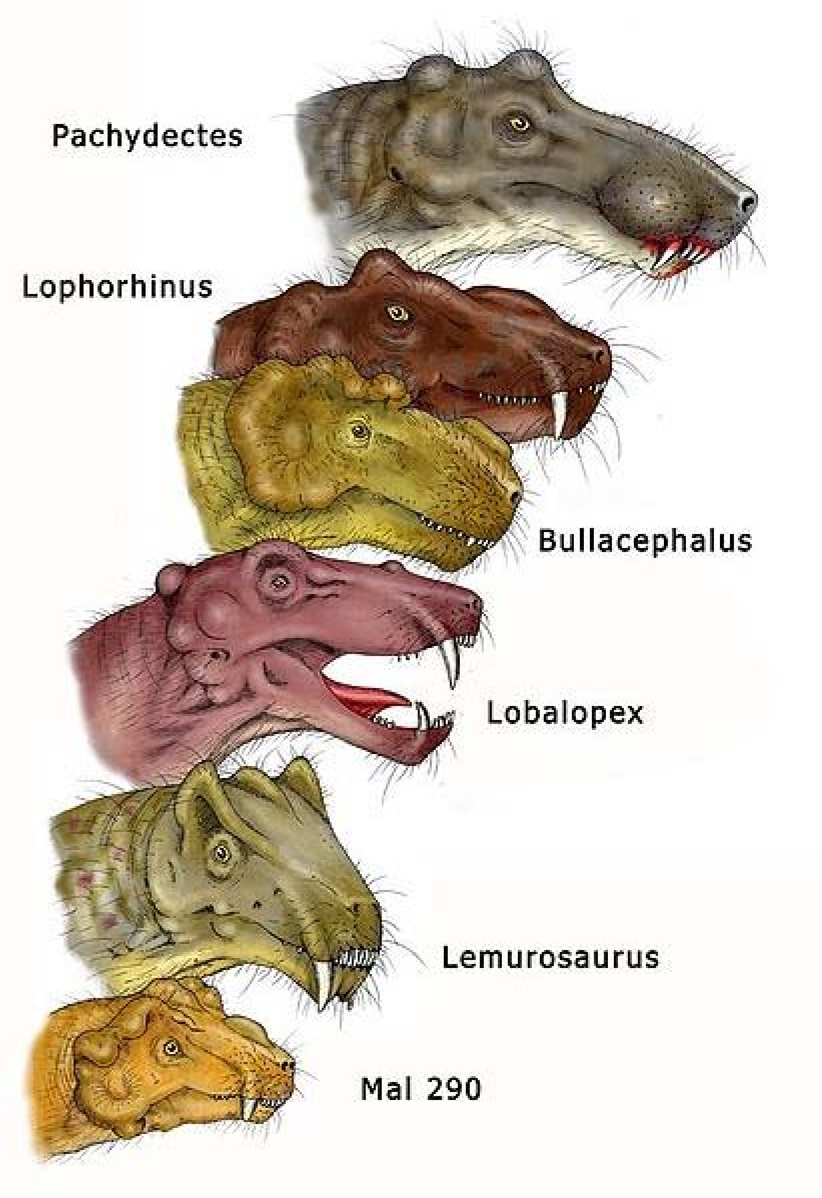
1. Burnetiamorpha X
2. Burnetiidae X
3. Lemurosaurus X

Burnetiamorpha



Burnetiamorpha - artwork by Mojcaj - Wikipedia

More text to be added (eventually)...

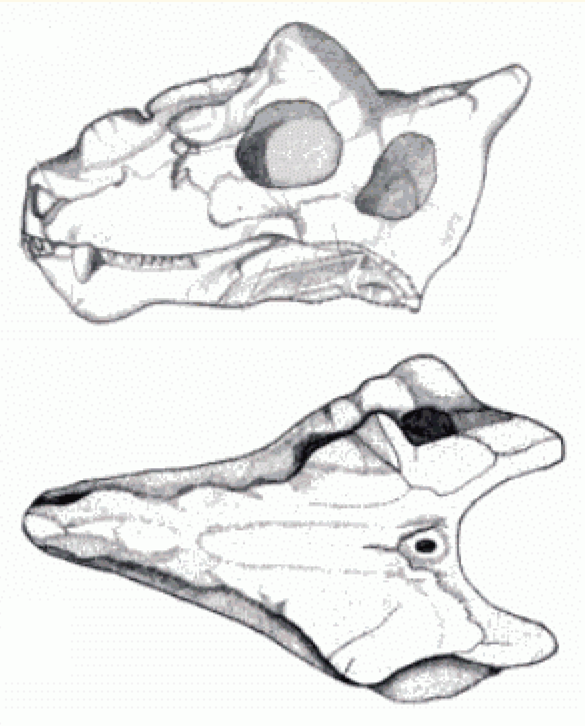
Burnetiamorpha: *Bullacephalus, Burnetia, Lemurosaurus, Proburnetia* etc

Range: Middle to Late Permian of South Africa

Phylogeny: Biarmosuchia: Ictidorhinidae ::: * : *Lemurosaurus* + Burnetiidae

Characters: Distinguished by three sets of bony bosses (hornlets): supraorbital (above eyes), on ventral surface of squamosal lateral to level of quadrate, and on lower margin of zygomatic arch at level of postorbital bar (cheek); pit on lateral surface of lacrimal; median frontal ridge, which varies in shape (Sidor & Welman 2003 p.632). These bony decorations can be seen in the drawing of the skull (right)

Illustration: (right) *Proburnetia viatkinenses* in lateral (top) and dorsal (bottom) views, showing bony bosses and ridges - from



Rubidge and Sidor 2002, via Kemp 2005 p.32

References: Sidor & Welman 2003, Jacobs *et. al.* 2005. MAK091111.

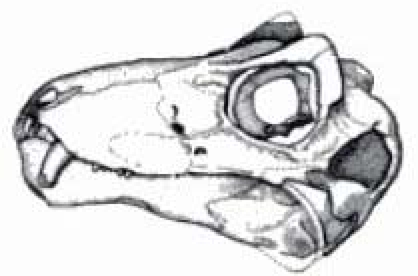
Burnetiidae: *Bullacephalus, Burnetia, Proburnetia*

Range: Middle to Late Permian of South Africa and Russia (*Niuksenitia sukhonense*)

Phylogeny: Burnetiamorpha: *Lemurosaurus* + *

Links: Burnetiidae - Wikipedia (stubby)

References: Sidor & Welman 2003 pp.638-9. MAK091111.



Lemurosaurus: *Lemurosaurus pricei* Broom 1949

Range: Late Permian (Wuchiapingian) of South Africa

Phylogeny: Burnetiamorpha: Burnetiidae + *

Characters: A primitive, unspecialised form. Small boss at dorsal apex of lateral temporal fenestra; low, ridge-like frontal crest; very coarse serrations on posterior margin of postcanine teeth. Lacks typical Burnetiamorph features of pachyostosed skull roof, nasal boss; and backwardly-pointing squamosal horns. (Sidor & Welman 2003 p.634).

Illustration: *Lemurosaurus pricei* in lateral view, from Sidor & Welman 2003, via Kemp 2005 p.32

References: Sidor & Welman 2003. MAK091111.

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Therapsida: Dinocephalia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|-Raranimus
`+-Biarmosuchia
 `--Eutherapsida
  `--+--Dinocephalia
     |  |--Stenocybus
     |  |--Estemmenosuchidae
     |  `--+--Anteosauria
     |     `--Tapinocephalia
     `--+--Anomodontia
        |  |--Venyukovioidea
        |  `--Dicynodontia
        `--Theriodontia
           |--Gorgonopsia
           `--+--Therocephalia
              `--CYNODONTIA
```

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Taxa on This Page

1. Dinocephalia X
2. Eutherapsida
3. *Stenocybus* X

Dinocephalia

The giant carnivorous anteosaur *Doliosauriscus* prowls through the tropical forest of equatorial Pangea - artwork by Dmitry Bogdanov - Wikipedia.

***Titanophoneus* *potens*. Early Capitanian epoch. Length 3 to 5 m. Image © Kelly Taylor -- reproduced with permission.**

The Permian **Dinocephalia** -- the name means "terrible head" and is a reference to their fierce appearance, were in many ways the most archaic of the higher therapsids, and among the earliest as well. Although these synapsids showed therapsid adaptations such as the expansion of the ilium and the general posture of the limbs, they retained various primitive characters of the pelycosaurs. For example they had no secondary palate, and their dentary was of moderate size In the more mammal-like group, the cynodonts, the dentary grew increasingly large, until it constituted the entire lower jaw, which is the mammalian condition. The dinocephalians are also distinguished by their large size. The biggest were the size of an adult rhinoceros. The dinocephalians also developed pachyostosis, or thickening, of the bones in the skull, perhaps as an adaptation for intra-specific rivalry (head-butting) to procure territory or a mate.

A number of writers have included the dinocephalians in the suborder Anomodontia, but it is now acknowledged they constitute a separate group. The dinocephalians are divided into three main groups, the mostly carnivorous Anteosauria (which included giants up to 6 meters and more in length), and the medium to very large herbivorous estemmenosuchids and Tapinocephalia. The tapinocephalians are again divided into two branches, the titanosuchids, which were large ponderous herbivores or omnivores, and the tapinocephalians, which were equally large and ponderous but more specialized as purely herbivores, both of which reached the size of an ox or even a rhinoceros in the larger species. The tapinocephalians also have the dubious distinction to be -- almost without dispute -- the ugliest vertebrates that nature has ever produced. The anteosaurs clearly preyed largely on their estemmenosuchid and tapinocephalian cousins.

The Dinocephalians are an ancient group and their ancestry is not clear. It is assumed that they must have evolved during the earlier part of the Ufimian/Roadian, or possibly even the Kungurian epoch, but no trace has been found; the fauna described by Olson of this age has turned out, on reinspection, to be not therapsid but misinterpretation of caseid remains [ref. pers. communication Christian Kammerer, and Sidor & Hopson 1995]. Even the earliest members, the estemmenosuchids and early brithopodids of the Russian Ocher fauna, (late Roadian? / early Wordian age) were already a diverse group of herbivores and carnivores.

All Dinocephalians are distinguished by the interlocking incisor (front) teeth. Correlated features are the distinctly downturned facial region, deep temporal region, and forwardly rotated suspensorium. The way the jaw mechanism works is shown in the figure.

Shearing contact between upper and lower teeth (allowing food to be more easily sliced into small bits for digestion) is achieved through keeping a fixed quadrate and a hinge-like movement at the jaw articulation. The lower teeth are inclined forward, and occlusion is achieved by the interlocking of the incisors.

The later dinocephalians improved on this system by developing heels on the lingual sides of the incisor teeth which met against one another to form a crushing surface when the jaws were shut.


The dinocephalian specialization of the jaw apparatus of the anteosaur *Titanophoneus*. The lower jaw closes with a simple hinge movement at the jaw articulation.

The dinocephalians were originally carnivorous, as represented by the anteosaurs, but even the earliest Estemmenosuchids, and then the somewhat later titanosuchids and tapinocephalids adapted to a herbivorous life-style, replacing the big Caseid pelycosaurs as the dominant vertebrate plant eaters. In all dinocephalians the synapsid opening for attachment of jaw muscles remained relatively small, and it is assumed that the power of the bite was provided by the sheer mass of the animals' jaw and muscles. This was a less efficient system than that developed by the anomodonts and theriodonts, but it clearly worked well, because these creatures dominated the large herbivore and large carnivore niche for some millions of years.

The Wordian and Capitanian epochs, during which the dinocephalians flourished, is generally said to have lasted only a million or two years each. Such evolutionary change over such a short period (say 3 million years in all) is difficult to accept, especially if one looks at comparable evolutionary rates among Mesozoic dinosaurs and Cenozoic mammals, which are at least several times slower. To be sure, evolution can proceed very fast, perhaps over periods of only hundreds or thousands of years in small, geographically isolated island populations. However, in general and in the large picture, the average lifetime of a terrestrial animal species is on the order of some two to three million years. For this reason it may be that the conventional dating is probably slightly in error. Generally, generally there is an uncertainty of some five or ten million years either way with radiometric dating. Thus, the total Dinocephalian span (perhaps beginning in the Ufimian/Roadian or even the Kungurian and going through to the middle or late Capitanian age) may have been on the order of some twelve million years or more.

At the end of mid-Permian time (mid or late Capitanian age) all the dinocephalians became extinct. The reason for this extinction is not clear, and the conventional explanation -- that they were out-competed by the more efficient herbivorous anomodonts and carnivorous theriodonts -- is about as persuasive as the old idea that the mammals out-competed the dinosaurs. Possibly disease, sudden climatic change, or other factors of environmental stress brought about their end. With their passing some of the most interesting prehistoric creatures this Earth has seen disappeared; they were replaced by much smaller dicynodonts and theriodonts. MAK000809.

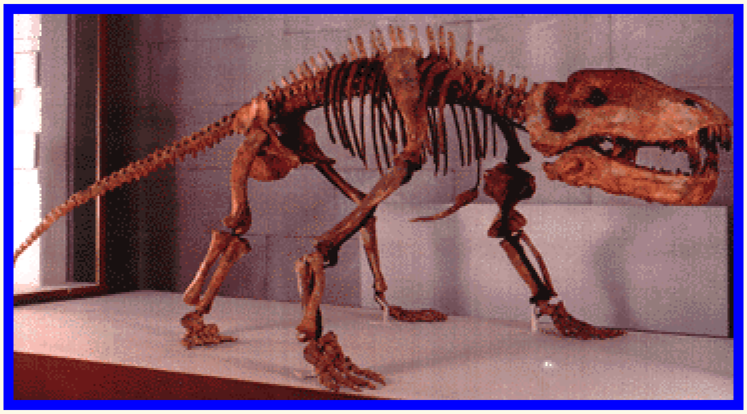
Eutherapsida: Dinocephalia + Anomodontia + Theriodontia. [RS01]

Range: from the Middle Permian.

Phylogeny: Therapsida:::: Eotitanosuchia + *: Anomodontia + Neotherapsida.

Characters: **$?** zygomatic arch bowed, with laterally expanded temporal fenestra [RS01]; **$?** ulna without distinct olecranon process [RS01]; **$?** pes V with only 3 phalanges [RS01].

References: Rubidge & Sidor (2001) [RS01]. 020219.



Dinocephalia: Medium to large (1-3 m) big-bodied, short-legged "dog-faced" forms.

Range: Middle Permian to Late Permian of Russia & South Africa.

Phylogeny: Eutherapsida: Neotherapsida + *: Estemmenosuchidae + (Anteosauria + Tapinocephalia).

Characters: Skull usually massive, **$** nares not terminal [RS01]; bone horns on maxillae or skull table; orbits small; temporal opening fairly large; some saggital crest; some with conspicuously thickened crania (head-butting?); highly integrated; no secondary palate; **$** premaxilla vomerine process absent (vomer contacts body of premaxilla directly) [RS01]; **$** pterygoid transverse process anterior to orbit [RS01]; **$** reflected lamina of angular smooth, without ridges or fossae [RS01]; **$** foramen on medial jaw, between angular and prearticular [RS01]; incisors interdigitate; canines sometimes long; cheek teeth small; tail very long; hindlimb posture somewhat upright, but forelimbs sprawl; metapodial V at least as long & robust as Mp IV [RS01]; phalangeal formula 23345 / 23333; carnivores (early) or herbivores (later).

Links: Early Mammal-like Reptiles; Schnellbestimmung anhand von typischen Schädelmerkmalen (in German); Notes From Other Vertebrates (go down to Christian Kammerer's comments); dinosaurs- titanophoneus potens; More Titanophoneus potens; BPI Palaeontology (includes life reconstruction); The first Karoo Reptiles and their origin; Early Mammal-like Reptiles; therapsid3a; therapsid4b (**Best on the Web**).

References: Rubidge & Sidor (2001) [RS01].

Image: *Titanophoneus potens* courtesy of mathematical.com. ATW020219.

Stenocybus: *S. acidentatus* Cheng & Li 1997

Stenocybus - artwork by Dmitry Bogdanov - Wikipedia

Range: Middle Permian (Roadian) of China.

Phylogeny: *Either:* Dinocephalia: Tapinocephalia + (Anteosauria + *) (if basal Anteosaur) *or* Dinocephalia: (Tapinocephalia + Anteosauria) + * (if basal Dinocephalian)

Location: Xidagou Formation, Dashankou, Yumen, Gansu Province, China.

Remains: One near-complete skull (IGCAGS V 361), plus the right premaxilla, maxilla and dentary of a second (IVPP V12008).

Size: Skull length 12-15 cm.

Diagnosis: Cheng & Li (1997) Skull high, narrow, slender without pachyosteosis; orbit large; temporal fossa small; maxilla high, triangular-shaped, with top above canine and connecting with prefrontal; lacrimal large and extending forward; frontal with no boss and interorbital ridge; anterior border of attachment depression for lower jaw adductor on dorsal surface of postfrontal; small teeth present on palatine and transverse process of pterygoid; marginal tooth formula I 5/4, C 1/1, PC 6-8/6; incisors large, procumbent, interlocked, with labial talon pointer and lingual heel.

Comments: *Stenocybus acidentatus* was a relatively small dinocephalian that lacked the pachyosteosis of more derived forms. It had a very high, narrow skull, triangular in dorsal view, with a large orbit compared to other dinocephalians.

Cheng & Li (1997) assigned their new form to the Dinocephalia on the basis of the lingual heel on the incisors and the position of the lower jaw adductor, but regarded it as basal within the clade due to the small skull without pachyosteosis, small temporal fenestra, lower jaw articulation not anteriorly moved, maxilla with apex above the canine rather than posteriorly, and lacrimal extended anteriorly rather than short. While Cheng & Li (1997) placed Stenocybus outside the Anteosauria + Tapinocephalia clade, they seem to have only compared it with members of Anteosauria and not directly to members of Tapinocephalia. Rubidge & Sidor (2001) place it closer to Anteosauria than Tapinocephalia, again without much comment.

Credits: CKT071010 (original page Palaeos org - Stenocybus)

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checked ATW031025; last modified MAK091111, 120127

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Therapsida: Dinocephalia: Estemmenosuchidae

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--Eutherapsida
`--+--Dinocephalia
   |  |--Stenocybus
   |  |--Estemmenosuchidae
   |  |  |--Anoplosuchus
   |  |  `--+--Estemmenosuchus
   |  |     |--Molybdopygus
   |  |     `--Zopherosuchus
   |  `--+--Anteosauria
   |     `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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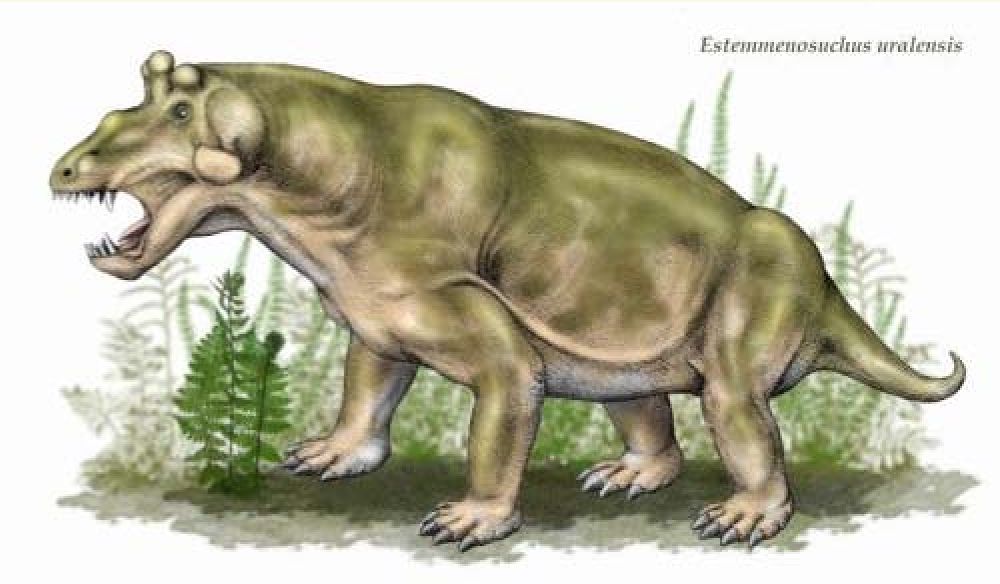
3. *Estemmenosuchus* X
4. *Molybdopygus* X
5. *Zopherosuchus* X

Dinocephalia: Estemmenosuchidae



Estemmenosuchus uralensis - life reconstruction artwork by Mojcaj - Wikipedia

With the decline of the Kungurian and Ufimian caseids, the herbivorous **Estemmenosuchidae** took over the role of top herbivore. These were massive, clumsy-looking animals, with a sprawling posture, reaching the size of an adult bull, although some types were smaller.

The skull is high and massive. The creature is equipped with several bizarre set of large horns projecting both upwards and outwards, probably used for intra-specific display. There are five large teeth on the maxillae (upper jaw bone), rather short canines, and at least twenty small and uniform post-canines. Each tooth has a swollen crown and a sharp, laterally compressed at the apex. There are also numerous small teeth on the palate (vomers, palatines and pterygoids). The reduced side teeth, with a bulky body for digesting volumes of plant food, indicate a herbivorous lifestyle, despite the large canines. Vegetable matter was grasped with the strong front teeth and swallowed without chewing, as the weak and thin side teeth only served to keep food in the mouth. These animals would nevertheless have taken carrion when they could find it, as the great force exerted by the chisel-like front teeth could cut up meat quite easily.

As with the tapinocephalids of the early Capitanian epoch, a number of types are known, and it seems that, for a short time, the estemmenosuchids constituted a successful evolutionary radiation. Connections are sometimes suggested with *Styracocephalus*, but in the estemmenosuchids the 'horns' are situated on the frontals and directed dorsally. In *Styracocephalus* the 'horns' are formed by the tabular and directed posteriorly. Otherwise their features very similar to those of *Styracocephalus*. It is not possible to say therefore whether the relationship is one of ancestor- descendent or simply evolutionary convergence due to similar lifestyle, although difference in the bones forming the horns would suggest the latter.

The remains of ***Estemmenosuchus*** have been found in a channel flood deposit, indicating that they probably frequented lowland and marshy areas. MAK000725.

Suborder	Dinocephalia			
Family	Estemmenosuchidae			
Species	***Estemmenosuchus uralensis*** *Chudinov 1960*	***Estemmenosuchus mirabilis*** *Chudinov 1968*	***Anoplosuchia tenuirostris*** *Chudinov 1968*	***Zopherosuchus luceus*** *Chudinov 1983*
Horizon:	Upper Kazanian or Lower Tartarian Substage, Middle Permian			
Locality:	Echovo locality, Ocher Province, Perm Region, Russia			
Possible age:	Middle or Late Wordian			
Known remains:	elements of skulls and postcrania	skull, lower jaw and vertebrae	incomplete skeleton and skull	poorly preserved skeleton and incomplete skull
Length	65 cm	40 cm	no information	no information

(skull):				
Length (total):	upto 4 meters	over 3 meters	intermediate in size	1.5 meters

Comments: The Estemmenosuchids represent the first major evolutionary radiation of therapsid herbivores. Still rare during the Roadian age, they come into their own during the Wordian, when a number of types of animals occur together; clearly representing a mature evolutionary assemblage, like the Capitanian tapinocephalids whose fossil remains are known from the South African Karoo (Beaufort Group). They range in size from medium-sized animals like *Zopherosuchus*, to the large *Estemmenosuchus* which was the biggest animal of its day. The fossil remains of the Estemmenosuchids are so far not known beyond the Permian deposits of the Urals, which at the time was an equatorial lowland environment. So these animals seem to have been tropical, possibly swamp loving, herbivores. The name *Estemmenosuchus* means "Crested Crocodile", and refers to the strange horns or bony antlers. These animals are distinguished by their bizarre crests and flanges of bone, which were probably for intra-specific behavior. There is great individual variation.


Estemmenosuchus mirabilis - illustration copyright © Satoshi Kawasaki

Zopherosuchus luceus was a fairly uncommon, relatively small estemmenosuchid (although still large relative to other animals in its environment). Some of bones at the front of the skull are particularly thickened.

Anoplosuchia tenuirostris was a fairly uncommon, medium sized estemmenosuchid with a comparatively narrow skull. There are no horns or thickening, except in the front nasal region.

Estemmenosuchus mirabilis was a fairly uncommon, large estemmenosuchid with spectacular moose-like "horns". It had a shorter face than the type species *E. uralensis*. According to Vickers-Rich and Rich, 1993 irt was about the size of a rhinoceros.

Estemmenosuchus uralensis was a common, very large (upto 4 meters long - Chudinov 1960 quoted in Olson, 1962 p.79) estemmenosuchid, about the size of a rhinoceros (Vickers-Rich and Rich, 1993), with less prominant horns then *E. mirabilis*. Originally all specimens were included in this species, but it was since realised that wthere were a number of different species (however, not all palaeontologists agree that these were different species. According to Ivakhnenko 1998 *Anoplosuchus* and *Zopherosuchus* are synonyms of *Estemmenosuchus uralensis*). This peaceful herbivore had much to fear from the giant Eotitanosuchid *Ivantosaurus*, the only creature in its environment big enough to take on an adult *Estemmenosuchus*.

References: Olson, 1962, King 1988, Vickers-Rich and Rich, 1993

Links: *Estemmenosuchus uralensis* skeleton; *Estemmenosuchus uralensis* skull; *Estemmenosuchus mirabilis* life illustration

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Estemmenosuchidae: *Parabradysaurus*?

Range: Middle Permian (uppermost Kazanian) to Late Permian (lower Tatarian) of Russia

Phylogeny: Dinocephalia: (Anteosauria + Tapinocephalidae) + *: *Anoplosuchus* + (*Estemmenosuchus* + *Molybdopygus* + *Zopherosuchus*)

Characters: medium to large size; skull with heavy pachyostosis [BS00]; often with numerous knob-like or horn-like protuberances [BS00]; teeth on vomers [BS00]; tail short; herbivorous.

Links: dinosaurs-estemmenosuchus uralensis; Gondwona Studios; Estemmenosuchus Printout - Enchanted Learning Software.

References: Battail & Surkov (2000) [BS00]. ATW020522.

Anoplosuchus: *A. tenuirostris* Tchudinov 1968b

Range: Middle Permian (uppermost Kazanian) to Late Permian (lower Tatarian) of Russia (Ocher District)

Phylogeny: Estemmenosuchidae: (*Estemmenosuchus* + *Molybdopygus* + *Zopherosuchus*) + *.

Characters: medium-sized [BS00]; skull narrow; preorbital region long, low & broad; outer edge of jaw in region of canine bears weak boss; preorbital skull without excrescences or thickening [BS00] except in posterior nasal region (?); postorbital (skull?) short, weak, broad & high; incisors more or less equal in size to canines [BS00]; numerous small post-canine teeth [BS00].

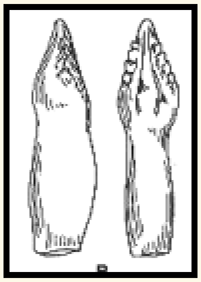
Links: paleng2_0p189abs (abstract of Ivakhnenko article stating that *Anoplosuchus* is synonymous with *Estemmenosuchus* & *Zopherosuchus*); RepTherapS.pdf;

References: Battail & Surkov (2000) [BS00]

Note: known from an incomplete skeleton and skull plus referred skull & jaw fragments. ATW020522, MAK000725.

Estemmenosuchus: *E. uralensis* Tchudinov, 1960; *E. mirabilis* Tchudinov, 1968.

Range: Middle Permian (uppermost Kazanian) to Late Permian (lower Tatarian) of Russia (Ocher District).



Phylogeny: Estemmenosuchidae:: *Molybdopygus* + *Zopherosuchus* + *.

Characters: bull-sized; massive skull [BS00]; rather spectacular "horns;" anterior nasal form unpaired boss on dorsal snout [BS00]; jugal & squamosal form massive lateral outgrowth (see image at right) [BS00]; long, curved incisors [BS00]; canines short & thick [BS00]; at least 20 weak marginal teeth [BS00]; note the typically herbivorous teeth in image at left.

Links: dinosaurs-estemmenosuchus uralensis; Estemmenosuchus Printout - Enchanted Learning Software; therapsid3b.

Note: *E. uralensis* is larger, with a longer skull in proportion to width. The postorbitals & postfrontals form a pair of partially fused horn-like protuberances on the skull table just posterior to the orbits. *E. mirabilis* is smaller, with a shorter skull. The horn pair is shorter, well-separated and the horns extend more laterally. Note that the image at right is a *mirabilis*. [BS00].

References: Battail & Surkov (2000) [BS00]. ATW020522.

Molybdopygus: (= *Deuterosaurus*) *M. arcanus* Tchudinov 1964

Range: Late Permian of Russia, Bolshoi Kitiak, Malmych, Kirov. Lower Tatarian Substage.

Phylogeny: Estemmenosuchidae: *Estemmenosuchus* + *Zopherosuchus* + *.

Characters: known only from pelvic bones. Smaller than *Estemmenosuchus*, but perhaps more massively built [BS00]; flat facets at posterior end of acetabulum; high pubo-ischiadic symphysis.

References: Battail & Surkov (2000) [BS00]. ATW020523

Zopherosuchus**:** *Z. luceus* Tchudinov 1983.

Range: Middle Permian (uppermost Kazanian) to Late Permian (lower Tatarian) of Russia (Ocher District).

Phylogeny: Estemmenosuchidae:: *Estemmenosuchus* + *Molybdopygus* + *.

Characters: small-bodied [BS00]; no cranial horns [BS00]; frontals & parietals particularly thick; temporal fenestrae short, but very tall [BS00]; relatively small number of postcanine teeth [BS00].

References: Battail & Surkov (2000) [BS00]. ATW020524.

checked ATW031025; last modified MAK091111, MAK091114

Therapsida: Anteosauria

Abbreviated Dendrogram

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SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Stenocybus
   |  |--Estemmenosuchidae
   |  |--Anteosauria
   |  |  |--Archaeosyodon
   |  |  `--+--Brithopodidae
   |  |     |  |--Chthomaloporus
   |  |     |  `--Brithopus
   |  |     `--+--Deuterosaurus
   |  |        `--Anteosauridae
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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Anteosauria

Two *Archaeosyodon* feast on the large semi-aquatic herbivore *Estemmenosuchus* - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

The family "Brithopodidae" was erected by Efremov in 1954 to include the carnivorous therapsids of the Russian Tatarian (Late Permian) Copper Sandstones and other Cis-Uralian localities, including both those of the Cis-Uralian Dinocephalian Complexes and the Isheevian Dinocephalian Complex. In the same year, Boonstra created the family Anteosauridae for the giant carnivorous dinocephalians of the South African Lower Beaufort (*Tapinocephalus* Zone). In his 1962 monograph on American and Russian Late Permian reptiles, Olson (1962) places the distinct herbivorous "brithopodid" *Deuterosaurus* in a family of its own. For several decades these three families were considered distinct if closely related. In her 1988 monograph on the "Anomodonta," King (1988) suggested a subfamily distinction, although rejecting the status of the Deuterosauridae. The current cladistic-based tendency is of course to do away with these Linnean taxa altogether. Hence our non-committal title, **Anteosauria**.

The basic technical diagnosis of the Anteosauria (Brithopodidae), which includes the three subfamilies, is as follows: A group of primitive carnivorous dinocephalians. The skull is high and narrow. The palatal teeth - the teeth on the roof of the mouth, a feature of many Paleozoic tetrapods - are enlarged and usually confined to a kidney-shaped cluster on each palatine (near the outer tooth row). Any palatal teeth on the pterygoid flange are reduced. The marginal teeth (teeth in the "normal" position) are of three types: anterior (front or incisor), canine, and cheek teeth. Here we have the further differentiation of tooth types along the line to the mammalian condition. The incisors (the teeth at the front) each have a small ledge or "heel", a distinctive dinocephalian feature that only the estemmenosuchids lack. The canine is very large in all anteosaurs, even the herbivorous ones. There are usually about ten cheek teeth (although the number is very variable, depending on age and tooth replacement), possessing bulbous crowns. The teeth may decrease in size from front to rear. There is a "step" or upturning in the premaxilla bone of the upper jaw, so the front of mouth curves strongly upwards. A somewhat similar "kink" (possibly a mobile joint) can be seen among some archosaurs such as proterosuchids and coleophysid dinosaurs. The postorbital bone and bar behind the eye are large, modified to produce an area for the attachment of the superficial adductor jaw muscles on the outer surface of skull. There is a tendency towards pachyostosis, the thickening of the roof of the head that is a common dinocephalian characteristic, perhaps indicative of "head-butting" intra-specific behavior (rivalry for mates and/or territory). This takes the form of a tuberosity around the pineal opening, in advanced forms as a bony "boss" (almost like a low mound). There is a large canal for pineal organ ("third eye", probably tied in with the animal's diurnal and seasonal cycles). The shoulder girdle is fairly light, with a narrow interclavicle, clavicle, and scapular blade. The femur (thigh bone) is slender and curved. These were, in spite of their size, probably quite agile animals.

Lifestyle

The stance of a typical anteosaur, such as *Titanophoneus* was primitive. Rather than the limbs being drawn in under the body, the stance was more sprawling. Olson (1962) notes that the Russian dinocephalian assemblages indicate environments tied to water, and Boonstra considered that the roughly contemporary *Anteosaurus* was a slinking crocodile-like semi-aquatic form. The long tail, weak limbs, and sprawling posture do indeed suggest some sort of crocodile-like existence. However the thickened skull-roof indicates that these animals were quite able to get about on land, if they were to practice the typically dinocephalian head-butting behavior. All other head-butters - pachycephalosaurian dinosaurs, titanothere ungulates, and goats - were or are completely terrestrial. Perhaps these animals spent some time in the water but were active on land during the mating season, and probably quite able to get about on land to hunt for prey (consider a modern sprawling/ambush predators such as the komodo "dragon" lizard).

The large anteosaurs were efficient predators, more specialized than earlier and more primitive Biarmosuchid and Eotitanosuchid carnivorous therapsids, as the temporal opening behind the eye socket was larger, indicating a greater muscle mass available for closing the lower jaw. And with skull lengths of 50 to 80 cm, overall lengths of 3 to 5 meters, and live weights of upto 500 kg, animals like *Titanophoneus*, *Doliosauriscus*, and *Anteosaurus* played the role of top predator in the terrestrial tetrapod assemblages of the Capitanian epoch that the large *Eotitanosuchus* did during the preceding late Roadian and early Wordian epoch, and the 3 meter long *Dimetrodon* did during the Early Permian.

Evolution

A full understanding of Anteosaur phylogeny has to await greater scrutiny of the available remains. Much of the Russian material is fragmentary, and a lot of this will no doubt turn out to be synonymous with the better known forms. It was originally thought that the earliest anteosaur was the very fragmentary American *Eosyodon* Olson, of Latest Kungurian age. It now seems that all of the proto-therapsids Olson described in his monograph are chimeras - mostly misinterpretations of caseid pelycosaurs (Sidor & Hopson 1995). That leaves the Russian Ocher fauna from Ezhovo (probably early Wordian age) as the oldest known anteosaurs. Two species are known from this period. Significantly, *Archaeosyodon* is known only from the skull, and *Chthomaloporus* only from postcrania. It is not unlikely that these two thus represent the same animal. The skull is typical of a fairly primitive anteosaur and indicates a reasonably large animal - perhaps a large predator intermediate in size between the dog-sized *Biarmosuchus*, the large *Eotitanosuchus*, and the huge *Ivantosaurus*, both of which were contemporary. The postcrania however include a pelvic girdle quite unique from that of other anteosaurs, indicating that this type represents a side-branch rather than a direct ancestor.

By the late Wordian / early Capitanian (late Kazanian - Bashkirian subzone), perhaps several million years later, the gigantic Eotitanosuchid super-predators are gone, along with most of their estemmenosuchid herbivore prey (perhaps the victims of a minor mass-extinction) and only a few smallish anteosaurs remain. They seem to have diverged into at least two distinct lineages - the primitive carnivorous types (*Syodon* and *Brithopus* - Brithopididae) and the more specialized herbivores (*Deuterosaurus*). The latter perhaps filled the ecological role vacated by the Estemmenosuchids.

A million or so years later, all the animals had grown in size, evolving into bigger and bigger types. A big species of *Brithopus* was joined by a giant *Admetophoneus* (subfamily Anteosaurinae), and the deuterosaurs had also increased in size, and were now existing alongside the big advanced tapinocephalid herbivores. These animals are by and large a lot bigger than those that existed during Bashkirian time.

By the time of the forms that have been found at Isheevo, the continuing basal primitive types like *Syodon* and *Brithopus*, and the advanced giant carnivorous forms like *Titanophoneus* and *Doliosauriscus*, are flourishing. The deuterosaurs are gone, perhaps replaced by the tapinocephalids. This seems to be the golden age of anteosaur diversity, and indeed of the dinocephalians in general. The South African *Anteosaurus* (*Tapinocephalus* zone), a representative of the titanophonine- doliosaur lineage (subfamily Anteosaurinae), seems to have existed at this time and also slightly later.

It is interesting that whereas in the South African temperate zone fauna there is only one anteosaurian predator (the giant *Anteosaurus*), in the tropical Isheevo fauna (yes, at the time Russia was located in the tropics!) there are four. Perhaps there were more ecological niches in the tropics for these animals. Perhaps some of the species will turn out to be synonyms or juveniles of other forms. Perhaps the smaller Russian anteosaurs like *Syodon* filled the same ecological niche as the similarly sized *Titanosuchus* did in the temperate regions. Much still remains to be known about these amazing animals. MAK000902. (revised MAK091114)

Anteosauria: *Sinophoneus, Stenocybus*

Range: Middle Permian to Late Permian of China, South Africa & Russia.

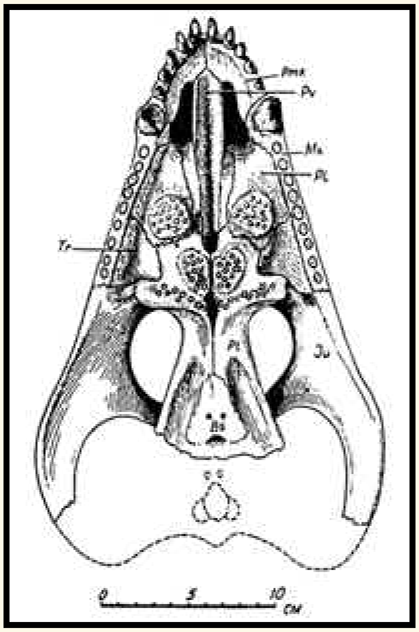
Phylogeny: Dinocephalia: Tapinocephalia + *: *Archaeosyodon* + (Brithopodidae + (*Deuterosaurus* + Anteosauridae)).

Characters: skull long, high and narrow [BS00]; skull pachyostosis common, especially around orbital rims & parietals [BS00]; premaxilla with "step" or upturning, so the front of mouth curves strongly upwards; pineal foramen large, with pronounced tuberosity; temporal fenestra well open dorsally [BS00]; palatal teeth enlarged and usually confined to kidney-shaped cluster on palatines; postorbital bone and bar large, modified to area for external attachment of superficial adductors; any teeth on pterygoid flange reduced; marginal teeth include incisors, canines, and cheek teeth; incisors with small ledge or "heel" [BS00]; canines very large [BS00]; usually about ten cheek teeth; (rather variable, dependent on age and tooth replacement); cheek teeth with bulbous crowns [BS00]; teeth may decrease in size distally; shoulder girdle is fairly light, with a narrow interclavicle, clavicle, and scapular blade; femur slender and curved; mostly carnivorous.

References: Battail & Surkov (2000) [BS00]; Rubidge & Sidor (2001) [RS01].

Note: possibly paraphyletic [RS01]. ATW020219.

Archaeosyodon: *A. praeventor* Tchudinov 1960.



Range: Middle Permian to Late Permian of Russia. (Ochersky area, near Ezhovo locality. Upper Kazanian)

Phylogeny: Anteosauria: (Brithopodidae + (*Deuterosaurus* + Anteosauridae)) + *.

Characters: medium (1.5-2.0 m) anteosaur; skull is massive & rather tall [BS00]; maxillary surfaces sculpted [BS00]; dorsal margin of orbits & fronto-parietal region strongly thickened; temporal openings broadly open dorsally; palate primitive, especially in arrangement of palatal teeth & anterior position of short, deep, choanae [BS00]; palatines and pterygoid flanges with numerous teeth [BS00]; upper canines short & recurved [BS00]; carnivorous.

Note: may be a primitive titanosuchid, not an anteosaur.

Links: PaleoNET | Библиотека.

References: Battail & Surkov (2000) [BS00]. ATW030518.

Brithopodidae: (= Brithopodinae)

Range: Middle Permian to Late Permian of Russia.

Phylogeny: Anteosauria:: (*Deuterosaurus* + Anteosauridae) + *: *Chthomaloporus* + *Brithopus*.

Characters: quadrate condyles narrowed anteroposteriorly. ATW020524.

Chthomaloporus: *C. lenocinator* Tchudinov 1964b.

Range: Middle Permian to Late Permian of Russia.

Phylogeny: Brithopodidae: *Brithopus* + *.

Characters: pelvic girdle lightly built [BS00] [K88]; acetabula closely spaced [BS00] [K88]; ischiadic symphysis well developed on anterior edge of ilia [BS00] [K88]; fused sacral vertebrae [BS00] [K88]; a powerful finger-shaped process on anterior edge of ilium [K88].

References: Battail & Surkov (2000) [BS00]; King (1988) [K88]. ATW020524.

Brithopus: (= *Orthopus* = *Rhopalodon* = *Dinosaurus* = *Eurosaurus*) *B. bashkyricus* Efremov 1954; *B. fischeri* Eichwald 1860; *B. ponderus* Efremov 1954; *B. priscus* Kutorga 1838.

Range: Middle Permian of Russia.

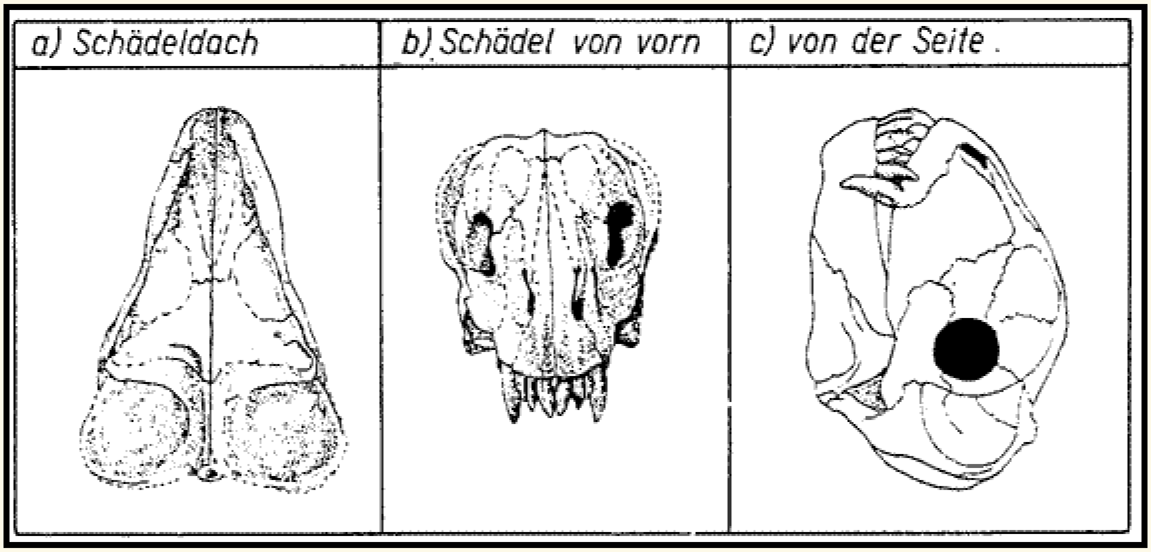
Phylogeny: Brithopodidae: *Chthomaloporus* + *.

Characters: fairly large (length 2.5 to 3 m) [K88]; choanal depression deep [BS00]; pterygoid flanges with row of teeth [BS00]; small palatal teeth on palatines [BS00]; postcanine teeth 9-10 [BS00] [K88]; shoulder girdle massive [K88]; glenoid somewhat screw-shaped (limited range of movement) [K88]; humerus with high supinator crest [BS00]; femur with strong 4th trochanter & short adductor crest [BS00].

Links: 0521554764WS.pdf (historical interest)

References: Battail & Surkov (2000) [BS00]; King (1988) [K88].

Note: all extremely scrappy material. ATW020524.



Deuterosaurus: (= *Eurosaurus* = *Mnmeiosaurus* = *Uraniscosaurus*) *D. biarmicus* Eichwald 1860.

Range: Late Permian of Russia.

Phylogeny: Anteosauria::: Anteosauridae + *.

Characters: Skull nearly as high as long (about 230 mm) [BS00]; pachyostosis reduced [BS00] & localized just anterior to orbital margin; jaw hinge displaced slightly anterior, but well below lower tooth row [BS00]; incisors with well-developed heels [BS00]; lower tusks (canines?) with longitudinal facets on enamel; postcanine teeth small [BS00]; postcanine teeth laterally flattened; complex crown structure in palatal teeth; tibia large with rounded and massive head; femur similar to that of sphenacodontids, with incipient development of trochanter major.

Note: Huxley thought *Deuterosaurus* was a dinosaur (see links below). Consequently, it is more famous today for *not* being a dinosaur, than for any quality it posessed as an anteosaur.

Image: *Deuterosaurus* skull in palatal, anterior and lateral views from Müller ("1968" (=1985?)).

Links: Triassic Dinosauria; On the Classification of the Dinosauria (1870); Revision of the Pelycosauria of North America.

References: Battail & Surkov (2000) [BS00]. ATW030521.

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Therapsida: Anteosauridae

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Stenocybus
   |  |--Estemmenosuchidae
   |  |--Anteosauria
   |  |  |--Brithopodidae
   |  |  `--Anteosauridae
   |  |     |--Syodontidae
   |  |     |  |--Notosyodon
   |  |     |  `--Syodon
   |  |     `--+--Titanophoneus
   |  |        `--Anteosaurinae
   |  |           |--Anteosaurus
   |  |           `--Doliosauriscus
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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4. *Doliosauriscus* X
5. *Notosyodon* X
6. *Syodon* X
7. Syodontidae X
8. *Titanophoneus* X

The Anteosauridae: into (or out of) Africa

Anteosaurus - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

In the world of the Early Permian, all of the major landmasses except Eurasia were consolidated into a single continent. Eurasia was located to the East of the other landmasses and was probably only in sporadic contact with the rest of the world from a biological point of view. However, during the course of the Permian, the Eurasian landmass (and Mongolia) steamed northwest into the higher latitudes of the Northern hemisphere at a rather fair clip. By the second half of the Permian, the northwesterly drift of Eurasia had brought it into relatively firm and regular contact with Greenland and the Laurentian (North American). Thus Pangaea was formed -- a single continent containing all of the world's major landmasses. At this point, Pangaea looked like the letter 'C'. The Cis-Uralian region was located at the top of the 'C' between about 35° and 50° north latitude.

By contrast, South Africa was almost at the bottom of the world, squeezed between South America and Australia at about 60° *South* latitude. The two were thus separated by over 10,000 km of land, including the gigantic howling deserts of eastern North America -- perhaps as large and almost certainly hotter than the Sahara today -- and a massive chain of equatorial mountains stretching across Pangaea from Texas to Spain.. Yet, somehow, dinocephalians made their way from one to the other. It is not completely clear which way the traffic was going. To judge by species diversity, the carnivorous anteosaurs spread from Russia to the far South; while the herbivorous Tapinocephalia came out of Africa to invade the Cis-Uralian north. In addition there is the unquantifiable possibility that both lineages diverged from some more central locality which has not conveniently left a Permian fossil record. In any event, the Late Permian witnessed the cosmopolitan spread of many therapsid lines which set the stage for the cynodont dominance of the Early Triassic. ATW020523.

Anteosauridae:

Range: Late Permian of Russia & South Africa.

Phylogeny: Anteosauria::: *Deuterosaurus* + *: Syodontidae + (*Titanophoneus* + Anteosaurinae).

Characters: ATW020525

Syodontidae: *Australocyodon* (a South African form!)

Range: Late Permian of Russia & South Africa.

Phylogeny: Anteosauridae: (*Titanophoneus* + Anteosaurinae) + *: *Notosyodon* + *Syodon*.

Characters: ATW020525

***Notosyodon*:** *N. gusevi* Tchudinov 1968b. Differs from *Syodon* mainly in larger size and greater pachyostosis and may be a junior synonym. [BS00]

Range: Late Permian of Russia.

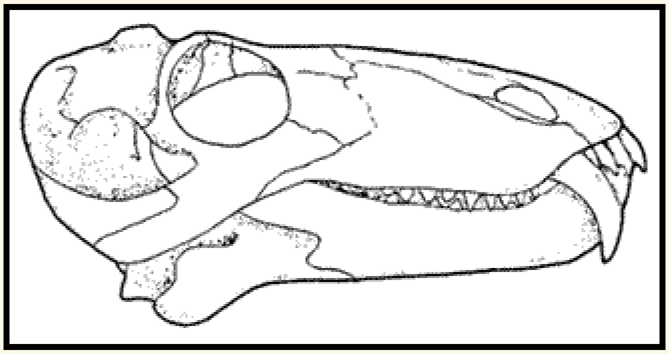
Phylogeny: Syodontidae: *Syodon* + *.

Characters: medium size [BS00]; massive skull [BS00]; orbital and parietal regions very strongly pachyostosed [BS00]; interorbital skull flat & straight, without median ridge [BS00]; orbits large [BS00]; parietal boss high & massive [BS00]; temporal fenestrae large [BS00]; upper portion of occiput strongly slanted posteroventrally [BS00]; occipital condyle very large [BS00].

References: Battail & Surkov (2000) [BS00].

Note: Known from a skull, missing the lower jaw and anterior rostrum, as well as 2 teeth and referred jaw fragments. ATW020927.

***Syodon*:** *S. biarmicum* Kutoroga 1838



Range: Late Permian of Russia.

Phylogeny: Syodontidae: *Notosyodon* + *.

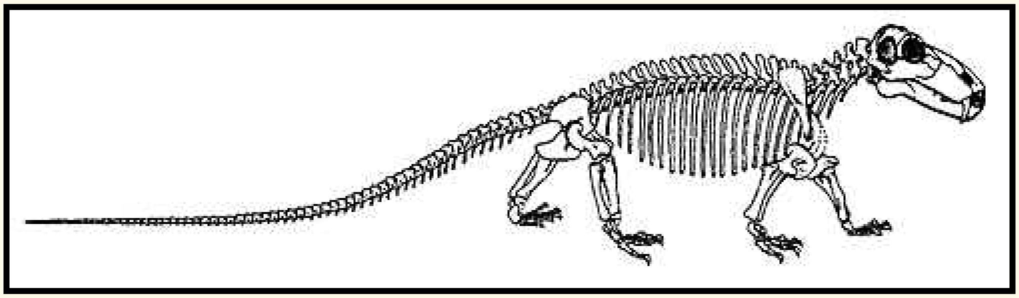
Characters: small body [BS00]; skull moderately high [BS00]; pineal opening and boss large [BS00]; orbits large [BS00]; postorbital hone large and thick, providing external area for origin of part of superficial adductor musculature [O62?]; palatines & pterygoids with teeth [BS00]; canines rounded and curved [BS00]; postcanines small & transversely compressed [BS00]; femora slender with ridges and condyles weakly developed, and with a slight curvature [O62?].

Image: from [O62].

References: Battail & Surkov (2000) [BS00]; Olson (1962) [O62].

Note: known from two skulls, one with lower jaw, and various postcrania. Kutoroga's holotype was a single canine. This extraordinary Russian scientist is largely forgotten now. However, he was the first to spot the connection between the early therapsids and the mammals. He seems to have had an anatomical intuition and depth of learning which suggests a comparison with Cuvier. 0521554764WS.pdf. ATW020525.

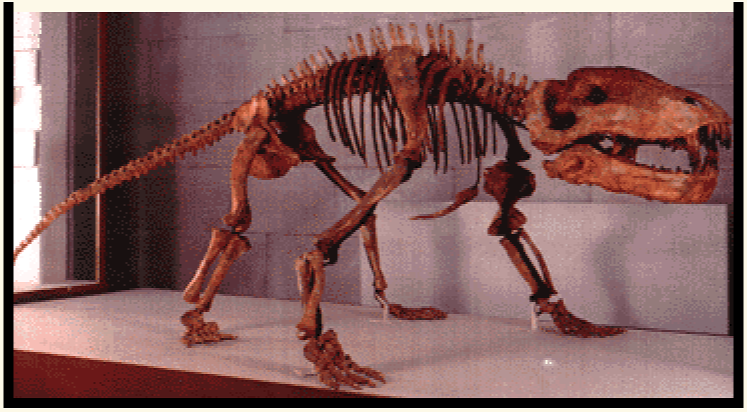
***Titanophoneus*:** *T. potens* Efremov 1938.



Range: Late Permian of Russia (Kamennyi Valley, near Isheevo, Perm region. Early Tatarian)

Phylogeny: Anteosauridae:: Anteosaurinae + *.

Characters: Medium to large-sized predator [BS00]; long snout [BS00]; pineal fossa in boss [BS00]; dorsal & posterior orbital margin thickened [BS00] (also prefrontals?); palatines with teeth [BS00]; 7-8 palatine teeth, recurved; pterygoid flanges with 2 teeth each [BS00]; lower jaw deep; canines large, transversely compressed, with anterior & posterior keels [BS00]; postcanine teeth



small [BS00] (implies reliance on mass of jaw for inertial biting, rather than strong jaw muscles); body lightly built [BS00]; pelvis very primitive; femur slender.

Note: Along with *Anteosaurus*, *Titanophoneus* was the largest of the anteosaurs, and clearly played the role of a top predator in its terrestrial tetrapod assemblage. The specimen usually illustrated (*above*) was found articulated and represents a young animal, with a skull about 26 cm in length. An adult skull would be almost one meter in length. The long snout, the long tail and the short limbs are all primitive, typically anteosaur features. It is interesting to compare the above drawing with the mount (see left), apparently of the same animal. In the photograph the back does not have the giraffe-like slope, and the tail appears shorter. MAK 000902.

Links: Titanopheus potens; dinosaurs- titanophoneus potens; Synapsid Classification & Apomorphies; Biology 356; Great Asian Dinosaurs! Unique Creatures from Russia's Vaults - opens December 26, 2001 - ROM Media Release (thumbnails link to *huge* jpgs); therapsid4a; Titanopheus potens; Synapsid Classification & Apomorphies

References: Battail & Surkov (2000) [BS00]. ATW030920.

Anteosaurinae: These are very specialized, very large anteosaurs. The postcanine teeth are further reduced. Deepening of the postorbital region of the skull (behind the eyes) produced a larger temporal opening, indicating more muscle mass. The boss on the angular (rear of the jaw) has become very prominent, again, another sign of powerful jaw muscles. These huge animals were clearly formidable predators.

In the Anteosaurinae, pachyostosis is taken to extremes. The dorsal (upper) surface of the nasal, frontal, and postfrontals (around and between/above the eyes) is thickened and rugose in the same manner as the tapinocephalids. Nevertheless these animals are two specialized and too late in time to have been the ancestors of the herbivorous tapinocephalids, so it is obvious that these characteristics evolved independently. Boonstra notes that the hip joint and the femur of *Anteosaurus* is comparable with those of the crocodile and that these animals may have had a crawling habit. In view of the carnivorous dentition, he believes them to have been slinking predators.

Range: Late Permian of Russia & South Africa.

Phylogeny: Anteosauridae:: *Titanophoneus* + *: *Anteosaurus* + *Doliosauriscus*.

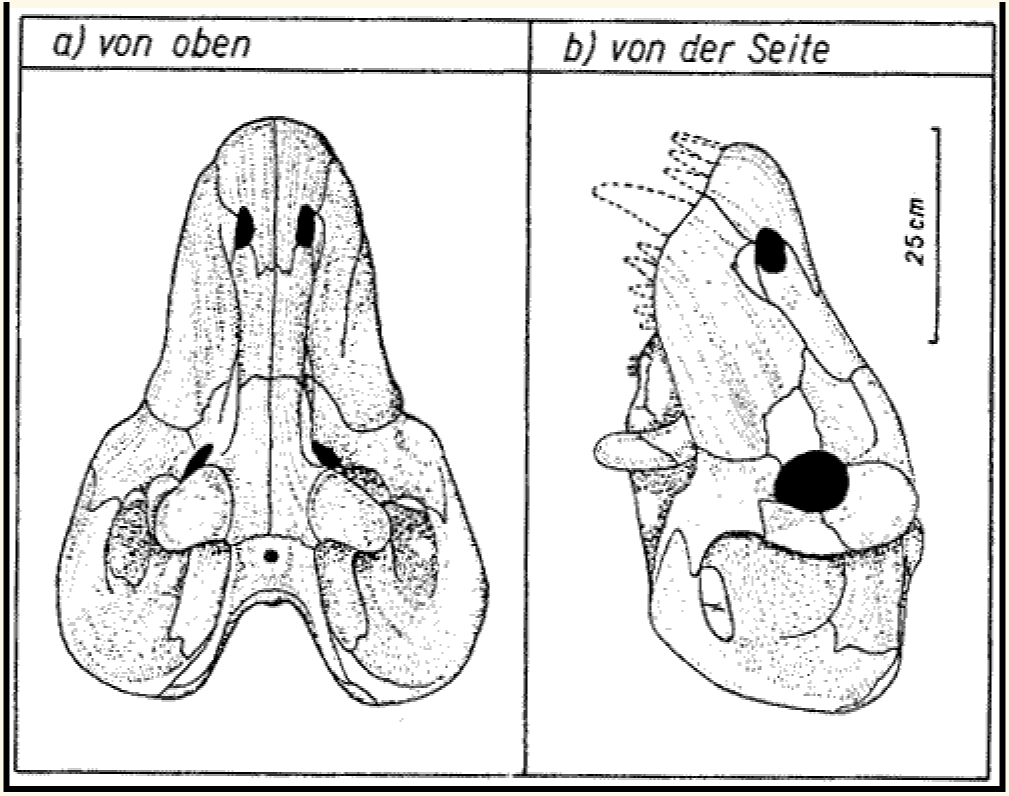
Characters: generally very large; peri- and inter-orbital region with strong pachyostosis; larger postorbital skull with larger temporal fenestra; angular with large boss; postcanine teeth further reduced. ATW020525.

Anteosaurus: *A. magnificus* Watson 1921. Known from 32 partial or complete skulls, assorted post-cranial elements. Probably the only valid genus and species of *Anteosaurus* [B69].

Range: Late Permian of South Africa (*Tapinocephalus* Zone - Capitanian epoch).

Phylogeny: Anteosaurinae: *Doliosauriscus* + *.

Characters: adult skull - 80 cm long; overall length probably 5- 6



m, weight 500- 600 kg; postfrontal forms a boss of variable size overhanging the dorso-posterior border of the orbit [B69].

Links: therapsid4b

Note: On this basis of his 1969 description, Boonstra [B69] synonymised six of the seven genera named from the *Tapinocephalus* zone: *Eccasaurus*, *Anteosaurus*, *Titanognathus*, *Dinosuchus*, *Micranteosaurus*, and *Pseudanteosaurus*. Of these, he says, *Dinosuchus* and *Titanognathus* can safely be considered synonyms of *Anteosaurus*. *Eccasaurus*, with a holotype of which the cranial material consists of only few typical anteosaurid incisors, appears to be only determinable as to family. The skull fragment forming the holotype of *Pseudanteosaurus* can best be considered as an immature specimen of *Anteosaurus*. *Micranteosaurus*, the holotype of which contains a small snout, was previously considered a new genus on account of its small size but is better be interpreted as a young specimen of *Anteosaurus*. And likewise, the large number of species attributed to the genus Anteosaurus can also be considered synonyms.

Boonstra still considers as valid the genus *Paranteosaurus*, which is defined as a genus of anteosaurids in which the postfrontal is not developed to form a boss. This is probably an example of individual variation and hence another synonym of *Anteosaurus*.

As with the genera, so the species are also mostly synonyms. The oldest species name, *A. magnificus*, is thus the only valid one. To quote Boonstra again:

"We have 32 skulls of *Anteosaurus*, of which 16 are reasonably well preserved and on them ten species have been named. To differentiate between the species the following main characters have been used: the number, size and shape of the teeth, skull size, shape and the nature of the pachyostosis. On re-examination it has become clear that the crowns of the teeth are seldom well preserved; basing the count for the dental formula on the preserved roots is unreliable. As this is affected by age and tooth generation; size of skull is a function of age and also possibly sex; skull shape is greatly affected by post-mortem deformation, and the variability in the pachyostosis, which may be specific in some respects, can just as well be the result of...physiological processes. Specific diagnosis consisting of the enumeration of differences of degree in features such as the above can hardly be considered as sufficient indication of the existence of discrete species.... *A. magnificus* thus has the following synonyms: *abeli, acutirostrus, crassifrons, cruentus, laticeps, levops, lotzi, major, minor, minusculus, parvus, priscus* and *vorsteri*."

The reason for the synonymy he gives as follows: the holotypes of *cruentus, levops, minor, minusculus*, and *parvus* are of immature animals; *lotzi* and *priscus* are specifically indeterminable; and in the case of *abeli, acutirostrus, crassifrons, laticeps, major* and *vorsteri* because the characters used are either due to post-mortem deformation or individual variation in the degree of pachyostosis. Ironically, a lot of these specific and generic synonyms were named by Boonstra himself, who reversed his earlier decisions later on.

Image: from [M85].

Links: Anteosaurus (excellent images); therapsid4c (notes on way of life); South African Museum - Fossil Reptiles of the South African Karoo (fauna); South African Journal of Science (abstract on fauna & biozone).

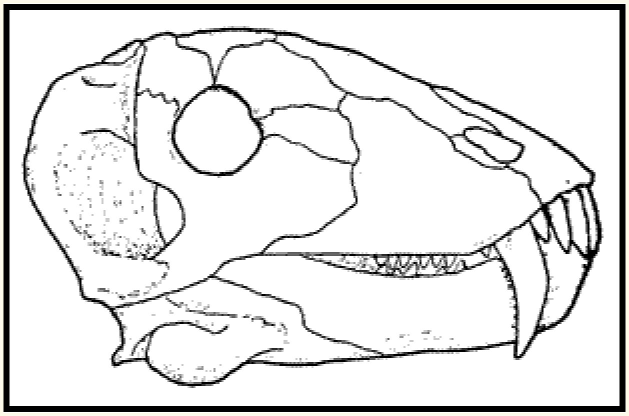
References: Boonstra (1969) [B69]; Müller (1985) [M85]. ATW030807.

Doliosauriscus: *D. yanshinovi* Kuhn 1961; *D. adamanteus* Orlov 1958 (distinguished by having shorter snout).

Range: Late Permian of Russia.

Phylogeny: Anteosaurinae: *Anteosaurus* + *.

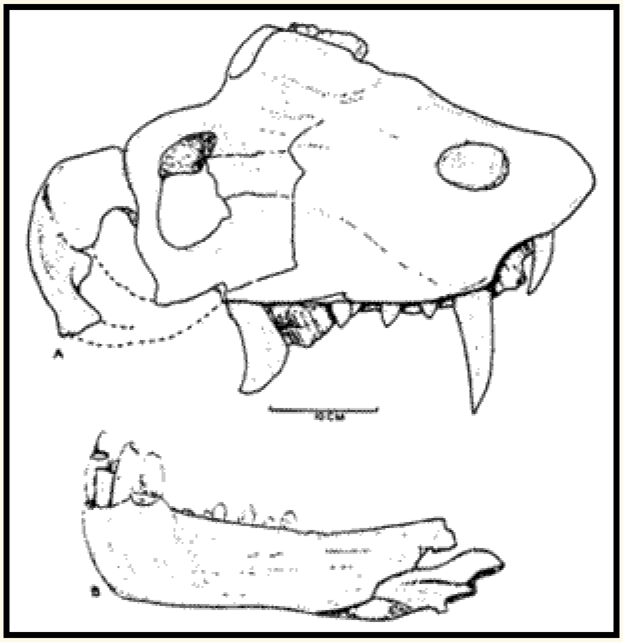
Characters: large [BS00]; skull high [BS00]; skull roof thickened, with tuberosities [BS00]; orbits small [BS00]; thick postorbital bar [BS00]; palatines & pterygoids with small teeth [BS00]; strong lower jaw with massive symphysis [BS00]; canines rounded [BS00]; palatal depressions house canines & first postcanine teeth [BS00].



***Doliosauriscus yanshinovi* (Orlov 1958)**
Type species
Locality: Kamennyi Valley, near Isheevo , Cis-Uralian, Perm region, Russia
Age: Lower Tatarian Substage, Middle Permian ("Zone II")
Material: skull (left), length 530 cm, and skeleton (below)

Along with *Titanophoneus*, this is the largest species of anteosaur from Isheevo. According to Olson (1962), there is an excellent skull (*right*), with some restoration and some flattening. The skull is high and straight, the orbits and pineal opening not very large. All dorsal (upper) skull bones thickened with tuberosities, the parietals (in the middle rear) greatly so.

Olson (1962) suggests that the crushing may be somewhat less extensive than Orlov's restorations suggest and that the skull was proportionately somewhat lower and broader than that of *Titanophoneus*. The postorbital bone is very large and forms a strong bar between the orbit and the temporal opening, for the attachment of the jaw musculature. In spite of the large size the skull is typically brithopodid, the basic structure much the same as in *Titanophoneus* and *Syodon*



***Doliosauriscus adamanteus* (Orlov 1958)**

Locality: Malyi Uran (Churan), Russia
Age: Lower Tatarian Substage, Middle Permian ("Zone II")
Material: known from the skull (*right*)
A,. Skull in lateral aspect as preserved B Lower jaw and teeth. There is no certainty these come from the same animal. Both from Malyi Uran locality. Skull length 500-550 mm.

This species is based upon a specimen from Malyi Uran (Malouran). Olson (1962) suggests that this specimen is sufficiently different from *D. yanshinovi* that it might well be considered a different genus, related more closely to Titanophoneus.

References: Battail & Surkov (2000) [BS00]; Olson (1962) [O62]. ATW020525.

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Therapsida: Tapinocephalia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   |     |--Styracocephalus
   |     `--+--Titanosuchidae
   |        |  |--Titanosuchus
   |        |  `--Jonkeria
   |        `--Tapinocephalidae
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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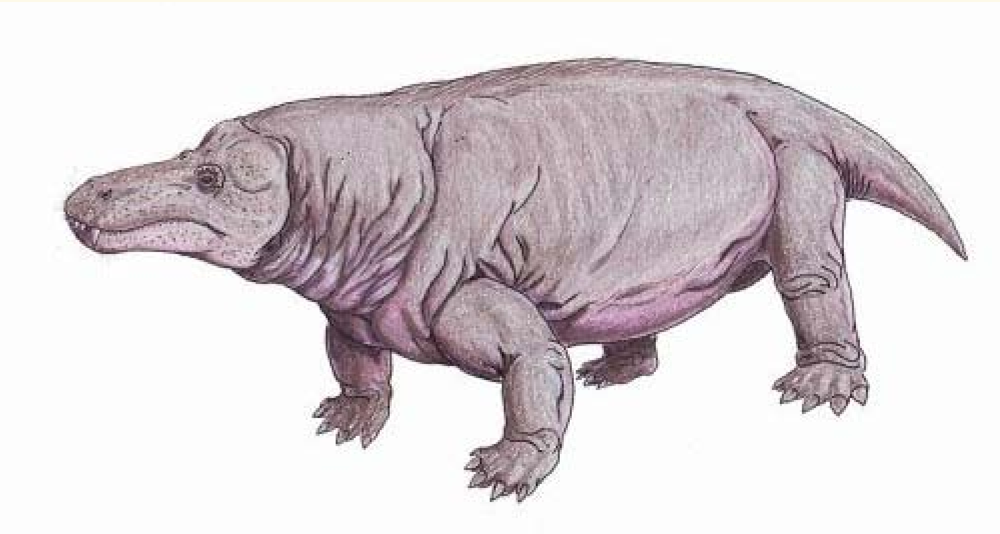
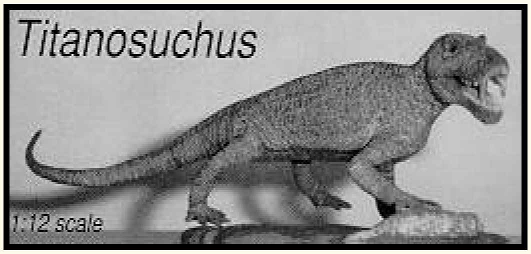
Tapinocephalia



Jonkeria - artwork by Dmitry Bogdanov - Wikipedia

The **Tapinocephalia** are the major herbivorous clade of the Dinocephalia. Unlike the anteosaurs and estemmenosuchids, the tapinocephalians are primarily an African group. The estemmenosuchids and pareiasaurs may have occupied this paleo-bovine niche in the north. Only one tapinocephalian, *Ulemosaurus*, is known from Russia. The Tapinocephalia are thought to consist of three clades: ***Styracocephalus*** (sometimes assigned to a family of its own, the Styracocephalidae), the **Titanosuchidae**, and the very successful Tapinocephalidae. ATW020524.

A number of rather imperfect skulls constitute the Styracocephalidae, small herbivorous dinocephalians who retained a moderate canine. Characteristic are the prominent posteriorly directed tabular bosses, weak, conical incisors and canine, and a long series of postcanines. The palatal teeth are very well developed, even on the vomer. All known forms come from a single species, *Styracocephalus platyrhynchus* Haughton 1929, from the *Tapinocephalus* Zone, Beaufort Beds, Beaufort West, Karoo, South Africa. These animals are similar to both the anteosaurs and the Estemmenosuchids, and are indeed believed to be closely related to both. MAK000809.



Among the **Titanosuchidae**, the large canine has been retained and the very strong incisors have a piercing talon and a crushing heel. Although the sharp front incisors and fanglike canines at the front of the jaws, might seem to indicate a carnivorous diet, the long series of post-canine teeth have leaf-shaped and serrated spatulate crowns, indicating these animals were at least partially herbivorous. Titanosuchids share with the more specialized tapinocephalids the presence of an enlarged heel on the incisor teeth, with a reduced canine, with the jaw hinge still further anterior. There is however very little pachyostosis (thickening of the skull).

There are only two genera, distinguished only by length of limb bones. It is sometimes suggested that the short-limbed ***Jonkeria*** was a herbivore, and the longer limbed ***Titanosuchus*** a carnivore. Boonstra (1969) has the family Titanosuchidae composed of two genera and nine species. I think this many species is excessive, it was probably no more than three or four species. Boonstra also states that the genera *Titanosuchus* and *Jonkeria* cannot be distinguished from one another on either cranial or dental characters, but in *Titanosuchus* the limb-bones are long, whereas in all the species of *Jonkeria* they are short and squat. However, King (1988) suggests a number of differences, including a large and massive skull in *Titanosuchus*, and a medium to large skull in *Jonkeria*, indicating *Titanosuchus*'s supposedly carnivorous lifestyle in contrast to the presumably herbivorous *Jonkeria* More probably both were omnivores, eating mostly plants, but sometimes carrion or even live animals (comparable omnivores today include bears, pigs, and baboons). MAK000802.

Tapinocephalia: *Tapinocephalia* > *Anteosaurus*. *Criocephalus.*

Range: Middle Permian to Late Permian of Russia & South Africa

Phylogeny: Dinocephalia **:** Anteosauria + * **:** *Styracocephalus* + (Titanosuchidae + Tapinocephalidae).

Characters: various horns & cranial protuberances [RS01]; pachyostosis of skull bones (head butting?) [RS01]; most have upper & lower canines [RS01]; incisors, even postcanine dentition may be interdigitating and equipped with heel & talon [RS01].

Links: Moschops;

References: Rubidge & Sidor (2001) [RS01]

Note: My personal candidate for ugliest tetrapod taxon of all time. ATW040312.

Styracocephalus:

Range: Middle Permian of South Africa (*Tapinocephalus* Zone).

Phylogeny: Tapinocephalia **:** (Titanosuchidae + Tapinocephalidae) + *.

Characters: prominent posteriorly directed tabular bosses; palatal teeth very well developed, even on vomer; weak, conical incisors and canine; long series of postcanines.

Links: therapsid4b

Note: Note that all three dinocephalian clades developed similar dentition independently. *Styracocephalus*, like the most basal therapsids, had numerous palatal teeth and relatively undeveloped incisors. Yet, as we will see, the advanced tapinocephalids, like the more derived anteosaurs and estemmenosuchids, increasing relied on powerful interdigitating incisors, with a very reduced complement of palatal teeth and relatively weak postcanines. ATW020524.

Titanosuchidae:

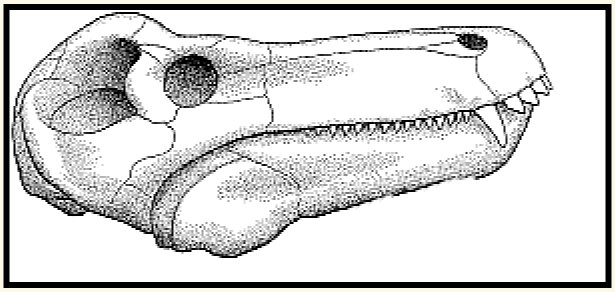
Range: Middle Permian of South Africa.

Phylogeny: Tapinocephalia **::** Tapinocephalidae + * **:** *Titanosuchus* + *Jonkeria*.

Characters: pachyostosis less pronounced than in tapinocephalids; jaw hinge further anterior than in tapinocephalids; incisors strong, with talon and a crushing heel; canines large; numerous postcanine teeth with leaf-shaped & serrated spatulate crowns. ATW020524.

Note: As is so often the case, the understanding of this group has been cluttered by a terrible excess of useless names, described on the basis of fragmentary material, and giving the impression that there were many more species around than there really were. The problems began when Sir Richard Owen, the famous English paleontologist, described *Titanosuchus ferox* in 1879 based on the roots of an incomplete set of teeth. As all the material from the Karoo was new to science at the time, even the poorest specimen warranted description.

In the race to name as many new species as possible Broom added a ballast of names on equally poor material. It has since been shown that even well-preserved batteries of teeth exhibit so much variation, with even the left and right sides of the same skull, that dental features are a very unreliable criterion for distinguishing between titanosuchids. MAK000802



Titanosuchus: (= *Scapanodon* = *Parascapanodon*) *T. ferox* Owen 1879.

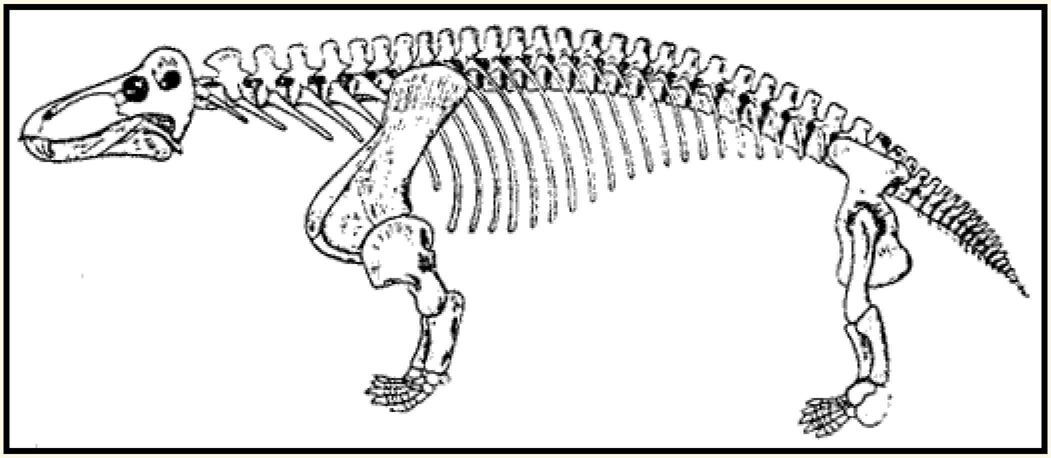
Range: Middle Permian of South Africa (*Tapinocephalus* Zone).

Phylogeny: Titanosuchidae **:** *Jonkeria* + *.

Characters: 2.5 m; legs short.

Links: South African Museum - Fossil Reptiles of the South African Karoo; Dinosaurios: Titanosuchus; Titanosuchus.

Note: Widely said to be a carnivore, but apparently this is incorrect. ATW020524.



***Jonkeria*:** (= *Phoneosuchus angusticeps*) *J. truculenta* Van Hoepen 1916b.

Range: Middle(?) Permian of South Africa.

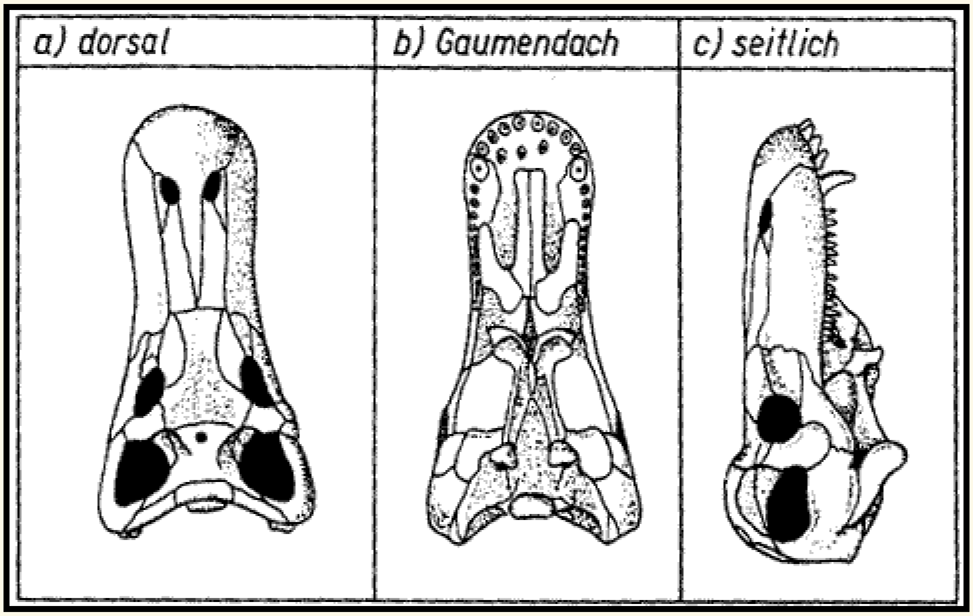
Phylogeny: Titanosuchidae : *Titanosuchus* + *.

Characters: Very large (4-5 m); elongated snout; large incisors and long canines; limbs stout & long. ATW020524.

Other species:

J. ingens Broom 1929. The holotype, originally *Dinophoneus ingens*, together with its synonym, *J. pugnax* Broom, 1929, and three other known skulls constitute a distinct species of *Jonkeria*.

J. vanderbyli Broom, 1929: The holotype is a good skull of *Jonkeria* which according to Boonstra is easily distinguishable from the other species of the genus.



J. haughtoni Broom, 1929: The type is a fairly good skull, with some limb-bones, which can be placed in the genus *Jonkeria*. It can be distinguished from the other species of the genus. Synonym: *Dinosphageus haughtoni* Broom, 1929 - original name *J. crassus* Broom, 1929. According to Boonstra, in the holotype consisting of dentaries and postcranial bones, the humerus cannot be distinguished from that of *J. haughtoni*, and as there are no other distinctive features it should be considered a synonym of *J. haughtoni*.

J. koupensis Boonstra, 1955: The holotype is a good pelvis readily distinguishable from that of any other known species of Jonkeria.

J. parva Boonstra, 1955: A small humerus is quite distinct from that of the other known species of Jonkeria. I think it is not unlikely this may turn out to a distorted or otherwise modified specimen.

J. rossouwi Boonstra, 1955: The holotype consists of postcranial bones readily distinguishable from those of the other species of the genus. Two other specimens are known that show the same distinctive features, indicating this is a valid type (probably corresponding to one of the species name on skull characteristics).

J. boonstrai Janensch, 1959: According to Boonstra, Janensch has given a convincing diagnosis of the specific features of the holotype skull. He also stresses the herbivorous nature of the dentition. MAK000809.

References: Boonstra (1969).

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Therapsida: Tapinocephalia: Tapinocephalidae

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Stenocybus
   |  |--Estemmenosuchidae
   |  |--Anteosauria
   |  `--Tapinocephalia
   |     |--Titanosuchidae
   |     `--Tapinocephalidae
   |        |--Ulemosaurus
   |        |--Tapinocaninus
   |        `--+--Struthiocephalus
   |           |--Tapinocephalus
   |           |--Keratocephalus
   |           |--Moschops
   |           `--Riebeeckosaurus
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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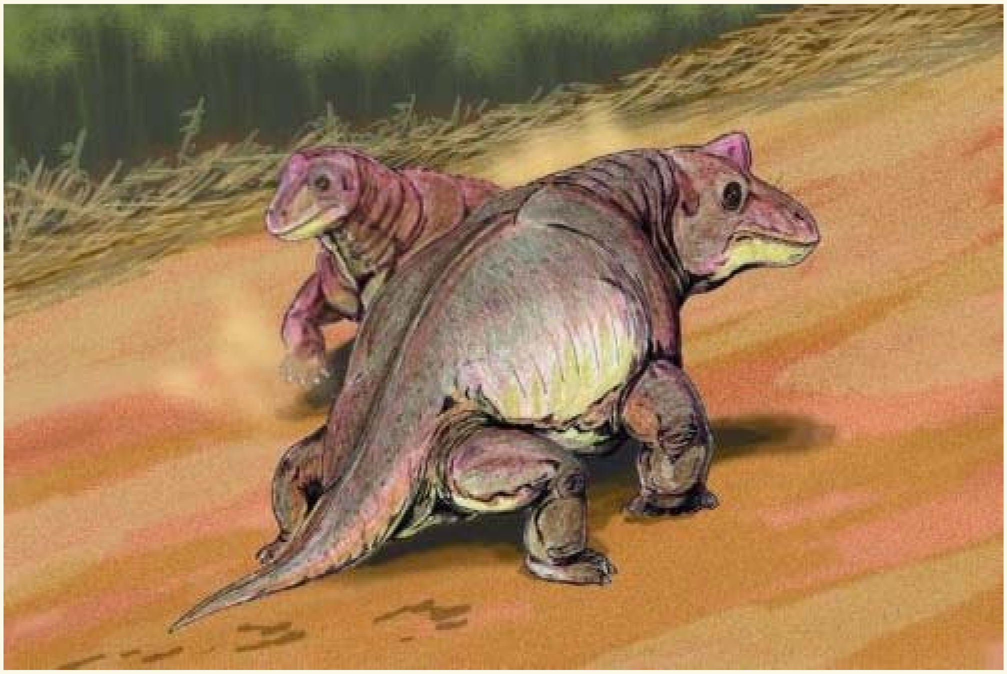
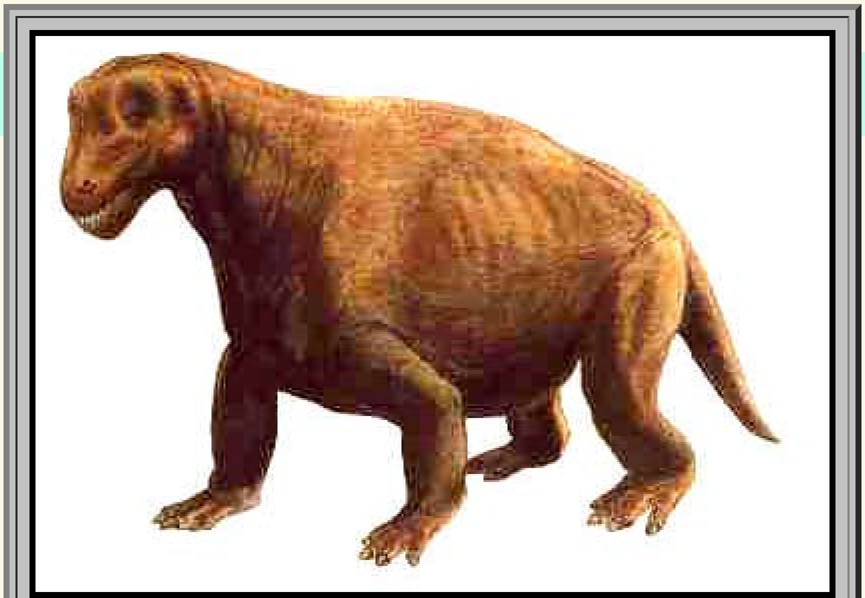
6. Tapinocephalidae X
7. *Tapinocephalus* X
8. *Ulemosaurus* X

Tapinocephalidae



Keratocephalus - life reconstruction artwork by Dmitry Bogdanov - Wikipedia

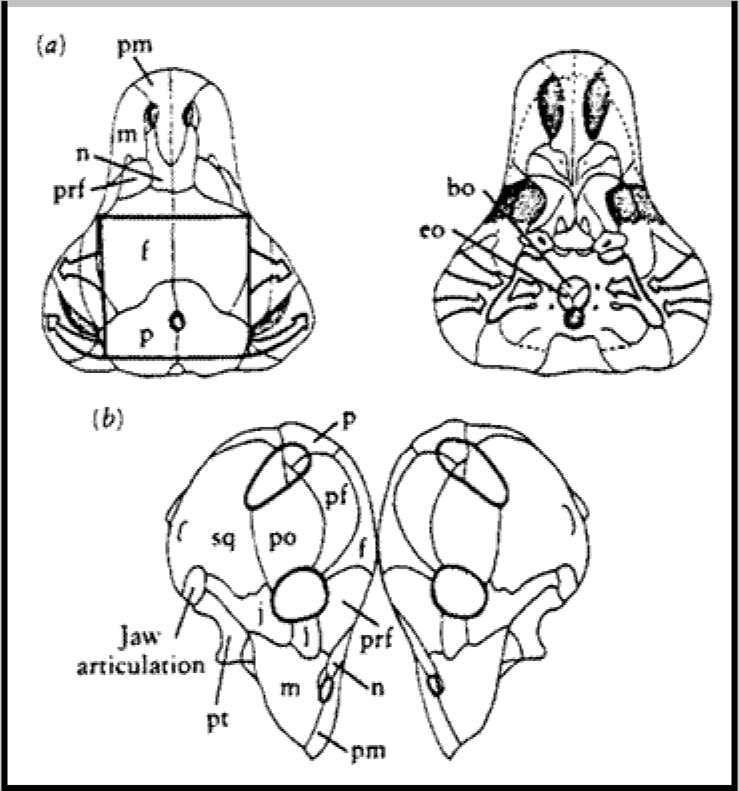
Tapinocephalidae



***Moschops capensis*, from the Karoo Series of South Africa. Length about 2.5 meters. Image from Cox *et al*. (1988)**

The **Tapinocephalidae** were an advanced family of giant herbivorous Dinocephalia, with an adult weight from about 500 to 1000 kg -- possibly up to 1.5 or 2 tonnes in the largest forms, such as ***Tapinocephalus*** *atherstonsi*. They are known from both Russia and South Africa. In all probability, the Tapinocephalidae had a worldwide (Pangean) distribution. The trend towards gigantism, so typical of many of the dinocephalians, was characteristic of even the earliest known members of this family. Along with pareiasaurs, these were the "heavies" of the Middle Permian. They flourished briefly during the Wordian and Capitanian ages, radiating into several lineages, existing simultaneously, and differing mainly in details of the skull and, to an even lesser degree, the skeleton. It is not clear how such similar animals could each find their own ecological niche, but such was obviously the case. There is a parallel here with the hadrosaur and ceratopsian dinosaurs of the Late Cretaceous. The cause of their abrupt extinction is not clear, since other smaller animals, and even the pareiasaurs, were not affected. Quite probably, like the extinction of the late Pleistocene megafauna, a number of factors were involved.

The tapinocephalid skull is massively constructed, and either long-snouted (e.g. ***Struthiocephalus***) or high and short (e.g.



Moschops **skull, showing areas of pachyostosis and distribution of forces in hypothetical head-butting combat. From Barghusen (1975).**

Moschops). Very often the top of the head is rounded, and the bones of the forehead are elevated into a sort of dome or boss, in the middle of which is a large pineal opening. In some specimens this boss is of only moderate thickness, while in others it has become greatly thickened into a huge mass of bone (pachyostosis). It has been suggested that these animals engaged in intra-specific head-butting behavior, presumably for territory or mates. A similar thickening of the skull occurs in pachycephalosaurian ("boneheaded") dinosaurs, and it is speculated that all of these animals practiced head-butting behavior like modern goats and bighorn sheep, or Late Eocene titanotheres.

In keeping with their vegetarian lifestyle, the chisel-edged teeth are undifferentiated, lacking canines, and rather peg-like. In maturity the teeth have a talon and a crushing heel and the upper and lower teeth of the whole battery intermesh.

The body is deep and capacious, allowing for a developed herbivore gut. The shoulders are much higher than the pelvic region, so that the back slopes, giraffe-fashion, from neck to tail. This seems to imply that they fed on vegetation of about a meter or more from the ground

The limbs are heavy, with sturdy forelegs that sprawled out to the sides, while the longer hind legs were placed directly under the hips (the dicynodonts had the same posture). The feet are broad and short.

Lifestyle and Metabolism

There is some disagreement over whether these animals lived in dry upland environments (Colbert), swamps, or either, depending on the species or tribe. There is no doubt that the Tapinocephalidae occupied different ecological niches. However, the tendency of earlier writers like Gregory (1926) and Boonstra (1965) to consider them semi-aquatic wallowers is reminiscent of the old fable of the sauropods consigned to the swamps because their limbs were too clumsy and their bodies too heavy for them to exist on dry land. In fact, if they were head-butters, it is unlikely they could have been clumsy swamp wallowers, since head-butting implies some degree of mobility.

Boonstra suggests that form such as *Tapinocephalus* and *Struthiocephalus* were semi-aquatic, while *Moschops* was terrestrial. It is quite likely that some tapinocephalid species may have frequented pond margins, feeding on soft vegetation, others preferred dry uplands. Gregory (1926) considered that dinocephalians were aquatic animals, the wide hands and feet and the extensive fore and aft reach being useful for propelling the animal through water and the massive forehead being an advantage in diving. He suggested that the pineal organ might have been phototropic, helping the animal to orient itself relative to the surface of the water. Tapinocephalines were seen by Boonstra (1956) as semi-aquatic animals. The cumbersome body, poor locomotor apparatus and feeble lower jaw and massive cranium all suggested to him that these animals could not have fed efficiently on land on tough vegetation. Instead he presented them as wallowers, being buoyed up by water, feeding on soft marsh vegetation.

Rescuing the tapinocephalids from a life of diluvian swamp-wallowing, Bakker (1975, 1986) argued that bone histology, geographic distribution, and predator-prey relationships showed that these were active, fully terrestrial and at least partially endothermic animals, midway between the ectothermic pelycosaurs and the fully endothermic theriodonts. Others like McNab and Geist suggest that the tapinocephalids were better considered inertial homeotherms, with the large barrel-like body and short tail being the most efficient surface for conserving heat.

My own position, for what it is worth, is that these were all fully or at least mostly terrestrial animals, although possibly (but not necessarily) evolving from semi-aquatic ancestors (many of the Russian dinocephalians seem to have lived a semi-aquatic lifestyle). They were inertial homeotherms, not endotherms, and rather than the ungainly antediluvian bumblers, were well adapted, successful animals that dominated their environment. Their demise was the result of a sudden environmental stress, perhaps a combination of climatic and vegetation change and exotic disease, which naturally hit these big, K-selected (slow to reproduce) creatures hardest. MAK020416.

Tapinocephalidae:

Range: Middle Permian to Late Permian of South Africa & Russia

Phylogeny: Tapinocephalia:: Titanosuchidae + *: *Ulemosaurus* + *Tapinocaninus* + (*Struthiocephalus* + *Tapinocephalus* + *Keratocephalus* + *Moschops* + *Riebeeckosaurus*).

Characters: extensive cranial pachyostosis, with reduction in size of temporal fenestrae [BS00]; pineal boss normally massive; jaw hinge displaced forward [BS00]; incisors with well-developed heels [BS00]; canines reduced [BS00]; teeth interdigitate [BS00].

Links: for once, we are more or less in complete agreement with the **Mikko's phylogeny**. Unfortunately, there is little else on the web worth mention. Most sites seem to be devoted to one of the particular members of this outstandingly ugly taxon, usually *Moschps* or *Ulemosaurus*.

References: Battail & Surkov (2000) [BS00]. ATW050930.

Ulemosaurus: *U. svijagensis* Ryabinin 1938

Range: Late Permian of Russia. Kamennyi Valley, near Isheevo, Perm region. Isheevo Dinocephalian Complex, Lower Tatarian Substage, Middle(?!) Permian ("Zone II"). 3 skulls. Postcrania also known.

Phylogeny: Tapinocephalidae: *Tapinocaninus* + (*Struthiocephalus* + *Tapinocephalus* + *Keratocephalus* + *Moschops* + *Riebeeckosaurus*) + *.

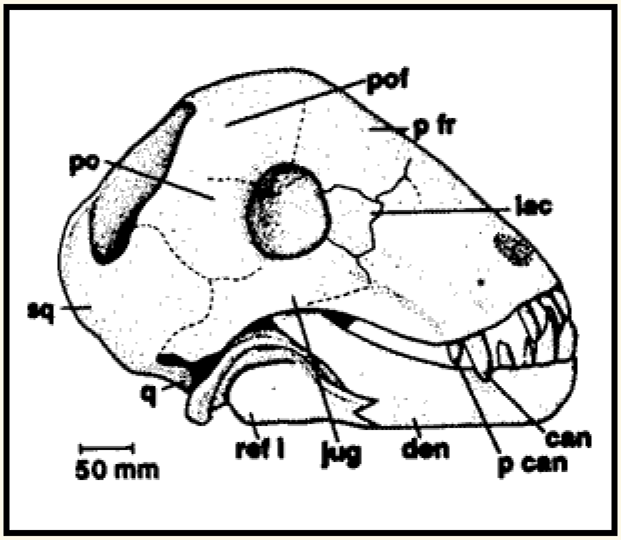
Characters: very large form [BS00]; snout narrow & tapering [BS00]; skull wide and very tall in postorbital region [BS00]; thick cranial roof [BS00]; dorsal border of roof strongly pachyostosed [BS00]; broad postorbital bar [BS00]; temporal opening relatively large [BS00]; incisors large [BS00]; canines of medium size [BS00]; anterior postcanines much larger than posterior postcanines [BS00].

Links: Gondwona Studios; Ulemosaurus; PERMIANO terapsídeos 1.

References: Battail & Surkov (2000) [BS00]; Boonstra (1963).

Note: This genus was originally taken for *Moschops* or perhaps a near relative. Boonstra (1963). It is now regarded as a considerably more basal form. ATW020526.

Tapinocaninus: *T. pamelae*

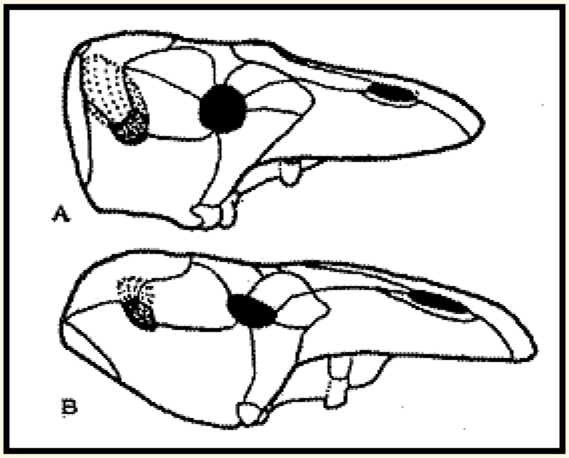


Range: Middle Permian of South Africa. *Eodicynodon* Zone, Karoo deposits, Beaufort series. Wordian Age.

Phylogeny: Tapinocephalidae: *Ulemosaurus* + (*Struthiocephalus* + *Tapinocephalus* + *Keratocephalus* + *Moschops* + *Riebeeckosaurus*) + *.

Characters: very large (3 m & 1000 kg).

Links: NAPC Abstracts, Ra - Ru; BPI Palaeontology (Wits University; University of the Witwatersrand, Johannesburg); paleontology; fossils; South Africa; therapsid2b; Albany Museum -- Karoo Fossils. ATW020526.



Struthiocephalus: *S. whaitsi* Haughton, 1915a.

Range: Middle Permian of South Africa. *Tapinocephalus* Zone, Karoo deposits, Lower Beaufort Beds; Beaufort West.

Phylogeny: Tapinocephalidae:: *Tapinocephalus* + *Keratocephalus* + *Moschops* + *Riebeeckosaurus* + *.

Characters: Fairly strong snout; moderate pachyostosis; "male" morph with large naso-frontal boss; perhaps 3m & 1000 kg.

Links: Albany Museum -- Karoo Fossils.

Image: *Struthiocephalus* skulls It is likely there is only one species, *Struthiocephalus whaitsi*. *Struthiocephalus* (A) probably represents the male form, *Struthiocephaloides* (B) the female. Illustration from Boonstra (1969).

References: Barghusen (1975), Boonstra (1965), Boonstra (1969), Brink (1956), King (1988).

Notes: Brink (1956) suggests that *Struthiocephalus* fed in or near water, the teeth being used for rooting up, gathering and grasping plant matter. Boonstra (1965) likewise considered that *Struthiocephalus* fed on soft vegetation, possibly under water. He suggested the postcranial skeleton possibly showed adaptations to living in marshy conditions (but see comments above), and the bone surface around the nostril might indicate the presence of a fleshy valve present used for closing off the nostril under water.

The long-snouted *Struthiocephalus whaitsi* would seem to be the only genus and species of this taxon. This animal has the largest head of any tapinocephalid. There area large number of synonyms. *Struthiocephalellus* is apparently a juvenile of *Struthiocephalus*. Boonstra showed that the seven named species of *Struthiocephalus* represent a growth series and are hence synonyms of the first described species, *whaitsi*.

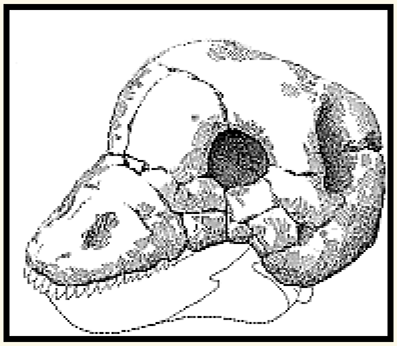
Struthiocephalus is characterized simply by a naso-frontal boss in mature specimens, whilst the very similar genus *Struthiocephaloides* lacks this character. This is consistent with a sexually dimorphic character, as well as a role in intraspecific combat. Barghusen (1975) considers would be more effective in flank butting than head-butting *per se*. In head-on combat the presumed horn would be deflected by the opponent's head and contact would be lost, but in flank butting a horned boss would concentrate the blow. Both "*Struthiocephalus*" and "*Struthiocephaloides*" have the same stratigraphic range - Lower to Middle *Tapinocephalus* Zone

Of the remaining two monospecific genera, *Struthionops intermedius* known from a single skull, possesses a naso-frontal boss moderate pachyostosis and a fairly short snout. Possibly this is a variant of another species. On the basis of the shorter snout, King (1988) includes this species among the Tapinocephalini.

Taurocephalus lerouxi, known from a single skull, has a fairly strong snout and 20 teeth in the upper jaw (more than usual for Tapinocephalids). Since tooth count tends to vary greatly among individual dinocephalians, again only this is also likely a variant individual, most probably *Struthiocephalus*

The remaining species *Moschosaurus longiceps*, Haughton is known from a single small and lightly built skull about 25 cm. long from the Upper *Tapinocephalus* Zone. It was originally placed in its own family, the Moschosauridae, and considered a good ancestral or primitive form (despite its late date). However, Boonstra (1969) identifies it as a juvenile *Struthiocephalus*. ATW020525

Tapinocephalus: *T. atherstonei* Owen 1876 (?)



Range: Middle Permian of South Africa. *Tapinocephalus* Zone, Karoo deposits, Lower Beaufort Beds; Beaufort West

Phylogeny: Tapinocephalidae: *Struthiocephalus* + *Keratocephalus* + *Moschops* + *Riebeeckosaurus* + *.

Characters: over 3m & 1500 kg; adult skull 45 cm; short weak *Moschops*-like snout., heavily pachyostotic skull roof; massive bony frontals.

Links: South African Museum - Fossil Reptiles of the South African Karoo; NAPC Abstracts, Ra - Ru; ALBANY MUSEUM - KAROO FOSSILS.(images in a sort of American Primitive style);therapsid2b (good, non- technical species account);

Comments: *Tapinocephalus atherstonei* is the only species of this genus. It is known from a number of skulls and postcranial bones. The skull is large with a heavily pachyostotic skull roof, a massive bony frontals and a short weak Moschops-like snout. *Taurops* is a synonym. This successful animal survived right until the end of the *Tapinocephalus* zone. *Phocosaurus megischion* differs from *Tapinocephalus* only in that the transition from the frontals to the snout is not abrupt. In view of the fact that it too continues until the upper *Tapinocephalus* zone, I would tend to see this as synonymous with *Tapinocephalus* zone, the differences being sexually dimorphic ATW030730, MAK020416.

Keratocephalus: *K. moloch*

Range: Middle Permian of South Africa. Lower and Middle *Tapinocephalus* Zone, Karoo deposits, Lower Beaufort Beds; Beaufort West.

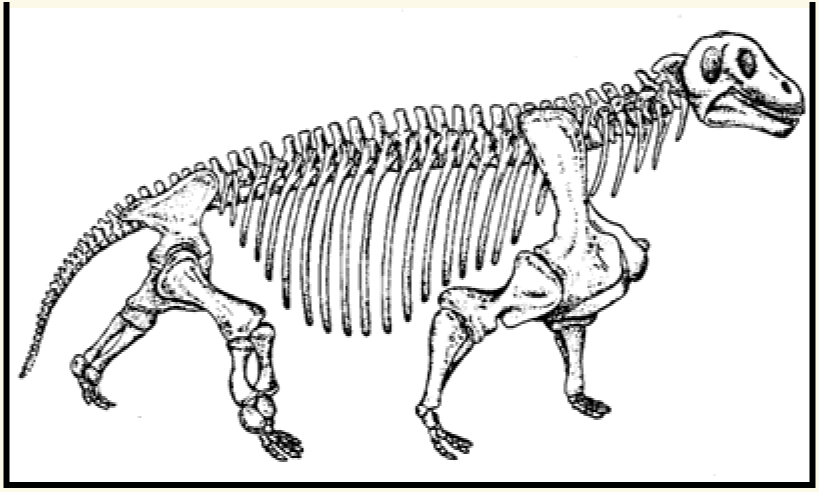
Phylogeny: Tapinocephalidae:: *Struthiocephalus* + *Tapinocephalus* + *Moschops* + *Riebeeckosaurus* + *.

Characters: 2.5 to 3 m long (skull 50 cm); 700 to 1000 kg; variable snout length; variable pachyostosis; nasofrontal boss raised into horn-like shape; .

Comments: *Keratocephalus moloch*, known from a number of greatly variable skulls, along with postcrania, from the Lower and Middle Tapinocephalus zone, shows considerable variability in the pachyostotic development. It may be not as derived as *Tapinocephalus*. The naso-frontal boss is raised into a sort of horn (hence the name - "horned head") and the length of the snout varies greatly. This in itself throws doubt on Boonstra's distinction between short and long-snouted forms. *Pelosuchus*, known only on the basis of postcranial features, is a synonym. ATW020525 MAK020416.

Moschops: *M. capiensis* Broom 1911

Range: Middle Permian of South Africa. Lower *Tapinocephalus* Zone, Karoo deposits, Lower Beaufort Beds; Beaufort West.



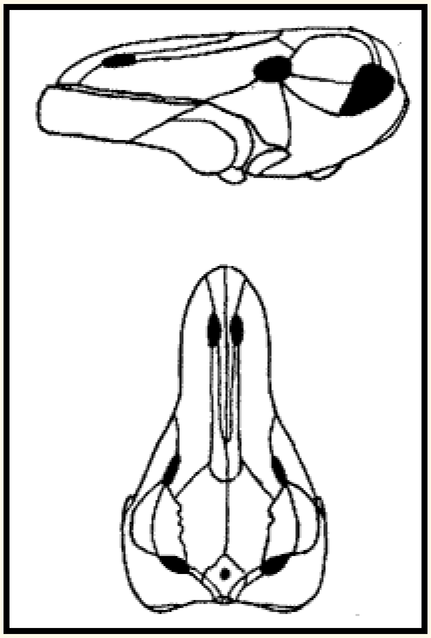
Phylogeny: Tapinocephalidae:: *Struthiocephalus* + *Tapinocephalus* + *Keratocephalus* + *Riebeeckosaurus* + *.

Characters: 2.5-5.0 m; skull very strongly pachyostosed; temporal fenestra strongly reduced; jaws short; marginal teeth chisel-shaped; front limbs sprawling, but rear limbs may have been columnar; tail very short.

Links: Moschops; Moschops Printout - Enchanted Learning Software; Paleontology and Geology Glossary: Mo; Dinosaurios (Spanish); Moschops, an early herbivorous therapsid; PANGEA (Italian); LPermian.html; South African Museum - Fossil Reptiles of the South African Karoo; Moschops (basic data and some small images); [모스콥스(Moschops)] (Korean); Moschops (Portuguese); Moschops - Dinocephalian Head Butting (the Therapsids site, always a good bet).

Comments: *Moschops* (with synonyms *Moschoides*, *Agnosaurus*, *Moschognathus* and *Pnigalion*) is distinguished by a strongly pachyostosed skull with a broad intertemporal region and greatly reduced temporal fossae. There are two species - *capensis* and *koupensis* - that are known from good material, and two species - *whaitsi* and *oweni* - of doubtful validity. It may be that *M. capensis* and *M. koupensis* are not distinct species at all, but gender morphs, and in any case they occupy the same stratigraphic range. The species *Delphinognathus conocephalus*, known from a single weathered skull, has a conical boss on the parietal surrounding the pineal foramen, and exhibits moderate pachyostosis. Boonstra suggests this may simply be a young specimen of *Moschops*; if so, *Moschops* becomes a junior synonym. *Avenantia kruuvleieusis* is only moderately pachyostosed, with a narrow intertemporal region and large temporal fossa. This apparently aberrant form may simply be a juvenile of *Moschops*. ATW031020 MAK020416.

Riebeeckosaurus: *R. longirostris* Boonstra 1952b.



Range: Middle Permian of South Africa. Middle *Tapinocephalus* Zone, Karoo deposits, Lower Beaufort Beds; Beaufort West.

Phylogeny: Tapinocephalidae:: *Struthiocephalus* + *Tapinocephalus* + *Keratocephalus* + *Moschops* + *.

Characters: Medium-sized (2.5 m est. 500 kg); very long, slender snout; narrow intertemporal region with narrow sagittal crest.

Note: Two skulls are known, both from the *Tapinocephalus* Zone. ATW020525 MAK020416.

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checked ATW041118; last modified MAK091111

Therapsida: Anomodontia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--Neotherapsida
      |--Anomodontia
      |  |--Venyukovioidea
      |  `--+--Dromasauria
      |     `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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4. Venyukovioidea X

The Anomodonts

Otsheria netsvetaevi - artwork by Dmitry Bogdanov - Wikipedia

One of the three major evolutionary lines (clades) deriving from the early Therapsida (the biarmasuchia - phthinosuchian - Eotitanosuchia base), were the **anomodonts**, mostly toothless herbivores. These developed at first (during the Wordian and Capitanian epochs) along several paths of adaptive radiation, such as the **Venyukovioidea**, the **Dromasauria**, and the Eodicynodont, Endothiodont. and the higher dicynodonts. Of those groups only the higher Dicynodontia were to be successful, and in fact these stocky, toothless and beaked animals remained the dominant terrestrial herbivores right up until the Carnian epoch (Late Triassic period).

The venyukovioid, represented by a handful of genera, seem to be intermediate in position between the ancestral therapsid condition and the dicynodonts. In these therapsids, as exemplified by the genus *Venyukovia* from the Capitanian (middle Permian) of Russia, there was a reduction in the dentition, and the skull exhibited changes in proportions that were clearly related to the highly evolved skull in the dicynodonts

Very different at first glance are the Dromasaurs. These are small therapsids, with a slight build, slender legs and long tail. The skull is short, with very large orbits (eye sockets). It has been suggested that these animals were actually juveniles, but no adult forms have been found, and it is more likely that they simply resepresent part of the early anomodont radiation.

Note by Christian Kammerer: Dromasaurs are undoubtedly an artificial group, and they are actually quite anomodontian if you consider venyukoviamorphs typical basal anomodonts. Actually, the most basal "dromasaurs" may form a clade (Galechiridae) consisting of *Galechirus*, *Galepus*, and *Patranomodon*, but *Galeops* is probably even closer to the dicynodonts than several "venyukoviamorphs". Several wonderful new basal anomdonts (for example *Suminia*, *Anomocephalus*) have been described recently and greatly elucidate basal anomodont relationships. Modesto *et al*. (1999).

Neotherapsida: Anomodontia + Theriodontia.

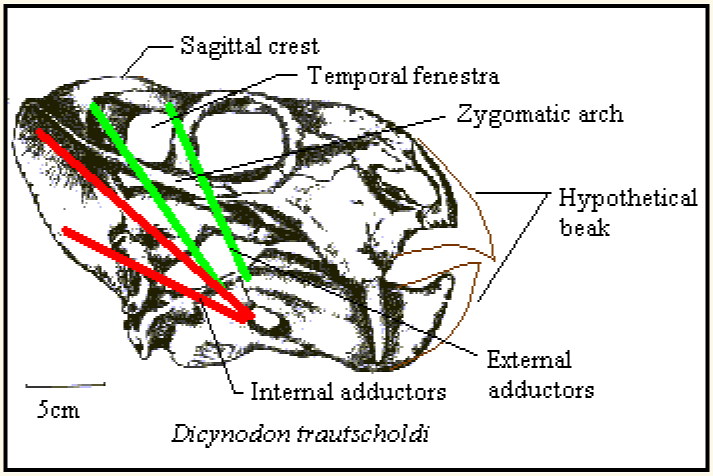
Range: from the Middle Permian.

Phylogeny: Eutherapsida: Dinocephalia + *: Anomodontia + Theriodontia.

Characters: **$** ventrally expanded squamosal [RS01]; temporal fenestra further enlarged; **$** squamosal covers most of quadrate and quadratojugal in posterior view [RS01]; **$** quadrate not sutured to skull; **$** epipterygoid broadly contacts parietal [RS01]; coronoid shortened below tooth row; **$** atlantal epipophyses present [RS01] (no, I *don't* know exactly what this means); **$** large obturator process present on suture between pubis & ischium [RS01].

References: Rubidge & Sidor (2001) [RS01] ATW020219.

Anomodontia: Dicynodonts and relations. *Anomocephalus, Patranomodon, Venjukovia.*



Dicynodon trautscholdi

Range: Middle Permian to Late Triassic worldwide.

Phylogeny: Neotherapsida: Theriodontia + *: Venyukovioidea + (Dromasauria + Dicynodontia).

Characters: Dominated Late Permian terrestrial vertebrate fauna at all size ranges. Only herbivorous therapsid group to survive PermoTriassic extinction; no teeth except maxillary fangs; beak presumably present; jaw articulation allowed anterior-posterior movement of jaw for slicing; long posterior process of premaxilla; nares not terminal; coronoid bone lost; masseter muscle probably absent or poorly developed, so that jaw was closed by very large adductors originating on sagittal crest and on strongly developed, dorsally bowed, zygomatic arch (squamosal + jugal); secondary palate (convergent with mammals), suggesting possible homeothermy and, perhaps, hair; temporal openings extend posterior to occipital condyle, creating central sagittal crest from parietals; post-orbital skull generally light and formed of arches; typical therapsid semi-sprawling posture with short heavy femur and humerus; reduction or loss of internal trochanter of femur.

Image: *Dicynodon trautscholdi* modified from More Dicynodon trautscholdi, courtesy of mathematical.com, and from a similar figure in Carroll (1988).

Note how the adductors operate almost horizontally to both close the jaw and pull it back in a slicing and clipping motion. This is characteristic of all anomodonts. ATW020526.

Venyukovioidea: *Venjukovia, Otsheria, Ulemica, Suminia.* Likely paraphyletic basal anomodonts, including dicynodonts.

Range: Middle Permian (to Late Triassic assuming paraphyly).

Phylogeny: Anomodontia: (Dromasauria + Dicynodontia) + *.

Characters: skulls small & short [C88]; premaxilla forms broad shelf anterior to nares [C88]; zygomatic arch high & thin, exposing adductor muscles broadly between arch & lower jaw [C88]; postorbital contacts squamosal [C88]; temporal fenestrae extended posteriorly beyond occipital condyle, but not as far dorsally as in dinocepahlians [C88]; palate with moveable basicranial articulation [C88]; pterygoid has distinct transverse flange, but without denticles [C88]; lower jaw with coronoid absent [C88]; dentaries may be fused at symphysis [C88].

References: Carroll (1988) [C88]. ATW020525.

Dromasauria: again, likely paraphyletic. *Galechirus, Galeops, Galepus*

Range: Middle Permian of South Africa.

Phylogeny: Anomodontia:: Dicynodontia + *.

Characters: small & slightly built; skull short; orbits very large; postorbital bar narrow [C88]; postorbital does not contact squamosal [C88]; high narrow zygomatic arch [C88]; temporal fenestrae open dorsally [C88]; squamosal narrow [C88]; partial secondary palate formed by premaxillae [C88]; outer surface of mandible grooved (insertion of external mandibular adductor?) [C88]; canines reduced [C88]; premaxillary teeth reduced in number [C88]; slender legs; long tail.

Links: NAPC Abstracts, Ka - Ku (Kurkin abstract); ANNOTATIONS 52 (Meyer abstract).

References: Carroll (1988) [C88]. ATW020913.

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checked ATW050913; last modified MAK091111

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Therapsida: Neotherapsida: Dicynodontia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      |     `--Diictodontia
      |        `--Pristerodontia
      |           |--Lystrosaurus
      |           `--+--Jachaleria
      |              `--Kannemeyeriidae
      |                 |--Kannemeyeria
      |                 `--+--Placerias
      |                    `--Ischigualastia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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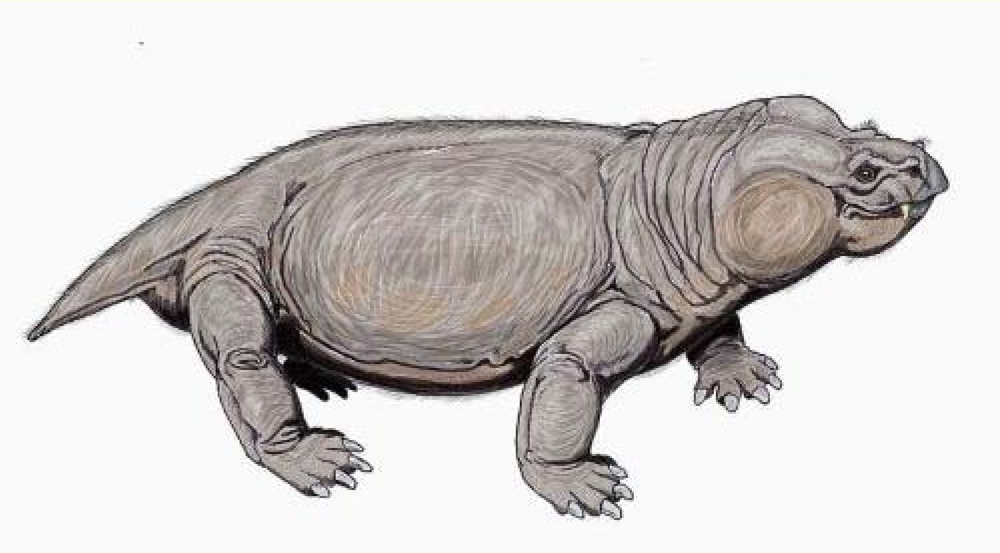
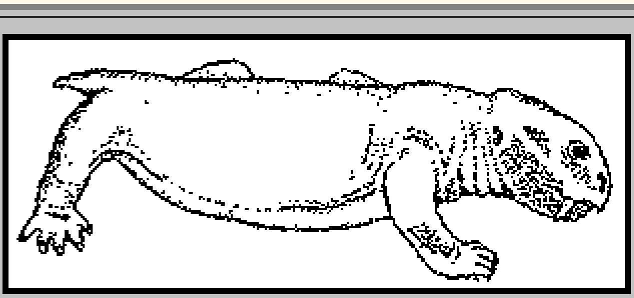
8. *Placerias* X
9. Pristerodontia X

Suborder Dicynodontia



The large Permian dicynodont *Aulacocephalodon baini* - artwork by Dmitry Bogdanov - Wikipedia



Diictodon **from King (1990)**

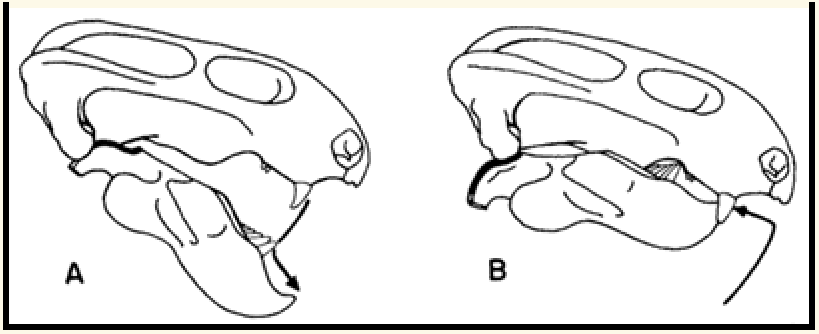
The **dicynodonts** were the most successful of the therapsids in terms of phylogenetic longevity, numbers of individuals, and the extent of distribution over continental areas. In fact they were the most successful and wide-ranging group of plant-eating animals of the time. They first appeared in mid Permian times (Wordian epoch) with the small *Eodicynodon*, and evolved in a remarkably uniform structural pattern, as seen in *Dicynodon*, through the Late Permian and the whole of Triassic period. During late Permian times they were among the commonest of all tetrapods, at least as indicated by the fossil record, and a large number of different lineages existed side by side, from small mole-like burrowers to giant ox-sized browsers.

They were greatly decimated by the increasingly harsh conditions of the terminal Permian, and only two lineages, the medium-sized *Lystrosaurus* (especially adapted not to swamps, as previously thought, but to arid conditions) and the tiny myosaurs, survived into the Early Triassic. The myosaurs eventually died out, perhaps through competition with other herbivores. The lystrosaurs evolved into the giant and very successful Kanneymeriids, pig to rhino sized animals that continued to the end of Carnian epoch (Late Triassic period).

The dicynodonts as a whole lasted some 50 million years, and the only group of therapsids to outlive them were the cynodonts, which were the direct ancestors of the mammals.

It is in the skull that the dicynodonts show their greatest specializations. There was no other quite like it, certainly not among the therapsids (although the large herbivorous rhynchosaurs also developed a similar beak). The advanced development of their skulls and jaws was the main factor in the success of these animals. The temporal openings at the back of the skull that are shared by all synapsids were greatly enlarged, so that the remaining bone formed long arches. These large openings supported very powerful jaw muscles. The dicynodonts skull is striking because of its light open construction and the presence of long, bony bars rather than broad plate-like areas behind the eye.

The hinge (see *Emydops* jaw movement, *right*) between the lower jaw and the skull permitted the jaws to move forward and backward, with a strong, shearing action. *See* images at



Dicynodonts - the Two-Tuskers for some variations on the basic dicynodont jaw mechanism. The dentition of these therapsids was unique. The front of the skull and the lower jaw were narrow and beak-like. Apart from a pair of large, upper tusks in some species, teeth were reduced to tiny remnants or were completely absent. In many dicynodonts the tusks are present in about half of the individuals, indicating that these were probably sexual characters, presumably present in one gender morph and absent in the other.

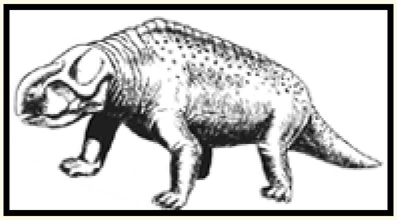
The upper and the lower jaws were certainly covered with horny beaks in life, like the beak in turtles and, it can be assumed, in the Triassic rhynchosaurs.

The body was short and broad, and was supported by strong limbs thick limbs that supported the body in the typical therapsid fashion. The ilium as expanded and strong, and likewise he shoulder girdle was large and strong. It seems that the hind-limb was held straighter than the forelimb (at least in the case of the Triassic *Dinodontosaurus*), making them slow plodders but nevertheless with a very powerful thrusting movement. The tail was short, even more so than in other types of therapsids.

In size the dicynodonts ranged from small rodent-like animals about 20cm in length, such as *Cistecephalus* and other small Permian forms, to giant, massive animals, such as the late Triassic genera *Stahleckeria* (known from Brazil) or ***Placerias*** (from Arizona), which were as big as the largest dinocephalians (reaching weights of over a tonne). MAK000813, ATW040201.

It has become increasingly clear that, as might be expected from this pattern of evolution, the classical taxa of dicynodonts are actually evolutionary grades in a continuous series. That is, the Kannemeyeriidae evolved from Pristerodontia, who evolved from Diictodontia, and so on. Surkov *et al.* (2005). So as not to lose these useful benchmarks of the course of dicynodont evolution, we have taken the liberty of redefining them as successive crown groups defined by their eponymous genera plus the highly derived dicynodont, *Ischigualastia*. Thus Kannemeyeriidae = *Kannemeyeria* + *Ischigualastia*, Pristerodontia = Pristerodon + *Ischigualastia*, etc. ATW050828.

Descriptions



Dicynodontia: *Ischigualastia* > *Galepus*. Examples: *Eodicynodon, Cistecephalus*.

Range: Middle Permian to Late Triassic.

Phylogeny: Anomodontia :: Dromasauria + * : Diictodontia

Characters: postorbital contacts squamosal [C88]; specialized jaw (see discussion, *supra*); squamosal elaborated to broad lateral plate of bone [C88]; temporal fenestrae very long and large [C88]; braincase sutured to pterygoids, without moveable basicranial articulation [C88]; secondary palate formed from premaxillae, maxillae, & palatines [C88]; pterygoid transverse flange absent [C88]; internal nares open behind midpoint of skull [C88]; premaxillae & dentaries fused at symphysis [C88]; keratinous beak present [C88]; teeth eliminated except canines (lost in some forms) with massive canine bosses at anterior maxilla [C88]; body short & stout [C88]; forelimbs sprawling, but hind limbs erect [C88]; phalangeal formula 23333 [C88].

Links: Schnellbestimmung anhand von typischen Schädelmerkmalen; South African Museum - Fossil Reptiles of the South African Karoo; sh: Prehistoric Animals - Brooke Bond tea cards offered in the interest of education; Samantekt um Dicynodontia (Icelandic); Paleontology and Geology Glossary: Di; Lystrosaurus; BPI Palaeontology (Wits University; University of the Witwatersrand, Johannesburg); paleontology; fossils; South Africa; Fossil Picture Gallery; Dicynodontia (Mikko's Phylogeny); Unterordnung Dicynodontia; Dicynodonts - the Two-Tuskers (**Best on the Web**);

References: Carroll (1988) [C88]. ATW020527.

Diictodontia: *Diictodon* + *Ischgualastia*. Examples: *Diictodon, Robertia*

Range: Late Permian to Early Triassic of South Africa, Antarctica

Phylogeny: Dicynodontia **:** *.

Image: *Cistecephalus* from BPI Palaeontology (Wits University; University of the Witwatersrand, Johannesburg); paleontology; fossils; South Africa; Fossil Picture Gallery

Links: Diictodontia; Synapsida.htm; South African Museum - Fossil Reptiles of the South African Karoo; Two life-size models of Diictodon; Biology 356; South African Museum - Trace Fossils of the Ancient Karoo; National Geographic Magazine @ nationalgeographic.com; Fossil Feature - A local scene from about 230 million years ago...; therapsid5a; Representative Faunas of the Four Lowland Empires of the Late Permian and Triassic of Southern Africa. ATW020809.

Pristerodontia: *Pristerodon* + *Ischigualastia*. Examples: *Pristerodon, Kingoria, Jachaleria*.

Range:

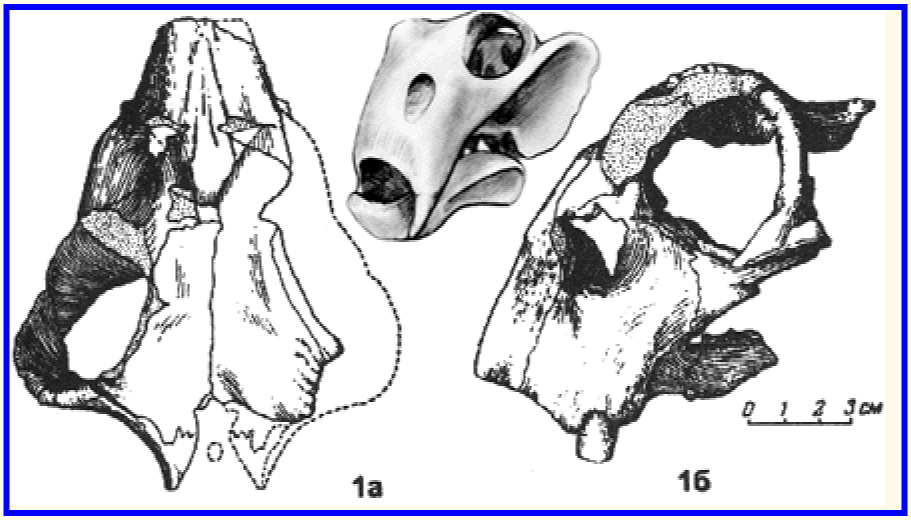
Phylogeny: Diictodontia **:** * **:** *Lystrosaurus* + (*Jachelaria* + Kannemeyeriidae).

Characters:

Links: Pristerodontia. ATW020527.

Lystrosaurus: Cope 1870. *L.* ("*Dicynodon*") *murrayi* Huxley 1859; *L.* ("*Dicynodon*") *curvatus* Owen, 1876; *L. declivis* ("*latirostris*") Owen, 1860; *L. georgi*, Kalandadze, 1975; *L. hedini* Young, 1935; *L. mccaigi* Seeley, 1898; *L. oviceps* Haughton, 1915; *L. platyceps* Seeley, 1898; *L. rajurkari* Tripathi & Satsangi 1963; *L. robustus* Sun, 1973; *L. shichanggouensis* Cheng, 1986; *L. weidenreichi* Young 1939.

Range: Late Permian to Early Triassic of South Africa, Antarctica, India, China & Russia.



Phylogeny: Pristerodontia **:** (*Jacheleria* + Kannemeyeriidae) + *.

Characters: medium- to large-sized [BS00] [S+05]; snout short & very deep, extended ventrally [BS00] [S+05]; snout slopes forward [BS00]; anterolateral corner of snout angular [S+05]; orbits high [BS00]; nares directly anterior to orbits [BS00]; choana only slightly constricted [S+05]; rugose portion of palatine narrow & small [S+05]; ectopterygoid absent [S+05].

Links: LYSTROSAURUS; Lystrosaurus; Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; Lystrosaurus sp.; triassic image page 1; Paleontology and Geology Glossary: L; National Geographic Magazine: July 1996 @ nationalgeographic.com; kf_24b.jpg; Dinosaurios: Lystrosaurus; Marine and terrestrial geology and geophysics; lystro2; Lystrosaurus; ????????; South African Museum - Fossil Reptiles of the South African Karoo; lystro2; Triassic; LYSTROSAURUS (long) (was Re- Mammal - Like - Reptiles); Lystrosaurus (image of fossil *in situ*); Glossary; lystro2; ALBANY MUSEUM - KAROO FOSSILS; Triassic; triassic%20page%201.html.

References: Battail & Surkov (2000) [BS00]; Surkov *et al*. (2005) [S+05].

Note: Now you know where Alan Busby got his idea for the Demu. ATW050828.

Jachaleria: *J. colorata* Bonaparte 1971. *J. candelariensis*.

Range: Late Triassic of South America.

Phylogeny: Pristerodontia **::** Kannemeyeriidae + *.

Image: *Jachaleria* skull (60 cm) from the Universidade Federal do Rio Grande do Sul, Instituto de Geociências.

Links: UFRGS - Paleovertebrates; UFRGS - MSc THESES/PALEONTOLOGY.

Note: These giant dicynodonts constitute some of the last known members of the dicynodont line. *J. colorata* is the only tetrapod collected from the base of the Los Colorados Formation, which immediately overlies the Ischigualasto. *J. candelariensis* is found together with the herbivorous cynodont *Exaeretodon* sp. MAK991017. ATW020527.

Kannemeyeriidae: *Kannemeyeria* + *Ischigualastia*.

Range: Late Permian to Late Triassic

Phylogeny: Pristerodontia **::** *Jachaleria* + * **:** *Kannemeyeria* + (*Placerias* + *Ischigualastia*).

Characters:

Links: ischifauna; Synapsida.htm. ATW020527.

Kannemeyeria:

Range: Early Triassic of South Africa, South America, India & possibly Australia.

Phylogeny: Kannemeyeriidae **:** (*Placerias* + *Ischigualastia*) + *.

Note: This ox-sized dicynodont was a common herbivore in Spathian and early Anisian times. It is known from South Africa, Argentina, and possibly India, but in all likelihood had a world-wide distribution.

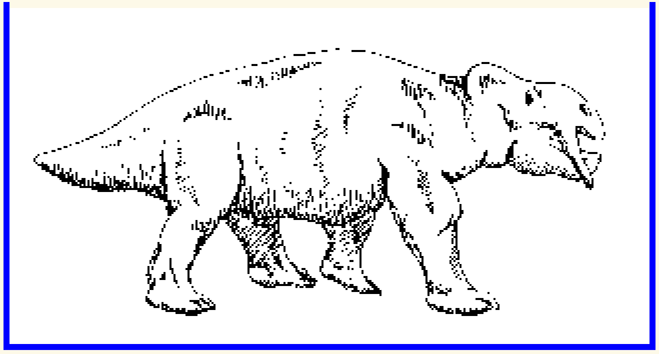
Links: Paleontology and Geology Glossary: K; South African Museum - Fossil Reptiles of the South African Karoo; BPI Palaeontology (Wits University; University of the Witwatersrand, Johannesburg); paleontology; fossils; South Africa; Fossil Picture Gallery; Kannemeyeria; Kannemeyeria (Korean); Abstracts, Ag - An; PANGEA (Italian); models.html. ATW020527.

Placerias: *P. gigas* (= *hesternus*)

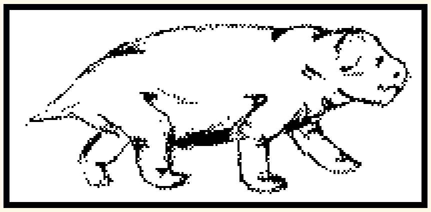
Range: Middle Triassic to Late Triassic of North America.

Phylogeny: Kannemeyeriidae **::** *Ischigualastia* + *.

Characters: to 3.5 m & 1000+ kg; hippo-like overall appearance.



Links: Walking with Dinosaurs - Fact File: Placerias; Petrified Forest National Park-Reptiles And Dinosaurs; Dinosaur museum (Chinese); Placerias - Paleontology and Geology Glossary; Placerias, a later herbivorous therapsid. Note the unusual tusk-like teeth. Middle Triassic, Arizona; Paleo Photos; Placerias, Drawing Nature Studio. ATW020527.



Ischigualastia: *I. jenseni* Cox 1964.

Range: Late Triassic of South America

Phylogeny: Kannemeyeriidae **::** *Placerias* + *.

Links: Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; ischifauna.

Note: An enormous dicynodont, with a short, high skull, and lacking tusks. It was a common member of the local fauna, although not as abundant as the medium-sized herbivores *Scaphonyx* and *Exaeretodon*. The only danger to such a huge animal was the almost equally large carnivorous pseudosuchian *Saurosuchus*. It is likely that pressure from this predator pushed *Ischigualastia* into extinction, for it becomes less common and finally disappears in the higher levels of the Ischigualasto Formation. A somewhat smaller relative or descendant, *Placerias*, survived in Laurasia. MAK991017. ATW020527.

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Therapsida: Theriodontia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--Eutheriodontia
            |--Therocephalia
            `--CYNODONTIA
```

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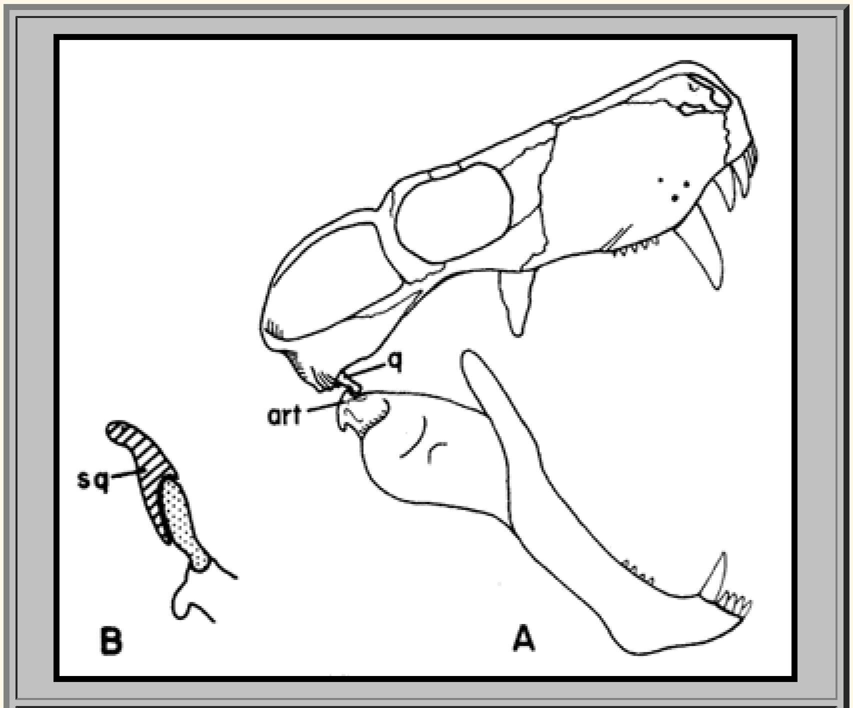
The Theriodonts

The late Permian gorgonopsid *Arctops* (= Scylacognathus?) *watsoni* - artwork by Dmitry Bogdanov - Wikipedia

The third great therapsid taxon, the **Theriodontia** ("beast tooth", referring to the mammal-like teeth), include the mammals. Even their most basal members are the most mammal-like of the Therapsida. The theriodonts included both carnivores and herbivores, and various lineages correlated to late Cenozoic wolves, weasels, otters, rodents, and shrews. Most diverse and successful during the Late Permian and Early Triassic, they were increasingly overwelmed by the archosaurian radiation of the later Triassic. During the latest Triassic (late Norian to Rhaetic) at least one line of **eutheriodonts** evolved into mammals. Even so, one family, the rodent-like tritylodontids continued right into the Late Jurassic (Oxfordian).



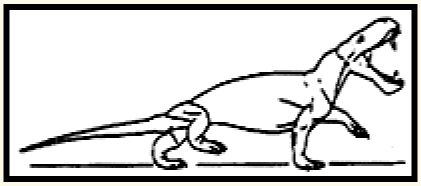
The theriodonts evolved a feeding mechanism much more successful than that of the Dinocephalia. The quadrate bone in the jaw was reduced in size. When the jaws are widely opened (drawing, *right*) the articular bone (***art*** in the diagram) toghtly grips the head of the small quadrate (***q***). The lower incisors pass entirely behind the upper incisors when the jaws are closed. The development of versatile jaw movements and a more precise type of dental occlusion also played a critical role in preadapting the elements of the theriodont articular complex for becoming the ossicles of the mammalian middle ear.

The small quadrate may have been loosely attached to the skull, probably by a fibrous pad in life; set in a squamosal recess (B) in the diagram above. The upper end occupies a hollow in the anterior face of the squamosal which also buttressed it from behind. Thus, as Hopson (1969) suggests, the quadrate was probably capable of a small amount of fore-aft movement at its lower end. Nevertheless the joint between the quadrate and articular was a tight one, with the articular firmly gripping the quadrate condyle, allowing only a hinge (and some transverse sliding) movement at the jaw joint, but no fore-aft sliding.

The theriodont specialization of the masticatory apparatus illustrated by the gorgonopsian *Dixeya*. In A, the jaws are widely opened; the articular (art) tightly grips the head of the small quadrate (q). The lower incisors pass entirely behind the upper incisor~ when the jaws are closed. B shows a diagrammatic cross section through the squamosal (sq) showing movable quadrate in squamosal recess. (A modified from Parrington.)

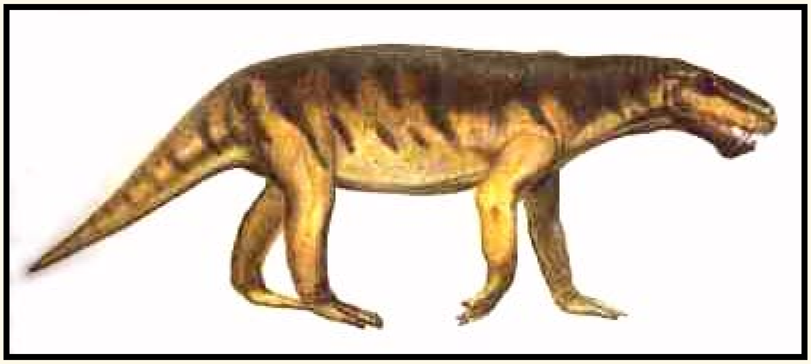
The reduced and movable quadrate was a key theriodont adaptation. In large carnivores with very long canines, such as the gorgonopsians and some therocephalians, a wide gape was necessary, and so a secure attachment of the lower jaw is required. This same adaptation is also found in mammalian carnivores. The theriodont quadrate also allowed the anterior (front) surfaces of the lower teeth to contact and shear against the posterior (rear) surfaces of the upper teeth as the jaws are closed. These teeth, which were sometimes serrated in gorgonopsian and other groups, could then function as very effective cutting instruments for dismembering a carcass or biting out chunks of flesh from it. In advanced herbivorous cynodonts, like the tritylodonts, the ability to move the lower jaws in a fore-aft direction was ex- ploited for the purpose of cutting up plant material by the cheek dentition.

Gorgonopsia



The theriodonts fall into three distinct groups, the **Gorgonopsia**; the Therocephalia, and the Cynodontia. A fourth group, the Bauriamorpha, are now generally included with the Therocephalia. The Gorgonopsia were the "sabre tooth tigers" of the Permian, medium-sized to large therapsids equiped with huge canine teeth, used to bring down large prey. These theriodonts, typified by animals like the dog-sized *Lycaenops* (below) and the bear-sized *Inostrancevia*, show some features that were further developed in the later theriodonts. Thus the dentary bone in the jaw was large, but not as large as in *Cynognathus*. In mammals, the jaw consists only of the dentary. The teeth, although differentiated, were not highly specialized. There was as yet no hard secondary palate (bony roof of the mouth, enabling the animal to eat and breath at the same time). The occipital condyle, which connects the skull to the backbone, was single.

These were efficient, very capable hunters, the dominant predators of the Late Permian terrestrial ecosystem. They may have hunted singly or in packs, and probably preyed on large, plant-eating animals like Pareiasaurs, Tapinocephalians, and large Dicynodonts. The canines were particularly long, giving the mouth a distinctly "sabre-toothed" appearance, and the front part of the skull was deeper than normal to accommodate their roots.



A medium-sized form like *Lycaenops*, represented by several species from the Late Permian (*Cistecephalus* and *Daptocephalus* zones) of South Africa, averaged about a meter in length. It was a lightly built carnivore, with long running legs, that almost certainly fed on the abundant dicynodont herbivores that shared its environment. Larger forms, like *Dinogorgon* and *Inostrancevia*, grew to be lion to bear sized, and prayed upon the ox- and hippo-like megaherbivores like the Pareiasaurs and the biggest Dicynodonts, both of which attained weights of a tonne. Gorgonopsids and Pareiasaurs may have formed a co-adaptive relationship (like Pleistocene megaherbivores and sabre-tooth cats), and significantly both became extinct at the same time (at the end of the epoch)

The Gorgonopsia are generally considered the most primitive members of the Theriodontia. It is also conceivable that the characters which they share with more mammal-like therapsids could perhaps be explained as convergences (parallel evolution), rather than as shared traits inherited from a common ancestor. The Gorgonopsia have thus been grouped by Boonstra with the Dinocephalia and other very primitive forms such as the Bairmosuchia, under the name

"Alphatherapsida". However there is no certain evidence for a close relationship between the Gorgonopsia and Dinocephalia, especially since many primitive forms (*e.g.*, the Ictidorhinidae) previously considered gorgonopsians are now generally accepted not to belong to this group at all. The most likely hypothesis at present is that the Gorgonopsia represent a distinct lineage of theriodonts. MAK000718.

The Therocephalia

The **Therocephalia** are at least as ancient as the Gorgonopsians, which they resemble, and in fact outlasted, making it through to the Early Triassic period. The earlier therocephalians were in many respects as primitive as the gorgonopsians, but they did show certain advances such as the enlargement of the temporal opening (for a lighter skull and mopre efficent muscle attachment) and reduction of the phalanges (finger and toe bones) to the mammalian formula. The later therocephalians included the advanced bauriamorphs, which carried some theriodont characters to a high degree of specialization. For instance, in *Bauria* there was no bar of bone separating the orbit from the temporal opening; a condition typical for primitive mammals. These and other advanced features led to the long-held opinion, now rejected, that the Ictidosaurs and even some early mammals arose from a bauriamorph stem. Rather, the situation seems to be that mammalian characteristics evolved in parallel among a number of different groups, and this makes the therapsid phylogeny a particularly tricky subject. [see for example Luo *et al*. (2002))

The fragmentary nature of some of these fossils, and the enthusiasm of early workers in the field to give each new scrap of bone a different species, genus, or even family designation, has led to a number of false taxa. It is not surprising that several therocephalian groups, like the Lycosuchidae and the Scaleposauridae, have turned out to be artificial, the former based on skulls which retain an extra set of canines (*i.e.* when the animal died one pair was in the process of replacing the other), and the latter based on mostly juvenile characteristics. MAK000907.

Cynodontia

To be added...

Theriodontia:

Range: from the Middle Permian.

Phylogeny: Neotherapsida: Anomodontia + *: Gorgonopsia + Eutheriodontia.

Characters: **$** Skull flat with wide muzzle (dorsal surface of nasals horizontal) [RS01]; dorsal process of premaxilla shortened; **$** skull roof narrow between tempral fenestrae (narrower than interorbital width) [RS01]; quadrate and quadratojugal shortened and lie in a pocket of the squamosal; **$** dentary has coronoid process, providing longer lever arm and more area for insertion of jaw adductor and temporalis (in later forms) muscles [RS01]; post-dentary bones reduced; dentary canines longer in relation to maxillary canines.

Links: Therapsida; Evolution of Mammals; dinosaurs-inostrancevia; Theriodontia; Annatherapsidus; Lecture 03 - Cont. Drift.

References: Rubidge & Sidor (2001) [RS01].

Note: Primitive forms were small and rather rodent-like carnivores and insectivores. This is the approximate place on the mammal road that features like fur and elevated metabolic rates are thought to have first occurred. ATW020206.

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checked ATW030505; last modified MAK091111

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Therapsida: Theriodontia: Gorgonopsia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--Eutheriodontia
            |--Therocephalia
            `--CYNODONTIA
```

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1. Gorgonopsia X

The Gorgonopsia

Inostrancevia alexandri, a bear-sized Gorgonopsian, from the Late Permian (middle Wuchiapingian to Changhsingian) of equatorial Pangeia (now, Russian Urals). Image from Mathematical com

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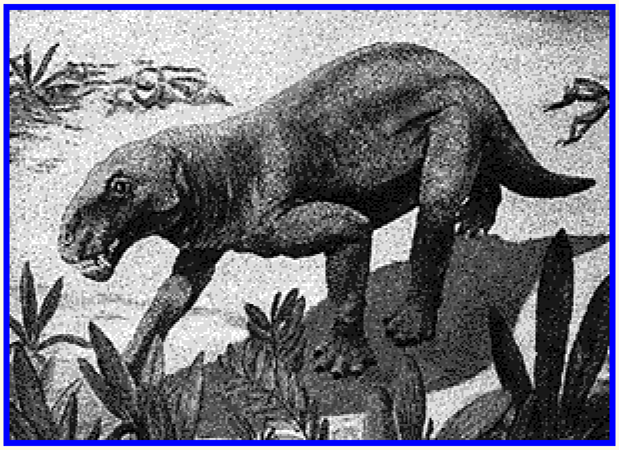

Gorgonopsia: *Lycaenops*.

Range: Middle Permian to Late Permian of South Africa & Russia.

Phylogeny: Theriodontia: Eutheriodontia + *.

Characters: Dog-sized, dog-like dominant carnivores of upP, with large fangs and flat heads; lightly built; skull similar to biarmosuchids, but longer and more massive; neomorphic medial preparietal at intersection of parietals and frontals; preparietal does not participate in pineal foramen [RS01]; orbits relatively small; jugal lacking postorbital process [RS01]; adductor chamber enlarged; quadrate without suture to squamosal [RS01]; quadrate bound to pterygoid & stapes[RS01]; articular slid sideways when jaw was opened [RS01]; vomer broad anteriorly, tapering rapidly posteriorly [RS01]; vomer with 3 parallel ridges with lateral ridges parallelling choanal margin [RS01]; palatines with extensive medial contact, separating vomers from pterygoids [RS01]; reflected lamina with attached dorsal margin, bearing distinctive ridge system [RS01]; long, blade-like serrated maxillary fangs; post-canine teeth fairly small and reduced number; teeth articulated?; no regular wear facets (no oral processing of food) [RS01]; forelimb posture still sprawling; femur similar to crocs & capable of either sprawling or parasagittal ("high walk") motion; pedal phalangeal count 23453; believed to be possibly endothermic, but only recovered skin fragment lacks hair.

Links: Introduction to the Gorgonopsia; National Geographic Magazine (nice gorgonopsid skull); Gorgonopsia Paleontology and Geology Glossary: G; New Scientist | Disaster: Meltdown (PT extinction generally); First complete fossil... ; permian image page; Life-size model of Scymnognathus parrangtoni v. Huene; Dinosaurs and other Italian reptiles - Tridimont (I don't know who this sculptor is, but he's a genius); Lapidarium; Early Mammal-like Reptiles.

References: Rubidge & Sidor (2001) [RS01]. ATW020220

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Therapsida: Theriodontia: Therocephalia

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--Eutheriodontia
            |--Therocephalia
            `--CYNODONTIA
```

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1. Eutheriodontia
2. Therocephalia X

The Therocephalia

Moschorhinus kitchingi

The advanced, felid-like Therocephalian *Moschorhinus kitchingi* - artwork by Dmitry Bogdanov - Wikipedia

page under construction...

I have decided to divide the Theriodontia page into several subpages to give better coverage to the various theriodont groups. The present page will be the main Therocephalia page. In the meantime, until all the appropriate links are revised, see the following:

Theriodontia page located here

Gorgonopsia located here

Sorry for any inconvenience!

MAK09111

Eutheriodontia: Therocephalia + Cynodontia [RS01]

Range: from the Middle Permian.

Phylogeny: Theriodontia: Gorgonopsia + *: Therocephalia + Cynodontia.

Characters: temporal roof reduced to sagittal crest [RS01]; posterior ramus of postorbital fails to meet squamosal [RS01]; epipterygoid anteroposteriorly expanded (= alisphenoid) [RS01]; respiratory turbinal bones may have been present (suggesting a degree of endothermy) [RS01]; palatine (*palatal*?) teeth absent [RS01].

References: Rubidge & Sidor (2001) [RS01]. ATW020219.

Therocephalia: *Bauria, Lycosuchus, Moschorhinus.*

Phylogeny: Eutheriodontia: Cynodontia + *.

Range: mP-mT of China, Antarctica, SAfr. & Rus.

Characters: Massive skull; postorbital bar may be incomplete (i.e. orbit and temporal fenestra are confluent); **$** stapes rod-like & stapedial foramen (for quadrate) absent [RS01]; epipterygoid expanded laterally

to braincase (also in cynodonts); jaw muscles expanded over braincase; some with complete secondary palate (evolved independently of cynodonts), but vomer participates in palate; **$** suborbital vacuities at intersection of pterygoid, ectopterygoid & palatines [RS01]; large canines; simple conical post-canine teeth, frequently lost; thin, small lumbar ribs; **$** ilium with finger-like projection from anterior margin [RS01]; long limbs; diverse small to large predators or insectivores; some herbivores.

Links: Theriodontia; Schnellbestimmung anhand von typischen Schädelmerkmalen; Vertebrates; BPI Palaeontology ... Fossil Picture Gallery (small picture in lower left corner); Annatherapsidus.

References: Rubidge & Sidor (2001) [RS01]

Image: *Annatherapsidus petri* from (as usual) mathematical.com. ATW000918.

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Therapsida: Dendrogram

Abbreviated Dendrogram

```
SYNAPSIDA
|
|-Raranimus
`+-Biarmosuchia
 `-+--Dinocephalia
   |  |--Anteosauria
   |  `--Tapinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

Contents

```
SYNAPSIDA
|
Therapsida MH, SN
|--Tetraceratops •X
|--Raranimus •X
`--+-?Phthinosuchidae •X
   `--+--Biarmosuchia X MH
      |  |--Biarmosuchidae •X
      |  `--Ictidorhinidae •X
      |     `--Burnetiamorpha  •X
      |        |--Lemurosaurus  •X
      |        `--Burnetiidae  •X
      `--+--Eotitanosuchia •X
         `--Eutherapsida
            |--Dinocephalia X MH
            |  |--Stenocybus
            |  |--Estemmenosuchidae X
            |  |  |--Anoplosuchus •X
            |  |  `--+--Estemmenosuchus •X
            |  |     |--Molybdopygus •X
            |  |     `--Zopherosuchus •X
            |  `--+--Anteosauria X MH
            |     |  |--Archaeosyodon •X
            |     |  `--+--Brithopodidae X
            |     |     |  |--Chthomaloporus •X
            |     |     |  `--Brithopus •X
            |     |     `--+--Deuterosaurus •X
            |     |        `--Anteosauridae X
            |     |           |--Syodontidae X
            |     |           |  |--Notosyodon •X
            |     |           |  `--Syodon •X
            |     |           `--+--Titanophoneus •X
            |     |              `--Anteosaurinae X
            |     |                 |--Anteosaurus •X
            |     |                 `--Doliosauriscus •X
            |     `--Tapinocephalia X MH
            |        |--Styracocephalus •X
```

```
|        `--+--Titanosuchidae X
|           |  |--Titanosuchus •X
|           |  `--Jonkeria •X
|           `--Tapinocephalidae X
|              |--Ulemosaurus •X
|              |--Tapinocaninus •X
|              `--+--Struthiocephalus •X
|                 |--Tapinocephalus •X
|                 |--Keratocephalus •X
|                 |--Moschops •X
|                 `--Riebeeckosaurus •X
`--Neotherapsida
   |--Anomodontia X SN MH
   |  |--Venyukovioidea •X
   |  `--+--Dromasauria •X
   |     `--Dicynodontia X MH
   |        `--Diictodontia X5
   |           `--Pristerodontia X MH
   |              |--Lystrosaurus •X
   |              `--+--Jachaleria •X
   |                 `--Kannemeyeriidae X MH
   |                    |--Kannemeyeria •X
   |                    `--+--Placerias •X
   |                       `--Ischigualastia •X
   `--Theriodontia Tax
      |--Gorgonopsia •X MH, Tax
      `--Eutheriodontia
         |--Therocephalia •X MH SN
         `--CYNODONTIA
```

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Therapsida: References

Abbreviated Dendrogram

```
SYNAPSIDA
|
THERAPSIDA
|--Biarmosuchia
`--+--Dinocephalia
   `--+--Anomodontia
      |  |--Venyukovioidea
      |  `--Dicynodontia
      `--Theriodontia
         |--Gorgonopsia
         `--+--Therocephalia
            `--CYNODONTIA
```

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Cynodontia

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIAFORMES
```

Contents

Cynognathus, a large Early Triassic cynodont that ranged widely across Southern Pangea (fossils are known from South Africa, South Ameriuca, and Antarctica). See BBC Cynodont for another illustration of this same animal.
Graphic copied from Science Positive, Antartica

In the unbroken evolutionary sequence from reptile to mammal, the cynodonts are intermediate between earlier and more primitive theriodont therapsids and the earliest mammals. These highly successful animals first appear in the late Permian, radiate quickly into a number of different forms (including both terrestrial and semi-aquatic) before the end of the period, reach their maximum diversity in the Early Triassic, and become increasingly mammal-like as the Triassic progresses, giving rise to true mammals in the later Triassic. By the start of the Jurassic, only the insectivore-like tritheledonts and rodent-like tritylodonts remained; the latter continuing alongside true mammals throughout the Jurassic and even into the early Cretaceous.

In cladistic nomenclature, the term "cynodont" is also used to include mammals, which evolved from cynodonts and hence are, phylogenetically speaking, derived cynodonts. MAK120206

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Cynodontia

Dvinia

Abbreviated Dendrogram

```
THERAPSIDA
|
Cynodontia
|--Dvinia
`--+--Procynosuchidae
   `--+--Galesauridae
      `--Eucynodontia
         |--Cynognathia
         |  |--Cynognathidae
         |  `--Tritylodontidae
         `--Probainognathia
            |--Tritheledontidae
            `--MAMMALIAFORMES
```

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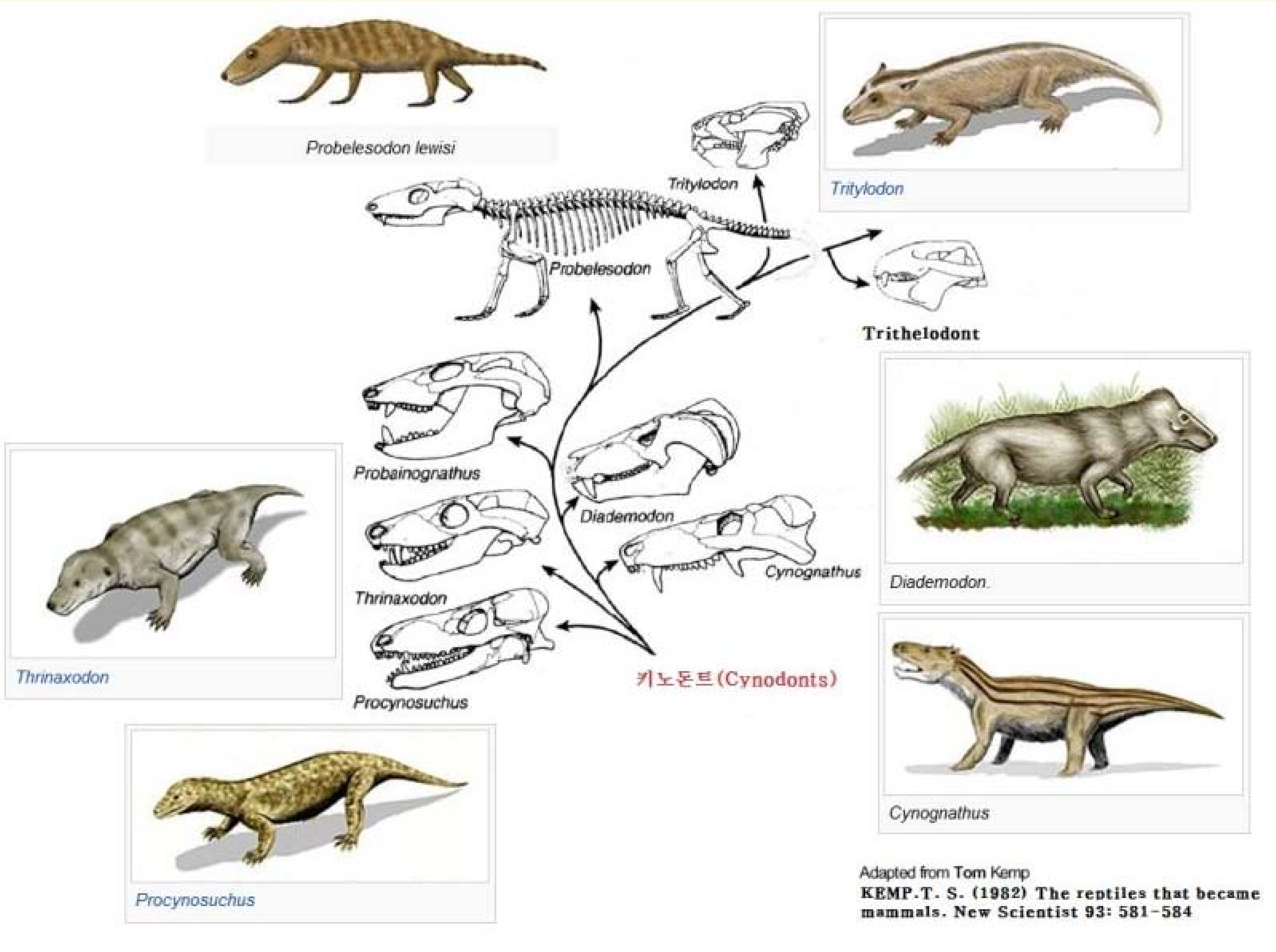
2. *Dvinia* X



Adapted from Tom Kemp
KEMP.T. S. (1982) The reptiles that became mammals. New Scientist 93: 581-584

Cynodont evolution, after Thomas Kemp (with Wikipedia life reconstructions), copied from Mammal-like Reptiles (Korean)

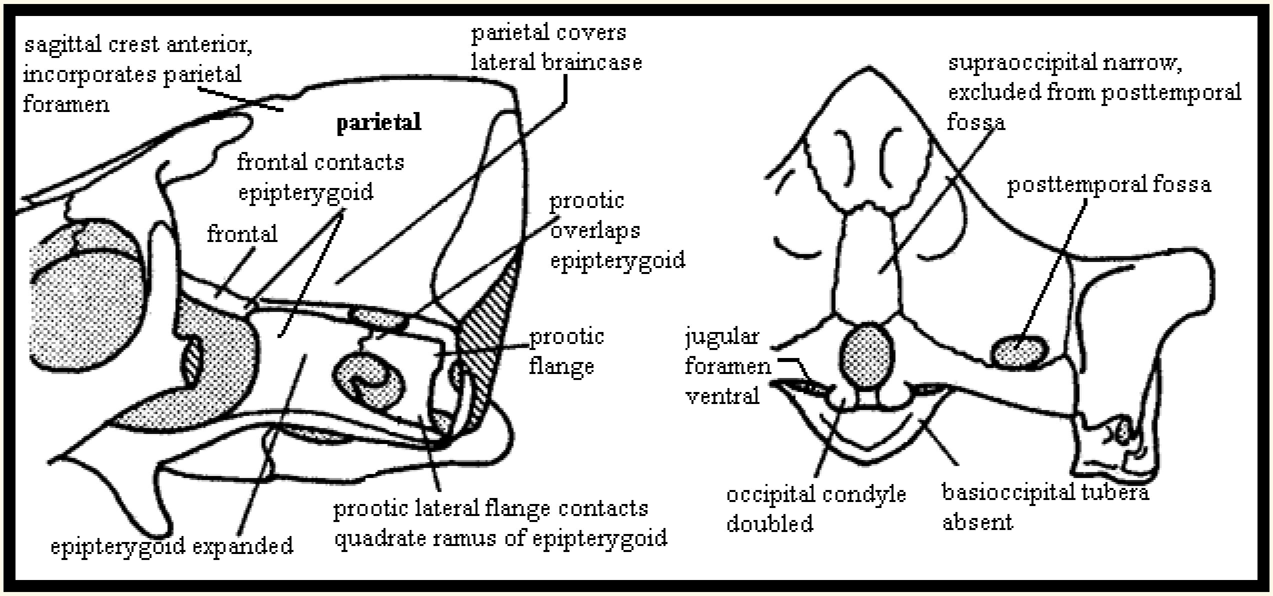
Descriptions

Cynodontia: Increasingly small-sized proto-mammals with higher metabolism.

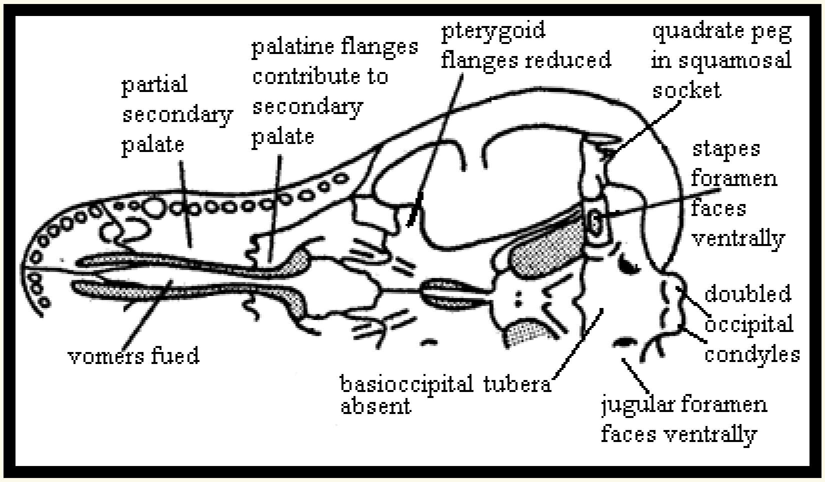
Range: from the Late Permian

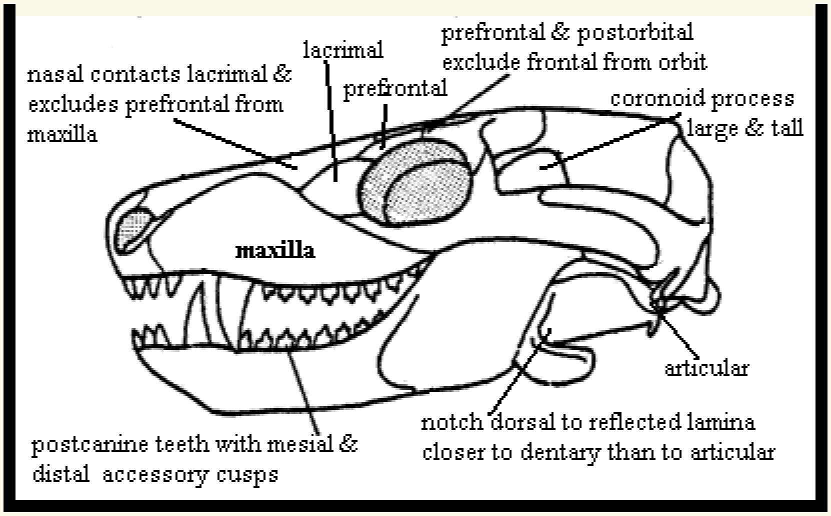
Phylogeny: Eutheriodontia : Therocephalia + * : *Dvinia* + (Procynosuchidae + Epicynodontia).

Characters: Continued reduction of cranial dermal bone number [S01]; rostral sculpturing suggests lips and mammal-like muzzle [K82]; premaxilla vomerine process present [SH98]; maxilla does not contact prefrontal [SH98]; posterior nasal expanded with reduction of frontal so that nasal contacts lacrimal & excludes prefrontal from maxilla [HB86$] [HK01$]; prefrontal contacts postorbital and excludes frontal from orbit [SH98] [HB86$] [HK01$]; postfrontal absent [SH98] [HB86$] [HK01$]; postorbital small [K82]; parietal dominates skull table [K82]; sagittal crest anterior to parietal foramen [SH98] [HB86$]; parietal extends ventrally to cover much of lateral braincase [RS01$] [HB86$]; ventral flanges of



the parietal and frontal meet flanges of opisthotic (anterior lamina) & epipterygoid; frontal contacts epipterygoid [HB86$]; outwardly bowed zygomatic arch (suggests grinding of food by masseter muscle located behind arch) [SH98]; great anteromedial expansion of temporal fenestra [K82]; quadratojugal extends into slit in squamosal [K82]; posteroventral quadrate peg fixed in squamosal notch [SH98] [HB86$] [HK01$]; tabular surrounds posttemporal foramen [SH98] [HK01$]; supraoccipital narrow & does not contact posttemporal foramen [HB86$]; occipital condyle doubled [HB86$] [HK01$]; *jugular foramen* faces ventrally (not posteriorly) [HB86$]; basioccipital tubera absent [HB86$]; stapes narrowest dorsoventrally & stapedial foramen oriented dorsoventrally [SH98] [HB86$] [HK01$]; stapedial dorsal process located distally [SH98]; prootic with lateral flange [HK01$]; prootic lateral flange contacting epipterygoid [SH98]; prootic flanges overlying (vascular?) grooves [HB86$]; anterodorsal prootic overlaps posterior epipterygoid (=alisphenoid) [SH98] [HB86$]; epipterygoid expanded anteroposteriorly to proportions of mammal-type alisphenoid [RS01**$**] [HB86$] (now broad sheet of bone sutured to prootic & forming part of braincase wall -- not narrow rod reaching skull roof); single, enclosed *trigeminal* foramen [SH98]; trigeminal foramen between prootic & epipterygoid [HK01$]; vomers fused at midline [S01] [HB86$] (*contra* [K82] vomers paired in *Dvinia*); epipterygoid contacts frontal [$RS01] [SH01] [HK01$]; **$**? at least partially ossified secondary palate [RS01]; maxilla & palatine flange participate in secondary palate [SH98] [HB86$] [HK01$]; pterygoid transverse flanges reduced [HB86]; pterygoid quadrate ramus connected to prootic by lateral flange of prootic [K82] [HB86$] **[4]**; ectopterygoid does not contact maxilla [HK01$]; large dentary and reduced postdentary jaw bones; very large coronoid process [K82]; coronoid process with at least some lateral excavation (*i.e.* *masseteric fossa*) [RS01**$**] [HB86**$**]; posterior dentary extensively overlaps surangular [HB86$] [HK01$]; increased use of post-dentary bones for hearing; ventral surangular & anterodorsal angular emarginated to form gap between them [HB86$]; intramandibular fenestra between surangular and prearticular [K82]; angular *reflected lamina* small [HB86$] [SH98]; angular reflected lamina with dorsal notch closer to dentary than to articular [SH98]; articular facets of articular face posteriorly [K82]; tooth row extends under orbit [SH98]; 6 upper incisors [SH98]; incisors not serrated [SH98]; incisors spatulate [HB86$]; incisors with "smoothly ridged" cutting margins [HK01$]; canines not serrated [SH98] [HK01$]; postcanines have 2+ cusps in a line [HK01$]; postcanine teeth have distal & mesial accessory cusps [RS01] [HB86$]; lingual cingulum present [RS01] [HB86$]; lower postcanines with mesial cingulum or mesial accessory cusp [HK01$]; pterygoid dentition absent [HB86$]; atlas centrum reduced and fused to axis [K82] [SH98]; atlas pleurocentrum with broad anterior projection [SH98]; differentiation of thoracic & lumbar regions [H91]; heads of ribs in at least lumbar vertebrae are confluent [K82]; lumbar ribs reduced or absent (development of diaphragm to defeat Carrier's constraint) [K82]; lumbar ribs sutured or fused to vertebrae [K82] [H91]; 4+ sacral ribs [SH98]; interclavicles with broad, parallel-sided posterior process [SH98]; scapula has laterally bent anterior and posterior edges enclosing a long vertical trough, the *spinatus fossa* [H91] [SH98]; coracoid and procoracoid reduced; orientation of humeral head mostly dorsal [SH98]; manus 4 with 4 phalanges [SH98]; ilium with large anterior process [K82]; ilium anterior process moderately elongated, with length 50-150% of acetabulum diameter [H91] [SH98] ([HK01] state 100-150%); pubis small and extends only just anterior to acetabulum [K82]





[H91]; obturator foramen very large & located on puboischiadic suture [SH98]; calcaneal heel present [H91]; fore-and-aft movement of hind limb; primitively insectivores, with later carnivorous and herbivorous derived forms; some degree of endothermy likely [RS01].

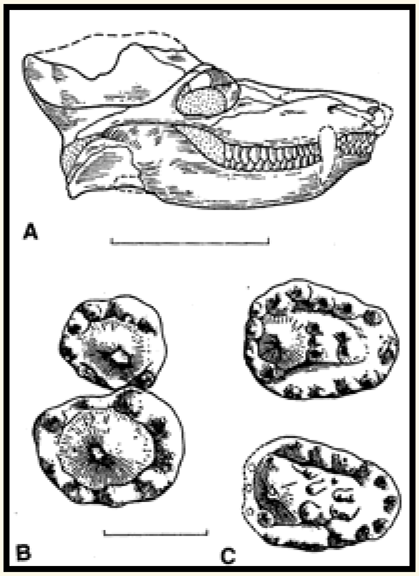
Notes: **[1]** [RS01] characterize cynodonts as showing a "fundamental reorganization of the jaw-closing musculature," with the beginning of the development of the muscular sling permitting palinal chewing. **[2]** from Biology 356: changes in frontal- parietal- epipterygoid structure strengthened the braincase and allowed jaw adductor muscles to have more room for their origin from the braincase. **[3]** from Biology 356: The excavation of the coronoid is the first indication of the mammalian masseter muscle. This was correlated with other changes in the jaw musculature. The jaw musculature of early tetrapods was composed of three muscles separated by maxillary and mandibular branches (V2 and V3) of the trigeminal nerve; the *adductor mandibulae posterior*, the *adductor mandibulae externus*, and the *adductor mandibulae internus* (including the pseudotemporalis and the pterygoideus). This pattern was retained in early therapsids. However, in cynodonts, most of the jaw musculature is composed of the *adductor mandibulae externus*. The medial portion of the externus is called the temporalis, while its new lateral portion is called the masseter (and has its origin on the zygomatic arch). **[4]** [HB86] refer to the quadrate ramus of the "epipterygoid." I assume this is a typographical error, something that seems to be unreasonably common in the cynodont literature.

Images: *Dvinia prima* courtesy of mathematical.com. Cynodont apomorphies all adapted from [HB86].

Links: Schnellbestimmung anhand von typischen Schädelmerkmalen; Prehistoric Animals; The cerebral hemispheres...; BBC Online - Walking with Dinosaurs - Fact Files; dinosaurs- dvinia prima; Reptile-Mammal (very nice page); mammalogy1.html (**Best on the Web**).

References: Hopson (1991) [H91]; Hopson & Barghusen (1986) [HB86]; Hopson & Kitching (2001) [HK01]; Kemp (1982) [K82]; Rubidge & Sidor (2001) [RS01]; Sidor (2001) [S01]; Sidor & Hopson (1998) [SH98]. ATW030209.

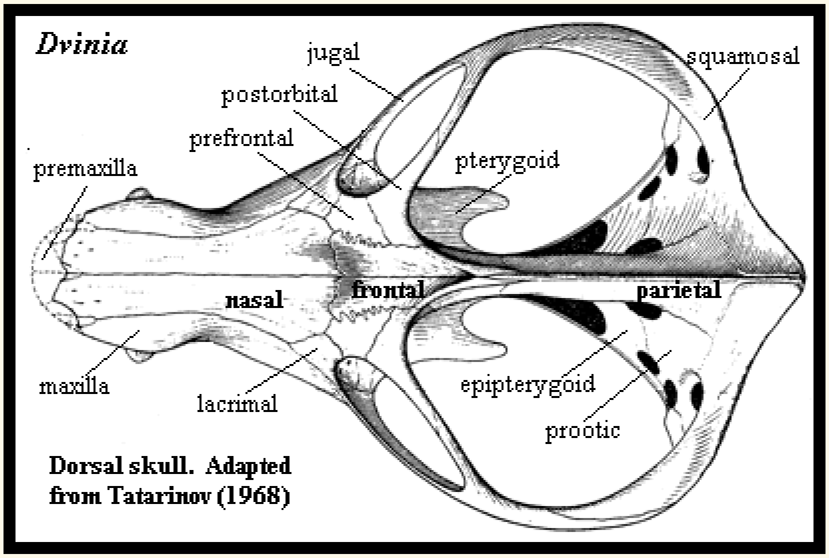
Dvinia: *D. prima* Amalitskii (= Amilitsky)1922 (= *Permocynodon sushkini*).



Range: Late Permian of Russia, Upper Tatarian deposits of Arkhangel'sk.

Phylogeny: Cynodontia **:** (Procynosuchidae + Epicynodontia) + *.

Characters: snout narrow [BS00]; distinct maxillary pit anterior to orbit [T68]; maxilla with 2 longitudinal grooves on ventral surface posterior to canines which may be attachments of labial muscles [T68]; relatively few other maxillary foramina [T68] **[3]**; very long, tall sagittal crest in which frontals participate [T68] [BS00]; parietal foramen absent [BS00] [T68]; sub- & postorbital bars & zygomatic arch narrow [BS00]; temporal fenestra very large, even for a cynodont [K82]; sagittal crest very high & long, without pineal foramen [BS00$] [HB86$]; sagittal crest extends posterior to occiput [K82]; squamosal lightly built [BS00]; squamosal without posterior expansion at rear of temporal fossa [HB86] [H91]; quadrate & quadratojugal exposed (not covered by squamosal) [BS00]; jaw articulation below level of occipital condyle [T68]; accessory quadratojugal-surangular articulation [T68]; *posttemporal foramina* relatively large [HB86] [H91]; paroccipital process anteroposteriorly narrow and almost entirely behind fenestra ovalis [HB86] [H91]; exoccipitals strongly developed [T68]; occipital condyles paired, but low and very close together, so that basioccipital is exposed only ventrally [T68]; stapes is thin-walled tube with very large stapedial foramen [T68]; stapes proximally in fenestra ovalis, distally with spur at the end of the paroccipital process **[4]** [T68]; possible external trace of auditory meatus present on squamosal [T68]; prootic and opisthotic completely fused [T68]; prootic & pterygoid sutured above trigeminal foramen [BS00] (but contact is very restricted [HB86] [H91]); well-developed secondary palate [T68]; secondary palate complete



Dorsal skull. Adapted from Tatarinov (1968)

[BS00] (*contra* [K82] anterior cleft exposing vomer); foramina for lower canines in palate [T68]; vomers paired [K82] (*contra* [HB86] paired vomers "could not be verified"); palatal processes of maxilla & palatine meet at midline [HB86$] (*contra* [H91]); interpterygoid vacuity present [T68] [BS00]; ectopterygoid substantial [T68]; *basipterygoid processes* closely appressed & immobile [T68]; dentary small [BS00] [K82]; shelf under incisors and 3 mental foramina at root of lower canine possibly for lip musculature and circulation [T68]; weak coronoid process [BS00]; masseteric fossa restricted to dorsal portion of coronoid [K82]; postdentary bones well-developed [T68] [K82]; *reflected lamina* fairly large [K82]; tooth rows roughly parallel [K82]; 6 incisors [BS00] [K82]; 6 lower incisors [SH98] [HB86$]; 1 very small vestigial upper precanine [BS00] [K82]; postcanines differentiated into "premolars" and "molars" [T68] **[2]**; premolars slender and simple [K82]; upper postcanines bit against outer shelf of dentary [K82]; upper molars inset from margin of maxilla [SH98]; upper molars with large central cusp with 7-9 accessory cusps around margin on a cingulum [T68] [K82]; lower molars transversely expanded, with low main cusp and many labial accessory cusps [BS00$] [K82] [HB86$]; lower molars bit against *secondary palate*, presumably on a *keratinous* sheath as in dicynodonts [K82]; lower molars with main cusp displaced buccaly and ~14 marginal accessory cusps [K82]; lower molars with additional accessory cusps lingual to main cusp in central area [T68] [K82]; (lower?) lingual cingulum greatly expanded [SH98]; believed to be at least partially omnivorous, including plants and insects in diet [K82].

Notes: [1] There are indications which suggest, at least to us, that *Dvinia* may have had the misfortune to become involved in some internal Soviet political squabble. *Verbum sap*. ... **[2]** The quotation marks are Tatarinov's. For simplicity, we will omit them in other places. **[3]** Tatarinov [T68] suggests that lips may have been present, but notes the general absence of the expected channels for nerves and vessels along the margin of the maxilla. However, the anterior nasals are "penetrated by numerous apertures." **[4]** Tatarinov [T68] speculates that the stapes was continued in cartilage to the quadrate. He includes an extensive discussion of hearing in *Dvinia* and the future middle ear ossicles. We have omitted this, as the results are inconclusive.

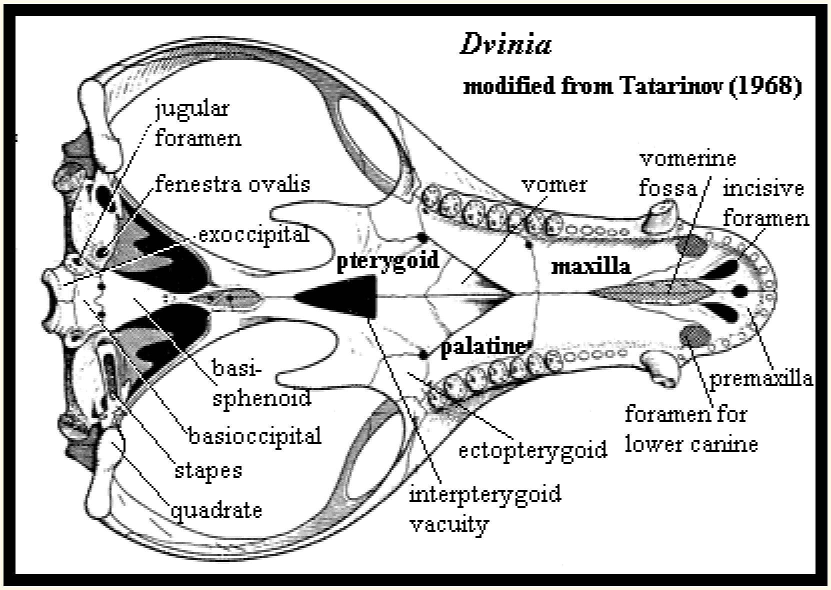


Image: (upper right) *Dvinia prima*, skull and right postcanines. Lingual is to the right, mesial (anterior) to the bottom. (B) upper 12th & 13th; (C) lower 11th & 13th. A strikingly derived design, but quite different from the mammalian system and vaguely reminiscent of Haramiyida. From [BS00].

Links: dinosaurs- dvinia prima; Biology 356; Chapter Two – Problems Carved in Stone.

References: Battail & Surkov (2000) [BS00]; Hopson (1991) [H91]; Hopson & Barghusen (1986) [HB86]; Kemp (1982) [K82]; Sidor & Hopson (1998) [SH98]; Tatarinov (1968) [T68]. ATW020530.

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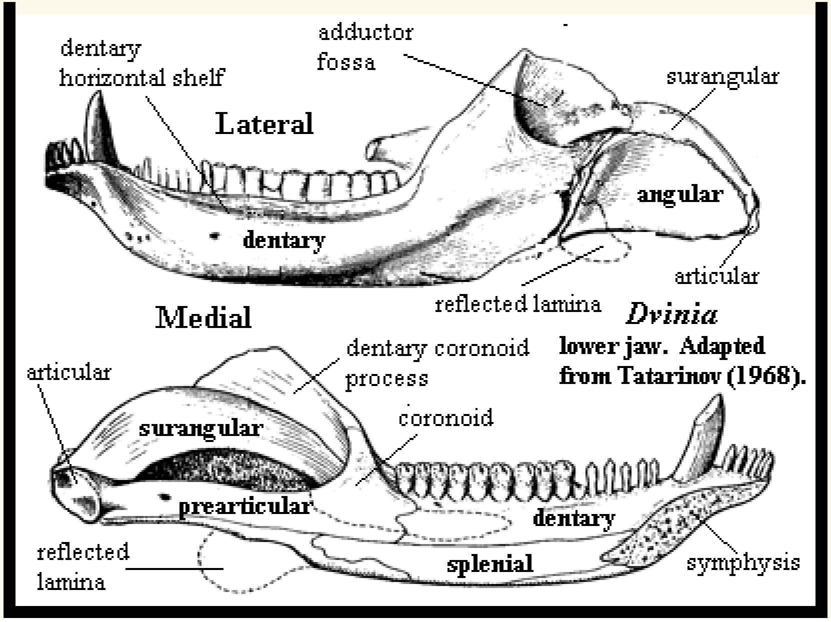

Dvinia **lower jaw. Adapted from Tatarinov (1968).**

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Cynodontia: Overview

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIAFORMES
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Contents

The Cynodont Radiation

The **cynodonts**, or 'dog teeth', were the most successful and one of the most diverse groups of therapsids. Their Late Permian and Triassic evolutionary radiation included such forms as the large, carnivorous **cynognathids**, equally large herbivorous traversodonts, and the small and extremely mammal-like **tritylodontids** and **tritheledonts**. The tritheledonts (ictidosaurs) are almost certainly close to the direct ancestry of the Mammalia. The extremely mammal-like structure of cynodonts has been known for nearly a century, but only within recent years have we learned enough about them and about the very early mammals to say with confidence that all mammals are indeed descended from a single group of cynodonts

Even the earliest cynodonts, the **Procynosuchidae** of the Late Permian, show many advanced mammalian characteristics, such as a reduced number of bones in the lower jaw, a secondary bony palate and a complex pattern of the crowns of their cheek teeth. It is likely that Cynodonts were at least partially if not completely warm-blooded, covered with hair, which would have insulated them and helped to maintain a high body temperature.

By Early Triassic times, cynodonts had diverged into large predaceous carnivores such as *Cynognathus* and moderate large omnivorous and herbivorous types such as *Trirachodon* and *Diademodon*. The Middle Triassic saw a major radiation of herbivorous forms included in the family Traversodontidae. From this family evolved the highly specialized and extremely mammal-like Tritylodontidae of the Late Triassic to Middle Jurassic, the "rodents" of the early Mesozoic and culmination of the herbivorous cynodont radiation. At the same time, the descendents of *Cynognathus* evolved into medium-sized to small carnivorous and insectivorous forms. It is interesting that as the archosaurian reptiles were becoming larger, the cynodonts became smaller, perhaps nocturnal. The hot arid Triassic conditions favored the ectothermic reptilian metabolism of the archosaurs over the warm-blooded mammalian organization of the cynodonts. (In his *Dinosaur Heresies*, Bob Bakker has clamed that even the early thecodont archosaurs like *Erythosuchus* were warm-blooded, and out-competed the cynodonts for this reason, but this position is almost never held nowadays.)

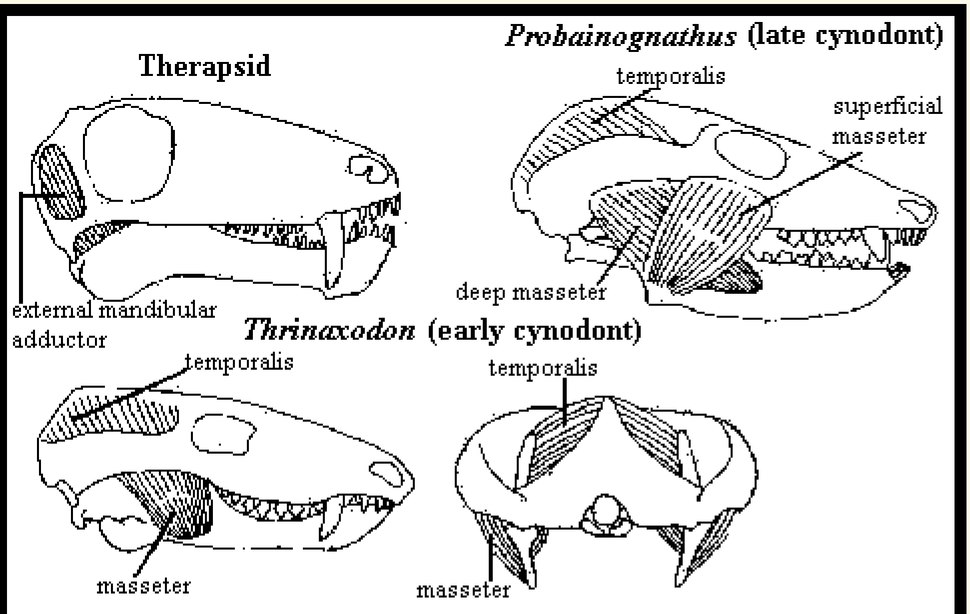
In the end, the small advanced cynodonts and their mammalian descendents became nocturnal, depending on hearing and smell and leaving the day to the visual-orientated archosaurs. Cynodont and early mammalian brains were larger than sauropsid (reptilian) brains not because they were more intelligent, but because of the enlarged olfactory and auditory bulbs. The small cynodonts and Mesozoic mammals owned the cool night, or lived in trees, the large thecodonts and dinosaurs ruled the day and the ground. It was to be some 150 million years before a combination of environmental stress and cometary or asteroid impact brought about the end of the dinosaurs and the other great reptiles, and allowed the mammals to emerge and take control of the Earth.

Masseter-Minds of the Mesozoic

The cynodonts are a very well-known and intensely studied volume of phylospace. In particular, a series of interdependent changes in the cynodont head -- mostly soft tissue changes -- has been the focus of much science and not a little inspired speculation. The principle issues are (a) the development of the characteristic mammalian jaw musculature and jaw articulation (b) the enlargement of the brain (c) the evolution of the mammalian middle ear, and (d) the beginnings of the unique mammalian feeding style and molar dentition. This is far too much to swallow all at one bite, even for well-educated hominids with all of the aforesaid brain, jaw, ear and dental equipment. **Palaeos** is an ambitious project, and we have not shied away from some reasonably technical matters. However, any attempt to integrate all of these issues at once would decisively cross the line between ambition and hubris. Of these four transformations, the change in jaw musculature may have been the most advanced at the end of the Permian. Accordingly, as a first iteration, we will outline the changes in jaw musculature and note how those developments may have related to some of the others on our list.

As Rowe (1996) points out, the early cynodonts were the first synapsids in which the brain filled the endocranial cavity. This is, perhaps, not the most impressive of accomplishments because the cynodonts were, quite literally, narrow-minded. That is, the brain was a long, tube-like affair (notably priapiform, in fact) trapped within a very narrow skull. **[1]** However, precisely because space was limited, any further expansion of the brain required remodeling the skull -- a constraint which had profound consequences for both the structure of the ear and the location of the jaw muscles. All three of these structures -- brain, jaw muscles and ear – compete for space at the back of the head. This is particularly true of the brain and jaw muscles since both are made up of a single basic type of cell and the power of both is, roughly speaking, a linear function of the number of cells.

In more basal therapsids, the jaw was closed reptile-fashion, by the *adductor mandibularis*, which originated on the braincase. The bulk of the muscle mass was located in an adductor chamber between the braincase and the dermal skull bones. The adductor mandibularis inserted on the *coronoid process* and internal surface of the lower jaw. Fenestration of the temporal area of the skull allowed more room for muscle mass. However, even the earliest cynodonts had taken this trend just about as far as it could go.



Development of the masseteric jaw musculature in cynodonts. From Carroll (1988).

One crucial change seems to have occurred in the precynodont therapsid lineage. In order to make more room for the adductor, the bar under the temporal fenestra (jugal + squamosal) became more robust and moved laterally, bowing out from the side of the skull. By itself, this development might have left the braincase overly exposed, but the parietal grew down and covered the braincase laterally. Thus, the attachment area for the adductor was both changed and split. The point is extremely important for later developments, and -- at the risk of beating a dead horse -- worth doing one more time, with feeling, and in more rigorous detail. See, generally, Carroll (1988).

FIRST In the old adductor chamber, the adductor attached to the *inner surface* of the parietal (which roofed the chamber) and to the braincase. In *Thrinaxodon*, this is geometrically impossible. Instead, the adductor attaches to the *outside surface* of the parietal, which *covers* the braincase. Thus the braincase no longer need be engineered to support muscle. There is also more room to expand. In this configuration, expansion of the braincase will actually increase the surface area available for muscle attachment, if some of the muscle body can be moved out of the way.

SECOND Expansion of the old subtemporal bar into a laterally flared *zygomatic arch* does exactly that, and more. Not only does it open up the space for muscle mass, but it creates a whole new surface for muscle attachment. The old *adductor mandibulae* therefore splits. The portion attaching to the external surface of the parietal is now referred to as the *temporalis*. The portion attaching to the inside surface of the zygomatic arch is referred to as the *masseter*. The temporalis attaches generally to the coronoid process and medial jaw, as before. But the masseter is not only posterodorsal to the jaw, it is also lateral. It attaches to the *outside* or lateral surface of the coronoid process. This creates an entirely new level of jaw control. Since we now have adductor muscles on both sides of the lower jaw, it becomes possible to develop controlled, lateral grinding movements.

The final step, taken by the late cynodonts, is illustrated in the figure of *Probainognathus*. Here, the masseter itself has split, with part moving anteriorly to originate on the anterior portion of the zygomatic arch, under the orbit and attach on the posterior end of the jaw. Now, we also have opposing adductors anterior and posterior, allowing front-to-back as well as side-to-side grinding. With this complete set of muscles, it becomes possible to make controlled grinding movements of the jaw in any direction. Since these are all adductor muscles, this can all be done while the jaw is closed. Given this level of fine control, it became possible, and advantageous, to evolve teeth with fixed and definite patterns of cusps. That is to say, all of this muscle reorganization set the stage for the waves of dental specialization which characterized the mammal lineage, as well as the expansion of the brain.

As Crompton & Parker (1978) point out, this suite of muscles also permits the animal to generate impressive jaw forces on the teeth without generating much pressure at all on the jaw joint. In fact, given the hypertrophied muscles developed by the cynodonts, the jaw joint becomes almost irrelevant. These jaws were not designed to slice or cut using the momentum of a rapidly closing hinge joint. Rather, the cynodont jaw was optimized to shear, tear and grind by lateral movement after the mouth was already closed. The jaw, as such, needed only to be fast enough to work around an appropriate food item. Depending on diet, this might not require a hinge joint at all. Accordingly, the reconstruction of the cynodont jaw muscles also freed up the post-dentary bones to be exapted for other uses, such as hearing, and permitted a gradual shift of the joint to a more mechanically advantageous articulation between the dentary and squamosal. Conversely, with opposing sets of muscles actin on the jaw at various points, it would be disadvantageous to divide the structure of the mandible among several bones. This could easily result in the jaw ripping itself apart. Thus the development of the dentary as the only bone in the lower jaw, to the exclusion of all other mandibular bones, can also be understood in terms of the structure of the jaw muscles.

But, to return to our starting point, one should not take this sort of simplistic analysis too seriously. Had we started with an analysis of brain expansion or dentition, we might have been able to make a similar case, creating the impression that these innovations drove all of the others. We can *understand* the various systemic changes in terms of their relationships with jaw musculature, but we should not confuse this understanding with actual causation. It is not even clear that "causation" is a meaningful concept when applied to co-evolving and interrelated systems of this sort. Rather, in focusing on jaw muscles, we have simply chosen a convenient point of view from which to observe certain points of a smooth series of state changes. ATW030214.

Notes: [1] Kemp (1982) suggests that the brain may have been much deeper, hence larger, than is usually supposed.

Image: (model) the Hammond reconstruction of *Procynosuchus*.

References: Barghusen (1968); Carroll (1988); Crompton & Parker (1978); Kemp (1982); Rowe (1996).

Cynodontia: Basal Cynodonts: Procynosuchidae

Abbreviated Dendrogram

```
THERAPSIDA
|
Cynodontia
|--Procynosuchidae
|  |--Nanocynodon
|  |--Parathrinaxodon
|  `--Procynosuchus
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
```

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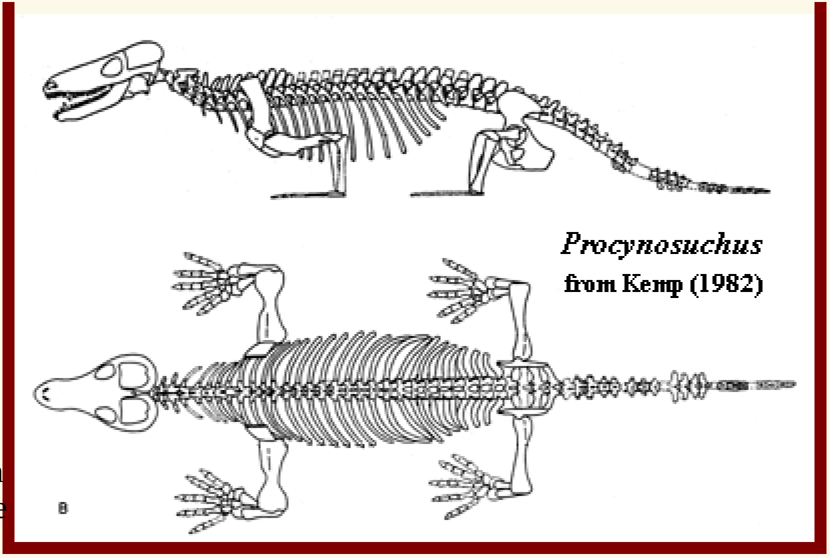
3. Procynosuchidae X
4. *Procynosuchus* X

Procynosuchidae: Late Permian Cynodonts

The **procynosuchids** were the earliest cynodonts. They flourished during the latest Permian (Cistecephalus and Daptocephalus Zones of South Africa and Tartarian Zone IV of Russia), evolving from the same basic therapsid stock as the therocephalians. Like some of the



Procynosuchus from Kemp (1982)

therocephalians, the cynodonts possessed a long series of small multicusped cheek teeth and a partial secondary palate. However, the cynodonts also possessed certain unique features as well, such as a closed braincase which probably served generally to strengthen the skull and to protect the brain and middle ear cavity from pressures generated by the contraction of the increased mass of jaw muscles. The cheek teeth had a much more complex cusp pattern than that of all but a few bauriamorph therocephalians (*e.g.*, the Bauridae). The complex cheek teeth and secondary palate show that the cynodonts were able to chew and breathe at the same time (which most reptiles cannot - they swallow their food in gulps). The food was broken down in the mouth rather than the stomach. Modifications in the jaw and the flared zygomatic arch reflect increased differentiation of jaw musculature. MAK000907. ATW030211.

Procynosuchidae: *Uralocynodon*. Possibly paraphyletic stem group of Permian cynodonts.

Range: Late Permian of South Africa, Europe & Russia. [BS00]

Phylogeny: Cynodontia :: Epicynodontia + * : *Nanocynodon* + *Parathrinaxodon* + *Procynosuchus*.

Characters: eyes generally forward-facing (possibly full stereoscopic vision); huge temporal fenestra, leaving parietal as steep sagittal crest; zygomatic arch robust and extends forward and lateral to dentary, allowing muscles to insert on lateral face of dentary [C88]; squamosal flares posteriorly in posterior wall of temporal fossa [HB86]; quadrate & quadratojugal well-exposed [BS00]; posttemporal foramen reduced [HB86]; paroccipital process expanded anteroposteriorly [HB86]; anterodorsal process of prootic extensively contacts epipterygoid [HB86]; premaxilla, palatine and maxilla expanded on palate but do not meet at midline [BS00]; probably had complete secondary palate, partially unossified [C88]; small interpterygoid vacuity present [BS00]; dentary bears coronoid process, laterally recessed for muscle insertion (*i.e.*, a *masseteric fossa*) [C88]; surangular articular displaced to retroarticular process on postero*ventral* surface of jaw; 6 incisors & 1-2 precanines in upper jaw [BS00]; cheek teeth with multiple cusps, but linear and do not occlude [C88]; cheek teeth slight compressed laterally [BS00] cheek teeth with labial cingulum and cusps [BS00]; teeth continuously replaced [C88]; thin, mammal-like tail (so did not rely on tail for locomotion) [C88]; neither set of limbs apparently sprawled, but forelimbs may not normally have been fully extended; digits unusually long; possibly strong digging and/or swimming; insectivorous? (perhaps more diverse diet).

Links: Procynosuchus delaharpeae Broom; Procynosuchus (in German).

Image: *Procynosuchus*, © 1999 Henssen PalaeoWerkstatt and reproduced by permission.

References: Battail & Surkov (2000) [BS00]; Carroll (1988) [C88]; Hopson & Barghusen (1986) [HB86]; Kemp (1982) [K82]; Rowe (1996) [R96]. ATW030209.

***Nanocynodon*:** *N. seductus* Tatarinov 1968.

Range: Late Permian of Russia

Phylogeny: Procynosuchidae **:** *Parathrinaxodon* + *Procynosuchus* + *.

Characters: very small [BS00]; at least 10 postcanines [BS00]; postcanines strongly compressed transversely and *sectorial* [BS00]; narrow lingual cingulum with accessory cusps [BS00].

Note: may be a thrinaxodontid.

Links: RepTherapS.pdf ATW030218, MAK000907.

References: Battail & Surkov (2000) [BS00].

Parathrinaxodon: *P. proops* Parrington 1936. Possibly synonymous with *Procynosuchus* [H91].

Range: Late Permian of Africa, Kawinga Formation of the Ruhuhu Valley, Tanzania.

Phylogeny: Procynosuchidae **:** *Nanocynodon* + *Procynosuchus* + *.

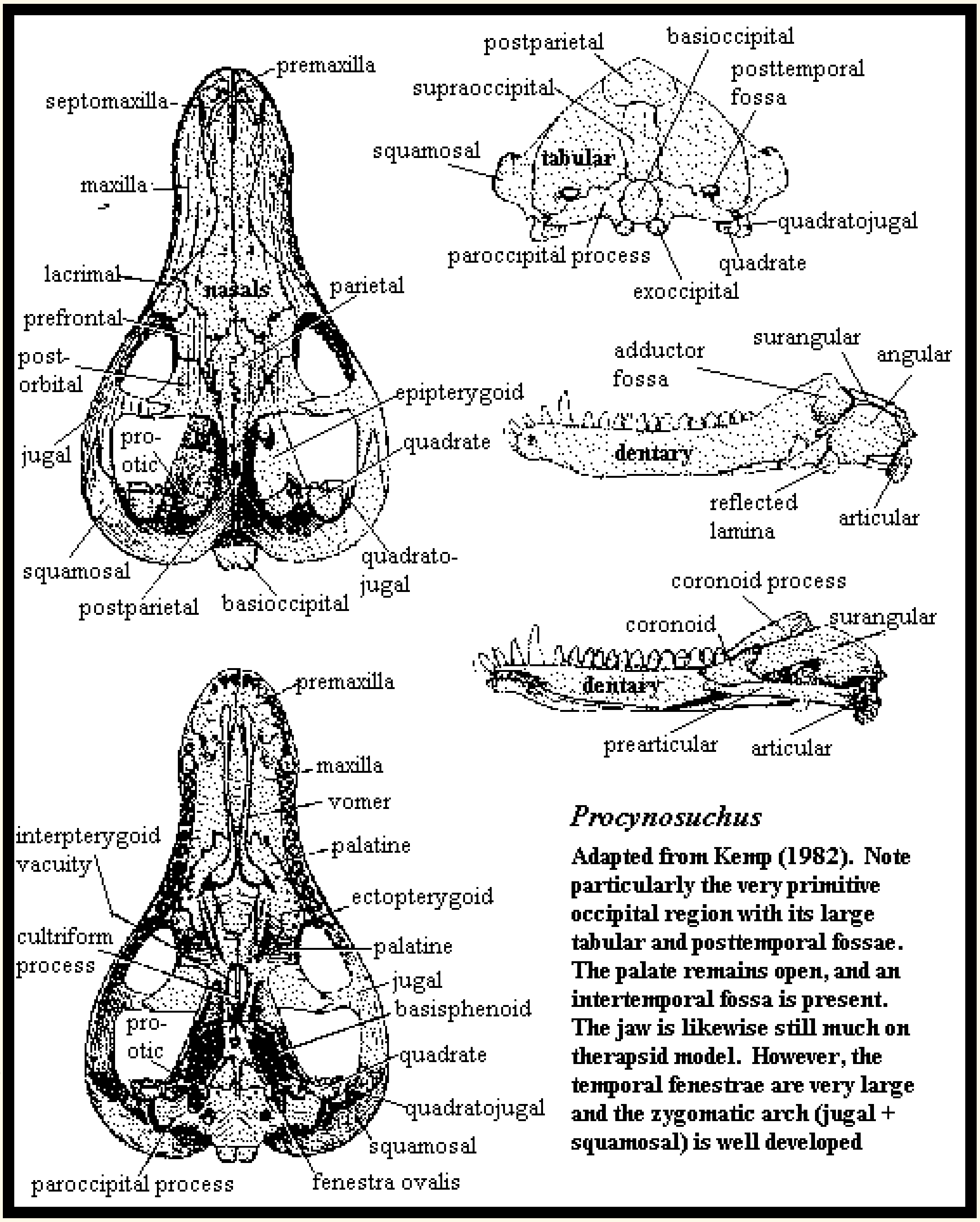
Characters: secondary palate probably not closed [H91]; postcanine teeth identical to *Procynosuchus* [H91].

References: Hopson (1991) [H91]. ATW030215, MAK000907

Procynosuchus: *P. delahareae* Broom. Synonyms: ?*Cyrbasiodon boycei* Broom 1931; *Procynosuchus rubidgei* Broom 1938; *Paracynosuchus rubidgei* Broom 1940a; *Nanictosuchus melinodon* Broom 1940a; *Mygalesaurus platyceps* Broom 1942; *Aelurodraco microps* Broom & Robinson 1948b; *Leavachia duvenhagei* Broom 1948; *Galeophrys kitchingi* Broom 1948; *Galecranium liorhynchus* Broom 1948; *Suphedestes polyodon* Broom 1949; *Protocynodon pricei* Broom 1949; *Suphedocynodon gymnoternporalis* Brink 1951; *Leavachia microps* Brink & Kitching 1951a; *Leavachia gracilis* Brink & Kitching 1951a; *Scalopocynodon gracilis* Brink 1961.

Range: Late Permian of Europe & South Africa, Daptocephalus Zone

Phylogeny: Procynosuchidae **:** *Nanocynodon* + *Parathrinaxodon* + *.



Procynosuchus

Adapted from Kemp (1982). Note particularly the very primitive occipital region with its large tabular and posttemporal fossae. The palate remains open, and an intertemporal fossa is present. The jaw is likewise still much on therapsid model. However, the temporal fenestrae are very large and the zygomatic arch (jugal + squamosal) is well developed

Characters: Size: 60cm long; snout broader than tall [SH98]; articular axis of quadrate somewhat anteromedially directed [K82]; quadrate and quadratojugal with simple articulations in squamosal [K82]; secondary palate very incomplete [K82]; vomers fused [K82]; tooth rows diverge posteriorly [K82]; articular surface of articular faced posterodorsally & somewhat medially [K82] **[1]**; 4 lower incisors [K82] [SH98]; precanine teeth on maxilla present [SH98]; anterior postcanines with a single large, slightly recurved central cusp and a labial ridge [K82]; posterior postcanines similar, but with ~5 accessory cusps on the lingual cingulum [K82]; lingual cingulum small [SH98]; buccal cingulum entirely absent [K82]; molariforms did not occlude but did shear past each other to some extent [K82]; trunk vertebrae with typical cynodont accessory zygapophyseal articulations absent [K82]; ribs without costal plates [K82]; rib heads fused into continuous synapophysis [K82]; thoracic and lumbar vertebrae somewhat differentiated, with lumbars being more massive and bearing shorter ribs [K82]; thoracic vertebrae with tight zygapophyseal articulations preventing lateral movement [K82] **[2]**; lumbar zygapophyses horizontal, permitting lateral undulation [K82]; posterior lumbar ribs are fused to transverse processes [K82]; may have had broad tail for swimming [K82]; limb bones & feet very flat [K82] (*contra* [H91] -- artifact of preservation); scapula broad & flat [K82]; coracoids large [K82]; glenoid widely open [K82] (*contra* [H91] -- artifact of preservation); forelimbs permanently sprawling [K82]; ulnar condyle present on humerus (not just a notch) [SH98]; ilium only slightly expanded anteriorly [K82]; hindlimbs probably capable of both sprawling & upright locomotion [K82]; insectivore? [K82]; aquatic? [K82] (*contra* [H91] -- supposed aquatic adaptations are all artifacts of preservation).

Note: [1] the significance of the articular angle is sketched at left. The fact that the articulation was angled implies that the musculature acting on the jaw was primarily a primitive adductor mandibulae, originating from the braincase. These muscles pull medially, and the jaw articulation is consequently angled to resist this medially- directed vector. **[2]** One, often repeated, speculation is that the earliest cynodonts had already acquired a diaphragm, hence the need to stiffen the thoracic region. This is also consistent with the reduction of lumbar ribs no longer needed for costal ventilation and the stiffening of the thoracic rib articulations. Kemp [K82] notes an abrupt change in angle, and more gradual change in length, beginning at the 21st rib as marking the possible posterior extent of the diaphragm.

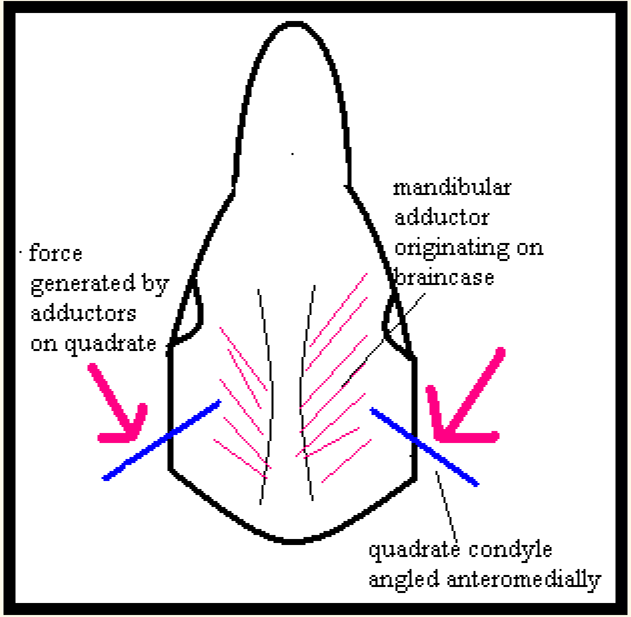


Image: (right) unfortunately, it was necessary to degrade this image considerably to fit it on the page.

Links: Skelettabguß von Procynosuchus delaharpeae Broom; Procynosuchus (German); Mounted skeletal reconstruction of the cynodon Procynosuchus delaharpeae Broom; Procynosuchus; Cuffey 2 - Mammal - Like Reptiles.

References: Hopson (1991) [H91]; Kemp (1982) [K82]; Sidor & Hopson (1998) [SH98]. ATW030214.

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checked ATW041118

Cynodontia: Basal Cynodonts: Epicynodontia

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--Epicynodontia
   |--Galesauridae
   |  |--Cynosaurus
   |  |--Galesaurus
   |  |--Nanictosaurus
   |  |--Platycraniellus
   |  `--Tribolodon
   `--+--Thrinaxodon
      `--Eucynodontia
         |--Cynognathia
         |  |--Cynognathidae
         |  `--Tritylodontidae
         `--Probainognathia
            |--Tritheledontidae
            `--MAMMALIFORMES
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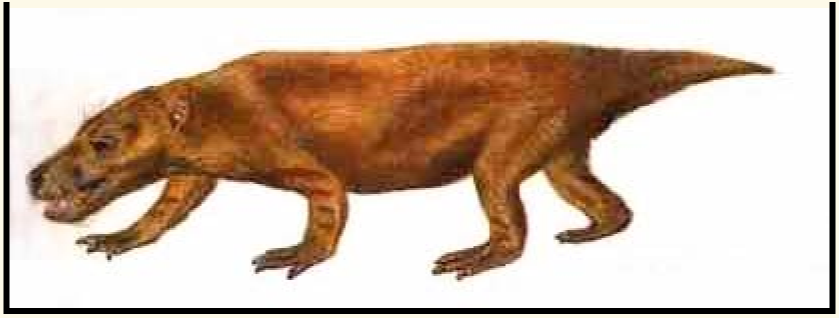
2. Epicynodontia
3. Galesauridae X
4. *Galesaurus* X
5. *Nanictosaurus* X
6. *Platycraniellus* X
7. *Thrinaxodon* X
8. *Tribolodon* X

The Epicynodonts: Early Triassic Cynodonts

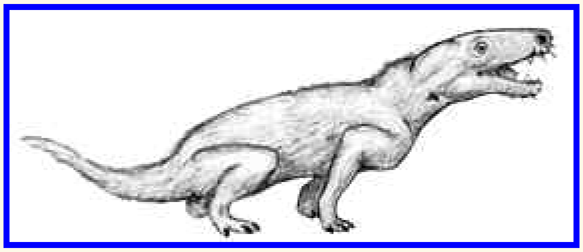
The **Galesauridae** and the very well-known ***Thrinaxodon*** make up the basal epicynodonts. The



epicynodonts are similar to, but more mammal-like than, their ancestors the Permian procynosuchids. Basal epicynodonts were small, solidly built carnivores, capable of running, to judge by the erect posture of their strong, if short, hind legs. An animal like *Thrinaxodon*, in its cranial anatomy and dental morphology must be close to the ancestry of the earliest mammals. Certain of its cheek teeth hear a striking similarity to those of the latest Triassic mammals.

Another mammalian trend is seen in the lower jaw of *Thrinaxodon*. The teeth on either side were set into a single bone, the dentary, which had become larger at the expense of the smaller bones at the back of the jaw. The effect of this trend among cynodonts, toward a single lower jaw bone, was to make the jaws stronger. The zygomatic arch of bone at the rear of the skull, behind the eyes, was also was heavier; the masseteric fossa and coronoid process were essentially mammalian in size and shape, indicating the presence of well-differentiated masseter and temporal muscles. As with the procynosuchids, there is a complete, ossified, secondary palate, which completely covered the roof of the mouth and separated the breathing passage from the mouth. This development allowed the animal to breathe at the same time as retaining food in its mouth for longer periods, chewing it up into small pieces for quicker digestion.

The body was long and - for the first time among vertebrates - divided into a distinct chest (thoracic) and lower back (lumbar) region. The division was marked by the extent of the ribs; only the thoracic vertebrae bore ribs, and these formed a distinct cage, which housed the vital organs such as the heart and lungs. As in living mammals, there was probably a sheet of muscular tissue, the diaphragm, that closed off the rib cage in Thrinaxodon. As the animal breathed, the movement of the diaphragm would have filled and emptied its lungs efficiently an essential development in the evolution of body temperature control.



Many other structural changes had occurred showed a number of progressive changes over their Permian procynosuchid ancestors. For example, one of the foot bones had developed a heel which, with the help of strong tendons, would have acted as a lever to lift the foot clear of the ground with each step. The toes were all of equal length, allowing the body weight to be evenly distributed over them. MAK000718 ATW030212

Image: *Thrinaxodon* (left) from drawing by Professor Paul E. Olsen - The Triassic World.

Descriptions

Epicynodontia: *Galesaurus* + Galileo

Range: from the Late Permian

Phylogeny: Cynodontia **::** Procynosuchidae + * **:** Galesauridae + (*Thrinaxodon* + Eucynodontia)

Characters: fusion of parietals at midline [S01]; zygomatic more robust and broader than in basal forms [K82]; squamosal flares posteriorly in posterior wall of temporal fossa [HB86]; squamosal auditory meatus groove moderately deep (deeper than basal cynodonts) [SH98] [HK01**$**]; squamosal with enlarged descending flange lateral to quadratojugal [SH98] [HB86**$**]; quadrate & quadratojugal smaller and more closely integrated into squamosal [K82] [HB86**$**]; quadrate contacts only squamosal & not paroccipital process [SH98]; occiput wide & low [K82]; posttemporal foramen reduced [HB86]; paroccipital process expanded anteroposteriorly [HB86]; anterodorsal process of prootic extensively contacts epipterygoid [HB86]; secondary palate complete in most except for small anterior fissure [K82] (*contra* [H91]); ectopterygoid reduced [K82]; pterygoid lateral processes slight [K82]; interpterygoid vacuity closed in adults [K82] [HB86**$**] [HK01**$**]; dentary larger & post-dentary bones smaller than in procynosuchids [K82]; coronoid process very large & extends dorsally well into level of temporal fenestra [K82]; coronoid process dorsal limit above level of orbit [SH98] [HB86**$**] or to mid-orbit [HK01**$**]; masseteric fossa extends to ventral margin of dentary [SH98] [HB86**$**] [HK01**$**]; height of postdentary bones less than 50% dentary height [SH98]; intramandibular fenestra between surangular & angular covered by dentary [SH98]; 4 upper incisors [SH98] [HK01**$**]; incisors 4/3 [K82] [SH98] [HB86**$**] [HK01**$**]; precanines absent [K82] [HB86**$**]; 7-9 postdentary (*sic* -- postcanine?) teeth [K82]; postcanines with accessory cingular cusps enlarged mesial & distal to main cusp, with rest of cingulum reduced or absent [K82]; vertebrae amphicoelous [SH98]; ribs with costal plates [SH98] [H91] [HK01**$**]; posterior process of ilium longer than acetabulum diameter [SH98] [HK01**$**]; pubis length shorter than diameter of acetabulum [SH98] [HK01**$**]; pes 4 with 4 phalanges [SH98].

References: Carroll (1988); Hopson (1991) [H91], Hopson & Barghusen (1986) [HB86]; Hopson & Kitching (2001) [HK01]; Kemp (1982) [K82]; Sidor (2001) [S01]; Sidor & Hopson (1998) [SH98]. ATW030722.

Galesauridae:

Range: Late Permian to Middle Triassic of Africa, Europe, Antarctica, Russia & probably everywhere else.

Phylogeny: Epicynodontia **:** (*Thrinaxodon* + Eucynodontia) + * **:** *Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon*.

Characters: snout broader than tall [SH98]; zygomatic arch enlarged; complete secondary palate; coronoid process with masseteric fossa; all postcanines on lower jaw on dentary; mesial accessory cusps absent [HB86**$**]; lower lingual cingulum absent [SH98] [HB86**$**]; distinct lumbar & thoracic regions, with ribs restricted to thoracic region; limbs somewhat more upright; calcaneal heel; diaphragm probably completely established.

References: Hopson & Barghusen (1986) [HB86]; Kemp (1982) [K82]; Sidor & Hopson (1998) [SH98]. ATW030215.

***Cynosaurus*:** (Genus *Cynosaurus* Schmidt 1927) *C. suppostus* (Owen 1876) (= *Cynosuchus* Owen 1876 = *Cynosuchoides* Broom 1931 = *A'anictosaurus* Broom 1936 = *Mygalesuchus* Broom 1942 = *Baurocynodon* Brink 1951).

Range: Late Permian of South Africa, Upper Daptocephalus Zone. [K82]

Phylogeny: Galesauridae **:** *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon* + *.

Characters: secondary palate not complete [K82]; teeth similar to *Thrinaxodon*, but without cingulum [K82].

References: Kemp (1982) [K82]. MAK 000718. ATW030419.

***Galesaurus*:** (= *Glochinodon* van Hoepen 1916 = *Glochinodontoides* Haughton 1924b). *G. planiceps* Owen 1859 (= *Glochinodon detinens* van Hoepen 1916 = *Glochinodontoides gracilis* Ilaughton 1924b = *Notictosaurus gracilis* Broom & Robinson 1948a = *Notictosaurus trigonocephalus* Brink & Kitching 1951b).

Range: Early Triassic of South Africa, Lystrosaurus Zone. (Possibly Permian)

Phylogeny: Galesauridae **:** *Cynosaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon* + *.

Characters: frontals with anterior "spine" projections inserting between nasals, persisting in adults; postcanines with large central cusp curving back to overhang distal accessory cusp [K82]; postcanines lack mesial cingula & mesial accessory cusps

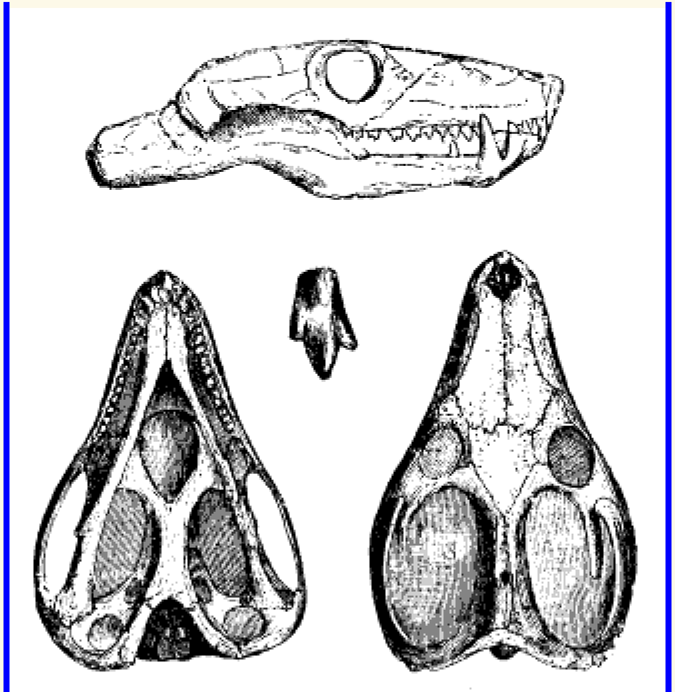


Fig. 78. Skalle af *Galesaurus* (efter Owen).

[K82].

Links: Triassic Dinosauria (historical interest); On the Classification of the Dinosauria (1870) (same); The Permo-Triassic Extinction; 68 (Människan. Hennes uppkomst och utveckling) (Swedish?); The Permo-Triassic Extinction; therapsid8b;

Note: Small, immature specimens have usually been referred to the genus *Galesaurus*, large, mature specimens to *Glochinodontoides*. MAK 000718.

References: Kemp (1982) [K82]. ATW030220.

Nanictosaurus: *N. kitchingi* Broom 1936 (= *N. robustus* Broom 1940b = *N. rubidgei* Brink & Kitching 1953).

Range: Late Permian of South Africa, Upper Daptocephalus Zone, Dicynodon laterticeps - Whaitsia Assemblage Zone.

Phylogeny: Galesauridae **:** *Cynosaurus* + *Galesaurus* + *Platycraniellus* + *Tribolodon* + *.

Note: *N. robustus* was previously considered a Procynosuchid and synonym of *Procynosuchus delaharpeae*; it is now known to be the same as *N. kitchingi*. MAK 000718. ATW040103.

Platycraniellus: (= *Platycranion* van Hoepen 1916 = *Platycranium* van Hoepen 1917) *P. elegans* vanHoepen 1916 (= *Platycranion elegans* van Hoepen 1916 = *Platycraniellus elegans* van Hoepen 1917).

Range: Early Triassic of South Africa, Lystrosaurus Zone.

Phylogeny: Galesauridae **:** *Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Tribolodon* + *.

Remarks: This species is known with certainty only from the type, which comes from Liarrismith, Orange Free State. A second specimen referred to this species by Brink is a *Galesaurus*. MAK 000718.

Tribolodon: Seeley 1894a. *T. frerensis* Seeley 1894a.

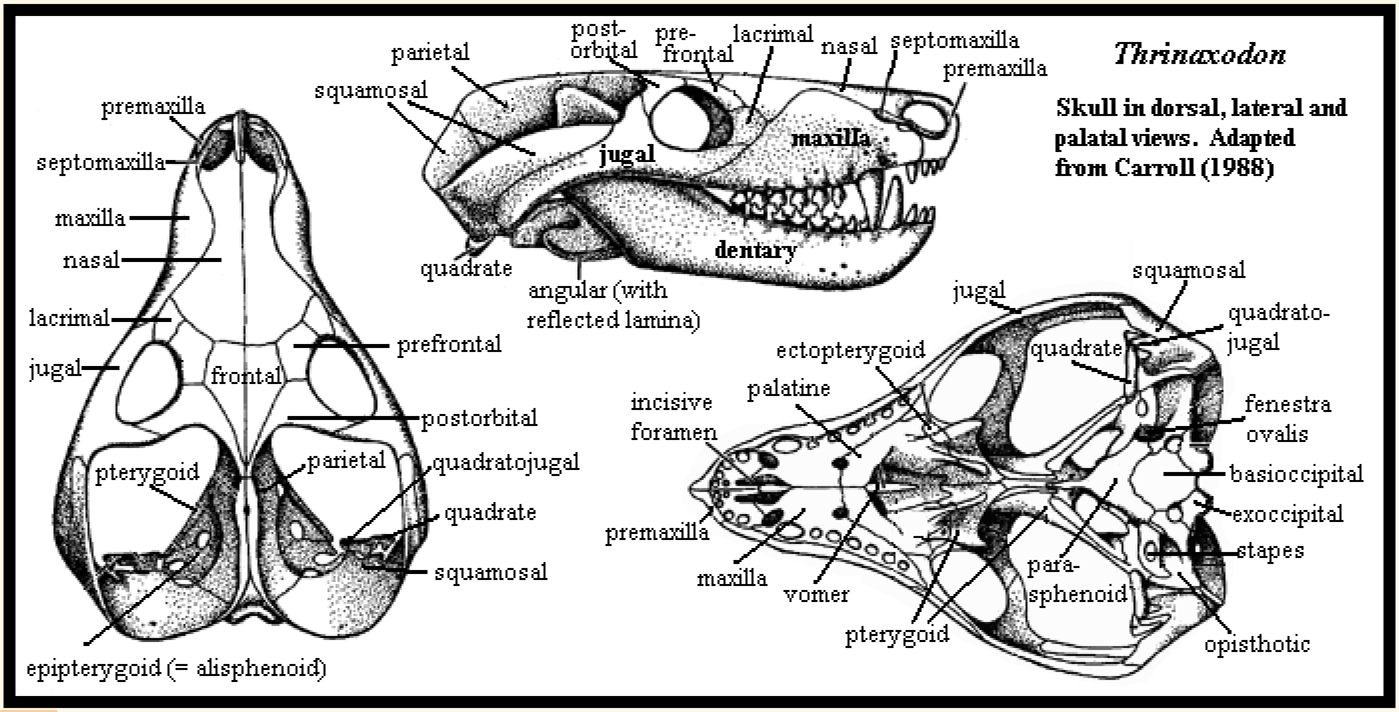
Range: Early Triassic of South Africa, Cynognathus Zone. [K82]

Phylogeny: Galesauridae **:** *Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *.

Characters: postcanine teeth tall & slender, with strong accessory cusps mesial & distal [K82]; labial cingulum present with additional accessory cusps [K82].

Note: [1] The name appears to be preoccupied by *Tribolodon* Günther 1877, a genus of cyprinid fish (dace). **[2]** This is the youngest species referable with certainty to the Galesauridae. Though frequently classified as a cynognathid, it is a typical galesaurid in its known features.

References: Kemp (1982) [K82]. ATW030215.



Thrinaxodon

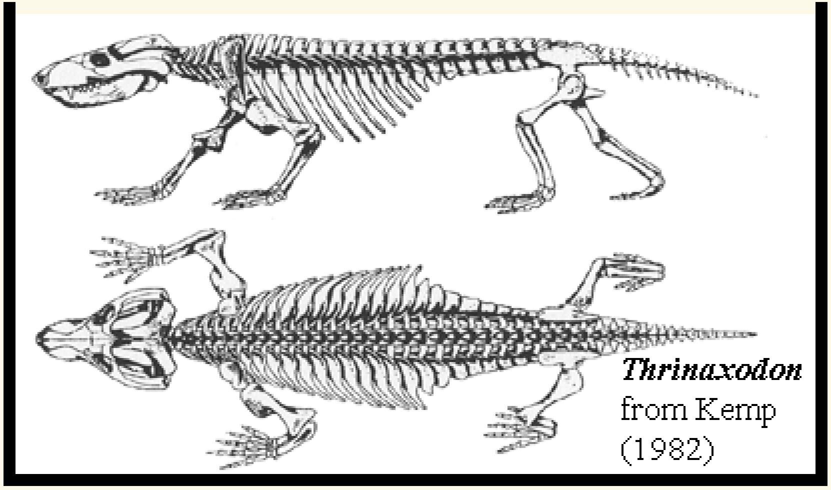
Skull in dorsal, lateral and palatal views. Adapted from Carroll (1988)

Thrinaxodon: *T. liorhinus* Seeley 1894a.

Range: Early Triassic Lystrosaurus Zone of South Africa & Fremouw Formation of Antarctica. [K82].

Phylogeny: Epicynodontia :: Eucynodontia + *.

Characters: 50 cm badger-like carnivore known from many remains [C88]; snout about as broad as tall [SH98]; postorbital and postfrontal merge [C88]; narrow braincase in sharp parietal crest [C88]; pineal opening present [C88]; robust zygomatic arch; adductor chamber almost half length of skull; squamosal covers posterior and forms most of adductor chamber & lateral surface of occiput [C88]; quadrate and quadratojugal much reduced & fit into sockets on squamosal [C88]; quadrate with posterior flange inserting in squamosal & capable of some anteroposterior motion [K82]; double condyle on occiput, but condyles remain below foramen magnum; ethmoturbinates present of type associated with homeothermic water-recovery system [H94]; fully ossified secondary palate [C88] [HB86]; incisive foramina present (shared with eucynodonts) [SH98]; palatine flanges in secondary palate meets at midline [SH98]; vomers with parallel sides, not expanded [SH98]; large dentary with coronoid reaching above zygomatic arch [C88]; masseteric fossa present and "reaches to its base" (base of dentary? or coronoid process?) [C88]; post-dentary bones lose sutural contact with dentary; reflected lamina large and deflected laterally [C88]; no evidence of a dentary-squamosal articulation [C88]; may have been a partial surangular - squamosal articulation [K82]; teeth with "reptilian" alternate replacement pattern [K82] **[2]**; dental formula 4/3,1/1,7-9/7-9 [C88]; cheek teeth regularly replaced, don't occlude, but have multiple cusps [C88]; upper cingulum much reduced or absent [K82]; lower lingual cingulum small [SH98]; proatlas present, but simplified atlas-axis articulation permits some rotation of head; long trunk; zygapophyses on dorsal vertebrae strongly angled upwards (limits lateral, but permits dorsoventral flexion) [C88]; zygapophyses with accessory articulations between peg below postzygapophyses and groove below prezygapophysis [K82]; 7 cervicals,13 dorsals, 7 lumbar, 5 sacrals, 10-15 caudals [C88]; rib *capitulum* articulates with *parapophysis* formed equally by 2 vertebrae [K82]; ribs proximally expanded to form overlapping costal plates (lateral stiffening) [C88] [K82]; lumbar ribs



have costal plates only [C88]; lumbar plates are vertical [K82]; tail short [C88]; limbs short [C88]; pectoral girdle remains primitive; ventral process of clavicle & interclavicle retained (resist lateral forces of sprawling posture) [C88]; coracoid somewhat reduced; scapula major weight-bearing element, directed vertically; scapular blade deeply concave, with narrowed base [K82]; coracoid plate reduced [K82]; small procoracoid present; dorsal (scapular) portion of glenoid almost flat, with restricting movement [K82]; humerus short, heavy, complex and horizontal [C88]; phalangeal count 23443 [C88]; pubes & ischium reduced [C88]; ilium expanded anteriorly [K82]; femur angled 55° outward, but capable of dorsoventral movement on angled humeral head; beginnings of gluteal-type musculature from iliofemoralis; greater trochanter moderately developed [K82]; calcaneal heel; simple hinge between astragalus (integrated with tibia) and calcaneum; gastrocnemius attaches to calcaneal tuber; plantigrade stance [C88].

Notes: [1] The best known epicynodont, and along with *Cynognathus* the best known cynodont. *Nythosaurus larvatus* Owen is based on the natural mould of a skull bearing impressions of the postcanine teeth. It is probably synonymous with either *Thrinaxodon liorhinus* or *Platycraniellus elegans*. MAK 000718. **[2]** in the typical sauropsid pattern, waves of tooth replacement move down each ramus of the jaw, keeping more or less in synchrony. The replacement wave affects only alternate teeth, avoiding any long gaps. The next replacement wave affects the teeth left intact on the first wave. The pattern in *Thrinaxodon* was somewhat more complex (*i.e.* we didn't understand Kemp's explanation), but followed the same general scheme.

Links: Thrinaxodon CAT Scan Rendering; Thrinaxodon CAT Scan Rendering; Estes, R., 1961; Thrinaxodon; TMM - Exhibits - Scratching the Surface - Thrinaxodon; Thrinaxodon sp.; Later Mammal-like Reptiles; Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; Ungewöhnliche Krokodilkonstruktionen der Vorzeit:; Mammalogy - Lecture 3; ??? ??????? (a great antidote to Bakker's unbearably cute image).

References: Carroll (1988) [C88]; Hillenius (1994) [H94]; Kemp (1982) [K82]; Sidor & Hopson (1998) [SH98]. ATW030212.

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Cynodontia: Galesauridae

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   |  |--Thrinaxodontidae
   |  `--+--Cynosaurus
   |     |--Galesaurus
   |     |--Nanictosaurus
   |     |--Platycraniellus
   |     `--Tribolodon
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
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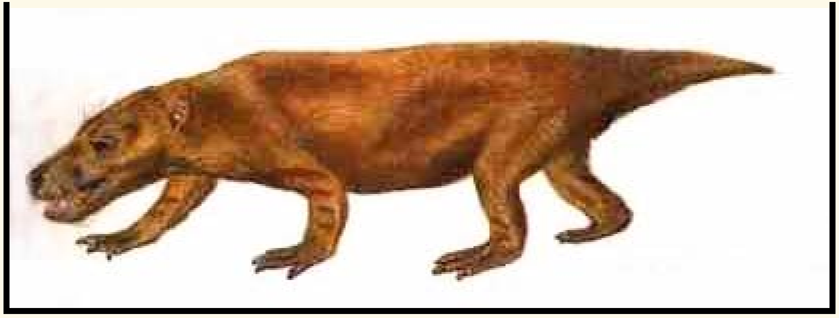
4. *Nanictosaurus* X
5. *Platycraniellus* X
6. Thrinaxodontidae X
7. *Tribolodon* X

The Galesauridae: Early Triassic Cynodonts

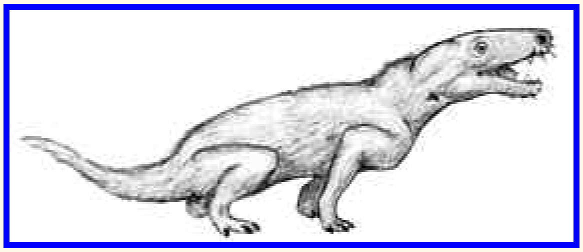
The **Galesauridae** are represented by a number of genera, the best known of which is ***Thrinaxodon***. The thrinaxodonts were similar to, but even more mammal-like than, their ancestors the Permian procynosuchids. These were small, solidly built carnivores, capable of running quite fast to judge by the erect posture of its



strong hind legs. An animal like *Thrinaxodon*, in its cranial anatomy and dental morphology is an ideal ancestor for the earliest mammals. Certain of its cheek teeth hear a striking similarity to those of the latest Triassic mammals of the family Eozostrodontidae.

Another mammalian trend is seen in the lower jaw of *Thrinaxodon*. The teeth on either side were set into a single bone, the dentary, which had become larger at the expense of the smaller bones at the back of the jaw. The effect of this trend among cynodonts, toward a single lower jaw bone, was to make the jaws stronger. The zygomatic arch of bone at the rear of the skull, behind the eyes, was also was heavier; the masseteric fossa and coronoid process were essentially mammalian in size and shape, indicating the presence of well-differentiated masseter and temporal muscles. As with the procynosuchids, there is a secondary or bony palate, which completely separated the breathing passage from the mouth. This development allowed the animal to breathe at the same time as retaining food in its mouth for longer periods, chewing it up into small pieces for quicker digestion.

The body was long and - for the first time among vertebrates - divided into a distinct chest (thoracic) and lower back (lumbar) region. The division was marked by the extent of the ribs; only the thoracic vertebrae bore ribs, and these formed a distinct cage, which housed the vital organs such as the heart and lungs. As in living mammals, there was probably a sheet of muscular tissue, the diaphragm, that closed off the rib cage in Thrinaxodon. As the animal breathed, the movement of the diaphragm would have filled and emptied its lungs efficiently an essential development in the evolution of body temperature control.



Many other structural changes had occurred showed a number of progressive changes over their Permian procynosuchid ancestors. For example, one of the foot bones had developed a heel which, with the help of strong tendons, would have acted as a lever to lift the foot clear of the ground with each step. The toes were all of equal length, allowing the body weight to be evenly distributed over them. MAK000718

Image: *Thrinaxodon* (left) from drawing by Professor Paul E. Olsen - The Triassic World.

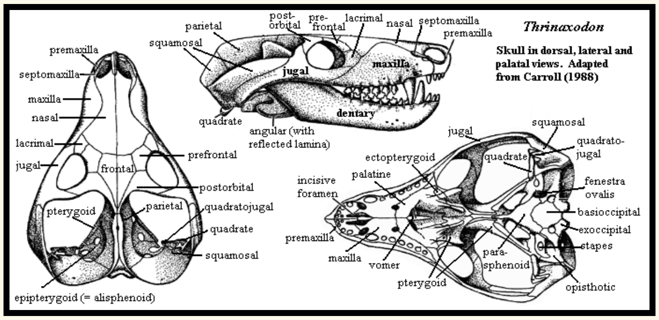
Galesauridae: used here *sensu lato*, as *Thrinaxodon* + *Galesaurus*.

Range: Late Permian to Middle Triassic of Africa, Europe, Antarctica, Russia & probably everywhere else.

Phylogeny: Cynodontia:: Eucynodontia + *: Thrinaxodontidae + (*Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon*).

Characters: zygomatic arch enlarged; complete secondary palate; coronoid process with masseteric fossa; all postcanines on lower jaw on dentary; distinct lumbar & thoracic regions, with ribs restricted to thoracic region; limbs somewhat more upright; calcaneal heel; diaphragm probably completely established. ATW020531.

Thrinaxodontidae: *Thrinaxodon*. *T. liorhinus* Seeley 1894a.



Thrinaxodon

Skull in dorsal, lateral and palatal views. Adapted from Carroll (1988)

Range: Late Permian to Middle Triassic. Best known from the Lystrosaurus Zone of South Africa; Fremouw Formation of Antarctica.

Phylogeny: Galesauridae: (*Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon*) + *.

Characters: 50 cm badger-like carnivore known from many remains. Large dentary with coronoid reaching above zygomatic arch; post-dentary bones lose sutural contact with dentary; reflected lamina large; dental formula 4/3,1/1,7-9/7-9; cheek teeth regularly replaced, don't occlude, but have multiple cusps; fully ossified secondary palate; robust zygomatic arch; postorbital and postfrontal merge; adductor chamber almost half length of skull; quadrate and quadratojugal much reduced & fit into sockets on squamosal; squamosal covers and forms most of adductor chamber & lateral surface of occiput; narrow braincase in sharp parietal crest; double condyle on occiput, but condyles remain below foramen magnum; proatlas present, but simplified atlas-axis articulation permits some rotation of head; long trunk; zygapophyses on dorsal vertebrae strongly angled upwards (limits lateral, but permits dorsoventral flexion); 13 dorsals, 7 lumbar, 5 sacrals, 10-15 caudals; ribs proximally expanded to form costal plates (lateral stiffening); lumbar ribs have costal plates only; pectoral girdle remains primitive; clavicle and interclavicle retained (resists lateral forces of sprawling posture); coracoid somewhat reduced; scapula major weight-bearing element, directed vertically; small procoracoid present; humerus short, complex and horizontal; phalangeal count 23443; pubes & ischium reduced; ileum expanded; short limbs; femur angled 55 deg. outward, but capable of dorsoventral movement on angled humeral head; beginnings of gluteal-type musculature from iliofemoralis; calcaneal heel; simple hinge between astragalus (integrated with tibia) and calcaneum; gastrocnemius attaches to calcaneal tuber; plantigrade stance.

Remarks: The best known Galesaurid, and along with *Cynognathus* the best known cynodont. In modern cladistic arrangements it is usually placed in a separate, mono-specific, family, but it can certainly be retained in the Galesauridae. *Nythosaurus larvatus* Owen is based on the natural mould of a skull bearing impressions of the postcanine teeth. It is probably synonymous with either *Thrinaxodon liorhinus* or *Platycraniellus elegans.*

Links: Thrinaxodon Specimen; Thrinaxodon CAT Scan Rendering; Thrinaxodon CAT Scan Rendering; Estes, R., 1961; Thrinaxodon; TMM - Exhibits - Scratching the Surface - Thrinaxodon; Thrinaxodon sp.; Later Mammal-like Reptiles; Lecture 9 - Triassic: Moenkopi, Karroo, Ischigualasto; CIENCIA HOY 32 - ARTÍCULO - La Escuela de Economía Política de Chicago - 1 (I'm a great fan of the Chicago School, but this is actually a mislabeled article on proto-mammals); Ungewöhnliche Krokodilkonstruktionen der Vorzeit:; Mammalogy - Lecture 3; ?????????? (a great antidote to Bakker's unbearably cute image). ATW011007.

Cynosaurus: (Genus *Cynosaurus* Schmidt 1927) *C. suppostus* (Owen 1876) (= *Cynosuchus* Owen 1876 = *Cynosuchoides* Broom 1931 = *A'anictosaurus* Broom 1936 = *Mygalesuchus* Broom 1942 = *Baurocynodon* Brink 1951).

Range: Late Permian of South Africa, Upper *Daptocephalus* Zone.

Phylogeny: Galesauridae:: *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon* + *. MAK 000718. ATW020531.

Galesaurus: (= *Glochinodon* van Hoepen 1916 = *Glochinodontoides* Haughton 1924b). *G. planiceps* Owen 1859 (= *Glochinodon detinens* van Hoepen 1916 = *Glochinodontoides gracilis* Ilaughton 1924b = *Notictosaurus gracilis* Broom & Robinson 1948a = *Notictosaurus trigonocephalus* Brink & Kitching 1951b).

Range: Early Triassic of South Africa, Lystrosaurus Zone. (Possibly Permian: see spec_id=7600)

Phylogeny: Galesauridae:: *Cynosaurus* + *Nanictosaurus* + *Platycraniellus* + *Tribolodon* + *.

Characters: frontals with anterior "spine" projections inserting between nasals, persisting in adults.

Links: Triassic Dinosauria (historical interest); On the Classification of the Dinosauria (1870) (same); The Permo-Triassic Extinction; Harrismith Commonage, Africa; 68 (Människan. Hennes uppkomst och utveckling) (Swedish?).

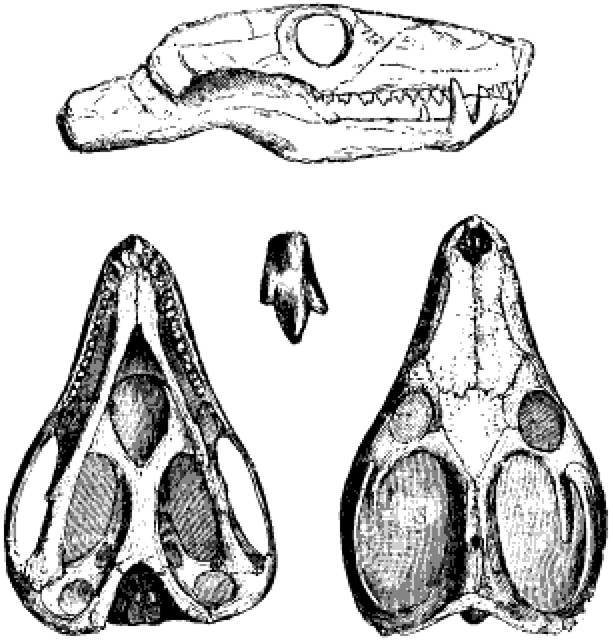


Fig. 78. Skalle af *Galesaurus* (efter Owen).

Note: Small, immature specimens have usually been referred to the genus *Galesaurus*, large, mature specimens to *Glochinodontoides*. MAK 000718. ATW020531.

Nanictosaurus**:** *N. kitchingi* Broom 1936 (= *N. robustus* Broom 1940b = *N. rubidgei* Brink & Kitching 1953).

Range: Late Permian of South Africa, Upper Daptocephalus Zone, Dicynodon laterticeps - Whaitsia Assemblage Zone.

Phylogeny: Galesauridae:: *Cynosaurus* + *Galesaurus* + *Platycraniellus* + *Tribolodon* + *.

Note: *N. robustus* was previously considered a Procynosuchid and synonym of *Procynosuchus delaharpeae*; it is now known to be the same as *N. kitchingi*. MAK 000718. ATW020531.

Platycraniellus**:** (= *Platycranion* van Hoepen 1916 = *Platycranium* van Hoepen 1917) *P. elegans* vanHoepen 1916 (= *Platycranion elegans* van Hoepen 1916 = *Platycraniellus elegans* van Hoepen 1917).

Range: Early Triassic of South Africa, Lystrosaurus Zone.

Phylogeny: Galesauridae:: *Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Tribolodon* + *.

Remarks: This species is known with certainty only from the type, which comes from Liarrismith, Orange Free State. A second specimen referred to this species by Brink is a *Galesaurus*. MAK 000718. ATW020531.

Tribolodon**:** Seeley 1894a. *T. frerensis* Seeley 1894a.

Range: Early Triassic of South Africa, Cynognathus Zone.

Phylogeny: Galesauridae:: *Cynosaurus* + *Galesaurus* + *Nanictosaurus* + *Platycraniellus* + *.

Note: **[1]** The name appears to be preoccupied by *Tribolodon* Günther 1877, a genus of cyprinid fish (dace). **[2]** This is the youngest species referable with certainty to the Galesauridae. Though frequently classified as a cynognathid, it is a typical galesaurid in its known features.

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Cynodontia: Eucynodontia

Cynognathids

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
```

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1. Cynognathia X
2. Cynognathidae X
3. Eucynodontia

Where is the "You" in Eucynodontia?

The answer to this question is still as unclear as it has been for many years. The **Eucynodontia** are an assortment of four groups: the **Cynognathia**, Probainognathia, Tritheledontia, Tritylodontidae. Even this division is not universally accepted. The traditional classification of the eucynodonts was into "traversodonts" and "gomphodonts," based on the structure of the teeth. Most workers now reject this division, since the tooth structure seems to correlate more with diet than with phylogeny. However, the branching sequence is still not well understood. Here, we treat the tritylodonts as part of the Cynognathia, with the probainognaths and tritheledonts on a separate branch. However, almost every permutation of these four taxa has some adherents.

In addition, it is uncertain whether the tritheledonts or tritylodonts led to the Mammaliformes. We treat the "you" in Eucynodontia as stemming from the tritheledont branch. This may now be, by a slight margin, the minority view; but, at this point, we have no real consensus to fall back on. ATW020531.

Cynognathus

A large and powerful predator, and dominant animal for many millions of years, *Cynognathus* was one of the largest cynodonts. The head was proportionally very large (up to 30 to 45 cm in length) and somewhat dog-like in appearance, hence the name *Cynognathus* ("dog jaw"). The skull is rather narrow, with a short temporal region, which served for the attachment of very powerful muscles for closing the jaws. Practically the whole of the lower jaw on each side was made up of a single bone, the dentary, into which were set the teeth: the cutting incisors, stabbing canines and shearing cheek teeth. Behind the small, peg-like incisors was a diastema, a gap, followed by the large canine. A great bony flange (the coronoid process) at the back of the dentary articulated with the skull, and enabled the jaws to be opened wide. This flange also provided a large area to which extra jaw muscles could attach, giving the jaws tremendous bite-power.

The body also was strongly built, with its hindlimbs placed directly beneath its body. The knee pointed forward and the elbow backward, giving an erect mammalian posture. Clearly this was an efficient predator, perfectly adapted to its environment, which persisted with little or no change for some five or ten million years. Review of the cynodonts gives only a single species, but it is possible that there were several very similar species, possibly in different parts of Pangaea, and perhaps succeeding each other as the Triassic period progressed.

Although a very successful animal, *Cynognathus* died out during the middle Triassic period, to be replaced by the smaller carnivorous Chiniquodontids and the small to large herbivorous "traversodontids." It is likely that the very arid conditions of the Triassic worked against the mammal-like *Cynognathus* and in favor of the reptilian archosaurs which had become the unchallenged masters of the land by the later Middle Triassic. MAK000906.

Eucynodontia:

Range: from the Early Triassic.

Phylogeny: Epicynodontia **::** *Thrinaxodon* + * **:** Cynognathia + Probainognathia

Characters: **$** supplementary dentary-squamosal jaw articulation [RS01]; **$** Very large dentary; post-dentary bones reduced and rod-like [RS01]; **$** dentaries fused at mandibular symphysis [RS01]; lower jaw pulled back into occlusion (?); carnivorous forms with blade-like post-canines; **$** scapula with acromion process on leading edge [RS01]; **$** phalangeal formula 23333 (mammalian) [RS01].

Links: A new carnivorous cynodont ... with comments on eucynodont phylogeny.

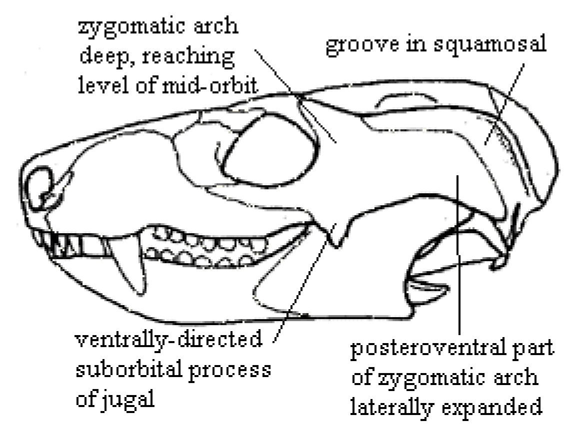
References: Rubidge & Sidor (2001) [RS01]. ATW020221.

Cynognathia: Stem group ~ *Cynognathus* > *Sinocodon*.

Range: Early Triassic to Early Cretaceous of Antarctica, South Africa, South America.

Phylogeny: Eucynodontia **:** Probainognathia + * **:** Cynognathidae + Tritylodontidae.

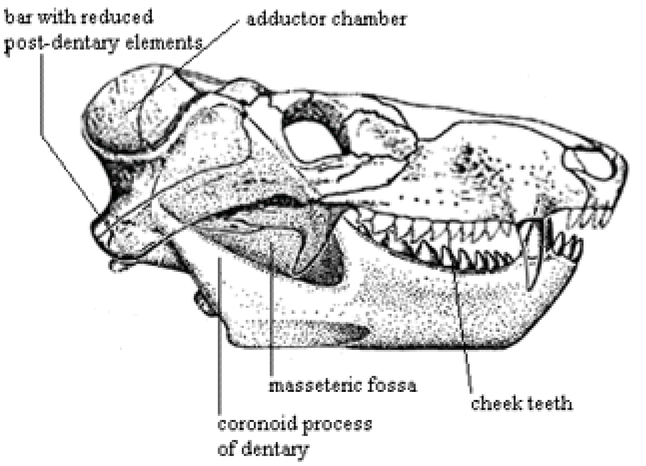
Characters: **$** Zygomatic arch, posteroventral part expanded laterally at or behind level of quadrate, so that skull has triangular outline in dorsal or ventral view; **$** dorsoventrally wide zygomatic arch, extending dorsally above mid-orbit [RS01]; **$** jugal with ventrally directed suborbital process for masseter attachment [RS01]; **$** deep groove on lateral surface of squamosal (analogous to external auditory meatus for aural connection to postdentary bones) [RS01].



Trirachodon skull in left lateral view. From Rubidge & Sidor (2000).

Links: Biology 356

References: Rubidge & Sidor (2001) [RS01]. ATW030324.



Cynognathus skull in right lateral view. Cranium shown as semi-transparant overlay on lower jaw. Modified from two figures in Carroll (1988).

Cynognathidae: Paraphyletic basal cynognaths. *Cynognathus*, *Diademodon*, *Massetognathus*, *Trirachodon***.**

Range: Early Triassic to Middle Triassic of Antarctica, South Africa, South America.

Phylogeny: Cynognathia **:** Tritylodontidae + *.

Characters: Large (2m?) carnivores and "gomphodont" herbivores; heavy, thick skull (~40cm); long snout; adductor chamber enlarged longitudinally or posterodorsally; narrow or absent post-orbital bar; jaw articulation primitive (articular & quadrate); dentary with large coronoid process; coronoid process with large masseteric fossa; articular, prearticular, angular, and surangular reduced to bar projecting posteriorly from behind the massive coronoid; large canines; cheek teeth laterally flattened, recurved and serrated; derived, "traversadont" herbivores with cheek teeth having two transversely aligned cusps anterior to basin; postcranial skeleton similar to more massive version of *Thrinaxodon*.

Links: Yale Peabody Museum: The Mural, Triassic; Evol.Page to Print: Clado Pic.Cynognathus (Mammal-Like Reptile); Mesozoic; Untitled Document; augtwoe.html; Cynognathus Printout - Enchanted Learning Software; PANGEA (Italian); Untitled Document.

Notes: [1] ***NOT*** a clade. This is a temporary place-holder for a series of basal cynognathians. The characters given are general cynognathian features. This includes the groups traditionally known as gomphodonts and traversadonts. **[2]** Generic and specific distinctions within the Cynognathidae have been based on characters which vary with age (tooth number and morphology, skull proportions) and are influenced by postmortem deformation. *Karoomys*, *Cistecynodon*, and *Nythosaurus browni* are based on tiny juveniles of *Cynognathus*. In their review of the Cynodontia, Hopson & Kitching (1972) recognize only a single species, pending a thorough revision of the family. MAK000906. ATW020222.

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checked ATW040208

Cynodontia: Tritylodontidae

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      |     |--Oligokyphus
      |     `--+--Tritylodon
      |        `--+--Bienotherium
      |           `--+--Kayentatherium
      |              `--+--+--Lufengia
      |                 |  `--Dianzhongia
      |                 `--+--Bocatherium
      |                    `--+--Yunnanodon
      |                       `--+-
-Stereognathus
      |                          `-
-Xenocretosuchus
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
```

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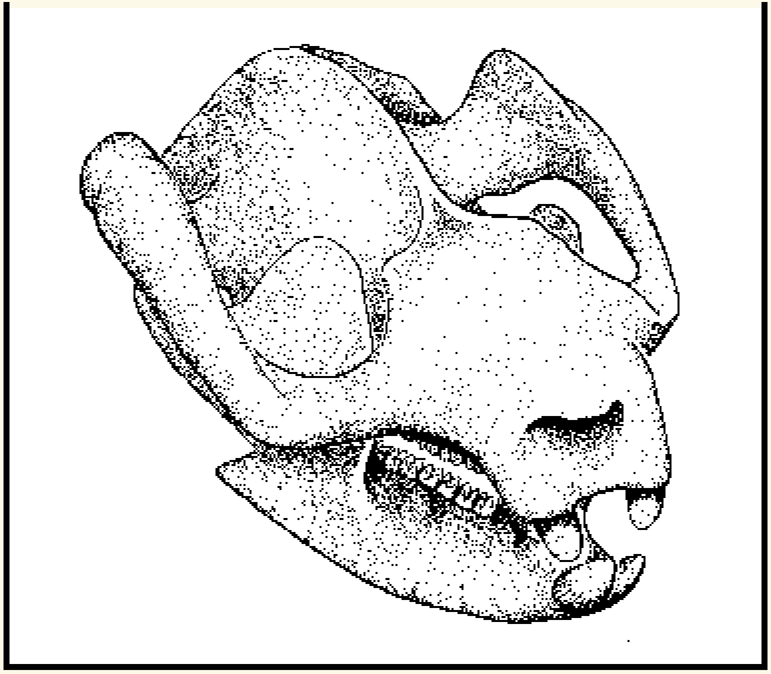
3. *Dianzhongia* X
4. *Kayentatherium* X
5. *Lufengia* X
6. *Oligokyphus* X
7. *Stereognathus* X
8. *Tritylodon* X
9. Tritylodontidae X
10. *Xenocretosuchus* X
11. *Yunnanodon* X

The **Tritylodontidae** were small to medium-sized, highly specialized and extremely mammal-like herbivorous cynodont synapsids. The tritylodonts were among the last of the cynodonts to appear, which evolved from more basal Cynognathia in latest Triassic times, and persisted well into the Jurassic period. In fact they were also the longest-lived group of all the therapsids, and, along with the Tritheledontidae (Ictidosaurs) the only mammal-like reptiles to endure into the Jurassic, and the only non-mammalian Theropsida (Synapsida) to make it through to the late Jurassic (the previous identification of an interesting Paleocene form (*Chronoperates paradoxus*) as therapsid is very unlikely, and HD Sues found it compared more closely with symmetrodont mammals). [Of course, it is always possible that the allotherians diverged from the mammalian stem earlier than is generally supposed. If so, the two statements are entirely consistent ... ATW020531]



Although in the past often placed in a separate infraorder Tritylodontia (e.g., Romer, 1966), the tritylodontids represent the culmination of the herbivorous cynodont radiation. These must have been quite common animals, and a number of fossil remains, including among them complete specimens, have been found in South Africa, western China, Europe, Arizona, and fragmentary but definitive remains from Argentina.

Tritylodon, after which the group is named, was first discovered in the Upper Triassic rocks of South Africa in the late 19th century, and was for decades considered to be a very early mammal. A typical tritylodontid, was like a modern weasel in appearance, with a long, slim body and tail. Its forelegs, as well as its hind-legs, were placed directly beneath the body, as they are in mammals (in contrast many more earlier and primitive therapsids, like the dicynodonts and the dinocephalians, had sprawling forelimbs).

The tritylodont's skull had a high flat crest and huge zygomatic arches (at the rear of the skull) for the attachment of very large jaw muscles. As in mammals, there was a well-developed secondary palate. The dentition of these animals was quite peculiar, and very different from that of other cynodonts. They had no canines, and the front pair of incisors were greatly enlarged, like those of a gnawing mammal like a rodent. As in the traversodonts, a large gap - the *diastema* - separated the incisors from the square cheek teeth (seven on each side). Each of the cheek teeth in the upper jaw had three rows of cusps, or projections, running along its length (i.e. longitudinally), with grooves in between; the lower teeth had two rows of cusps which fitted into the grooves in the upper teeth. This matching of the cusps allowed the teeth to occlude, or meet, in a precision bite. Given the advanced nature of the zygomatic arches, the secondary palate, and the specialized teeth, it is believed that these animals had feeding habits that were close to those of some mammals. The lower jaw apparently moved forward and back when the jaws were closed, thus grinding food between the teeth in somewhat the same fashion as some modern rodents chew their food. The multi-cusped cheek teeth, complex occlusion and extensive palinal power stroke were well suited for shredding fibrous plant material. Thus the tritylodonts can very much be seen as Mesozoic rodents. The structure of the shoulder girdle and forelimb suggests capability for digging, and wear on the enlarged incisors is consistent with digging for underground plant parts.

Tritylodonts clearly were active animals, probably burrowers in dirt or leaf litter like modern rodents and rabbits, without doubt warm-blooded animals. Yet, in spite of disadvantages, the tritylodonts still retained the reptilian joint between the quadrate bone of the skull and the articular bone of the lower jaw. But these bones were very much reduced, so that the squamosal bone of the skull and the dentary bone of the lower jaw involved in the mammalian jaw articulation were primary and in fact touching each other. In appearance these animals would have been almost indistinguishable from small mammals. MAK010421.

Image: Left *Bienotherium* yunnaense from china2001/0405.html (former site).

Tritylodontidae:

Range: Late Triassic to middle Cretaceous of South Africa, South America, North America, Europe, Russia, & China.

Phylogeny: Cynognathia: Cynognathidae + *: *Oligokyphus* + (*Tritylodon* + (*Bienotherium* + (*Kayentatherium* + ((*Lufengia* + *Dianzhongia*) + *Bocatherium* + (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*)))))).

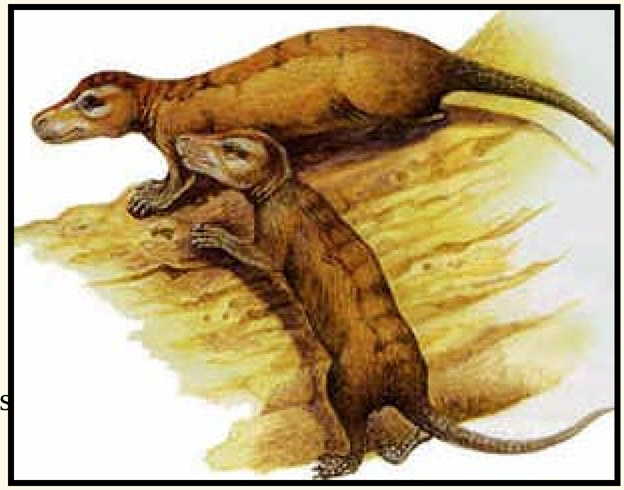
Characters: 50-100 cm long herbivores; prefrontal & postorbital absent; high, flat sagittal crest; temporal fenestra very large and confluent with orbit; zygomatic arch strongly enlarged; well-developed secondary palate; dentaries not fused at symphysis; mandible making strong bilateral retraction (as multituberculates) [RS01]; post-dentary bones reduced to slender rod located in deep groove on medial surface of the dentary; enlarged lower incisors, fitting between 2 enlarged upper incisors; canines absent; large diastema; **$** lower cheek teeth with 3 longitudinal rows of cusps which occlude against 2 rows in uppers [RS01]; long-bodied; postcranial skeleton generally mammal-like [RS01]; ilium rod-like [RS01]; pubes reduced and posteroventral to acetabulum [RS01]; greater trochanter separated from femoral head by notch as in mammals [RS01].

Links: Vertebrate Fossils; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; Tritylodontidae; Tritylodontoidea; PANGEA; Biology 356; Untitled Document; 4eern.pdf.

References: Luo *et al.* (2002) [L+02], Rubidge & Sidor (2001) [RS01].

Note: **[1]** This phylogenetic position is controversial, with many workers placing the tritylodonts as the sister of mammaliforms. Given the similarity of the dentition to allotherians, this seems possible. [L+02] regard linkage with allotherians as a conclusion from discredited notions of mammaliform paraphyly. But this need not be the case. **[2]** Possibly longest-lived therapsid group. ATW 020221.

Oligokyphus: (= *Chalepotherium* = *Mucrotherium* = *Uniserium*) *O. triserialis* Hennig 1922; *O. major* Kóhne 1956; *O. minor* Kóhne 1956; *O. lufengensis* Luo & Sun 1993.



Range: Early Jurassic (possibly Late Triassic) of Europe (Germany, England, Wales?), China, North America.

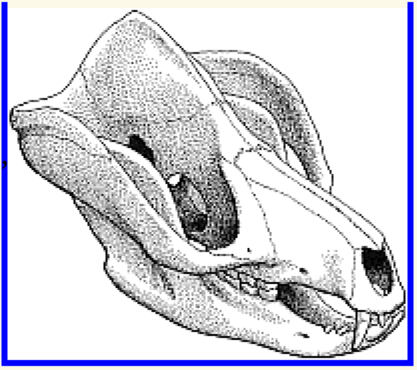
Phylogeny: Tritylodontidae: (*Tritylodon* + (*Bienotherium* + (*Kayentatherium* + ((*Lufengia* + *Dianzhongia*) + *Bocatherium* + (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*)))))) + *.

Characters: ~50 cm; double jaw joint; incisors enlarged; canines absent; alternate tooth replacement with double-rooted cheek teeth, but *without* mammalian-style tooth occlusion; More flexible neck, with mammalian atlas & axis and double occipital condyle; postcranial skeleton strikingly like monotremes; tail vertebrae simpler, like mammals; scapula substantially mammalian; forelimb is carried directly under the body; limb musculature and locomotion virtually fully mammalian.

Links: Transitional Vertebrate Fossils FAQ: Part 1B; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; PANGEA; Oligokyphus (Korean); FUR AND FANGS; Era Mesozoica Triassico - Epoca dei Dinosauri.

Notes: *O.* minor & *O.* major found in close association and were male & female morphs per Hopson & Kitching (1972). ATW020531.

Tritylodon: (= *Likhoelia* = *Tritylodontoideus*) *T. longaevus* Owen 1884 (= *Likhoelia ellenbergeri* Ginsberg 1961); *T. maximus* Fourie, 1962 (1963?).



Range: Early Jurassic (possibly Late Triassic) of South Africa, Antarctica. *T. longaevus* from the Hettangian - Sinemurian Red Beds and Cave Sandstone, especially Upper Middle Elliot (Tritylodon-acme zone) Formation, Stormberg Series, Orange Free State of South Africa, and Lesotho. *T. maximus* from the Sinemurian - Pliensbachian Clarens Formation, Stormberg Series, Orange Free State, South Africa.

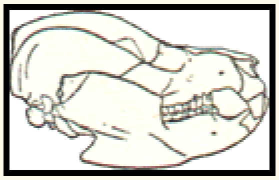
Phylogeny: Tritylodontidae:: (*Bienotherium* + (*Kayentatherium* + ((*Lufengia* + *Dianzhongia*) + *Bocatherium* + (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*))))) + *.

Links: South African Museum - Fossil Reptiles of the South African Karoo; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; UMGS Newsletter; exn.ca's Dinosaurs! Mammal-like reptiles: preying on baby dinosaurs; Encyclopedia of Dinosaurs: Hammer.

Image: *Tritylodon* skull from South African Museum - Fossil Reptiles of the South African Karoo.

Notes: **[1]** The generic name *Tritylodon* was in the past applied to isolated teeth from the Rhaeto-Lias of Europe (e.g. *Tritylodon fraasi* below), but these are in fact, generically indeterminate. As used now the genus is restricted to southern African forms. **[2]** *T. maximus* is either a large *T. longaevus* (Hopson & Kitching, 1972) or a distinct but closely related species. If the latter then this is a case of clear ecological succession, where an earlier smaller species dies out or is supplanted by or evolves into a later larger species. MAK010421. ATW020601.

Bienotherium: *B. yunnanense* Young 1940 (= *B. elegans* Young 1947); *B. magnum* Chow 1962.



Range: Early Jurassic of China. *B. yunnanense* from the Dull Purplish Beds, Lower Lu-feng Series of Yunnan, of Hettangian? age. *B. magnum* from the Dark Red Beds, Lower Lu-feng Series of Yunnan, of Sinemurian or early Pliensbachian age.

Phylogeny: Tritylodontidae::: (*Kayentatherium* + ((*Lufengia* + *Dianzhongia*) + *Bocatherium* + (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*)))) + *.

Links: JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; JURÁSSICO Répteis; Dinosaur museum (Chinese).

Note: *B. magnum* is recognized as a distinct species because it comes from a higher horizon than *B. yunnanense* and is much larger. MAK010421. ATW020601.

Kayentatherium: *K. wellesi* Kermack 1982 (= *Nearctylodon broomi* Lewis 1986)

Range: Early Jurassic of North America, Kayenta Formation, Arizona of late Sinemurian / early Pliensbachian age.

Phylogeny: Tritylodontidae:::: ((*Lufengia* + *Dianzhongia*) + *Bocatherium* + (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*))) + *.

Characters: highly specialized teeth with multiple rows of cusps, high mandibular condyle, teeth and jaw indicative of herbivorous diet.

Links: JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; Mesozoic; Vertebrate trace fossils; Vertebrate Fossils; Evolution of the mammalian cortex: past, present and future; MODERN CONCEPTS OF EVOLUTION; Tritylodontidae.

Image: image courtesy Dr Pamela Gore. MAK010421. ATW020601.

Lufengia: Chow & Hu 1959. *l. minor* Young 1947.

Range: Early Jurassic of China Dull Purplish Beds, Lower Lufeng Series of Yunnan.

Phylogeny: Tritylodontidae:::::: *Dianzhongia* + *.

Links: URASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory. MAK010421. ATW020601.

Dianzhongia: (= *Diazhongia*) *D. longirostrata* Cui 1981 (= *Lufengia delicata*? Chow & Hu 1959)

Range: Early Jurassic of China, Dark Red Beds, Lower Lu-feng Series of Yunnan, probably of Sinemurian or early Pliensbachian age.

Phylogeny: Tritylodontidae:::::: *Lufengia* + *.

Links: JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; bienoyokou.html (Japanese). ATW020601.

Bocatherium: *B. mexicanum* Clark & Hopson 1985.

Range: Middle Jurassic of North America, La Boca Formation of Huizachal Canyon, Tamaulipas, Mexico.

Phylogeny: Tritylodontidae:::: (*Yunnanodon* + (*Stereognathus* + *Xenocretosuchus*)) + *.

Links: The Journal of Vertebrate Paleontology; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; Un Pterosauro Tamaulipeco; Tritylodontidae; Los dinosaurios en México/Localidades del Período Jurásico en México (Spanish). ATW020601

Yunnanodon: (= *Yunnania*) *Y. brevirostre* Cui1976.

Range: Early Jurassic of China, from the Dark Red Beds, Lower Lufeng Series of Yunnan, probably of Sinemurian or early Pliensbachian age.

Phylogeny: Tritylodontidae:::::: (*Stereognathus* + *Xenocretosuchus*) + *.

Characters: skull length 3.5 - 4-5 cm; periotic bones combined in definitive petrosal with somewhat lengthened cochlea; buccal and labial cusps on uppers tend to form longitudinal crest; 2 cusps on lingual row (of uppers or lowers?); transverse dentine sheet connecting upper postcanine roots in the same row much less developed in *Yunnanodon* than *Lufengia*; anterolingual root of the upper postcanines small and rounded in transverse section.

Links: JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; bienoyokou.html (Japanese); paleng4_99p422abs; Untitled (Chinese). ATW030222

Stereognathus: *S. ooliticus* Charlesworth, 1855.

Range: Middle Jurassic of Europe, Stonesfield slate of Oxfordshire, (& a *S. sp.*, Forest Marble of Dorset), of Bajocian age.

Phylogeny: Tritylodontidae::::::: *Xenocretosuchus* + *.

Links: JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory.

Notes: *Stereognathus sp.* has been recorded from the Forest Marble of Dorset. For a long time *Stereognathus* was the latest known therapsid, but *Beinotheroides* discovered in China is younger. *Xenocretosuchus* is even younger again, but the fragmentary nature of the remains (teeth only) means it is not certain if it is a tritylodont, although it is certainly possible. ATW020601. MAK010421.

***Xenocretosuchus*:** *X. sibiricus* Tatarinov & Matchenko 1999.

Range: Early Cretaceous II of Russia. Shestakovo, Kemerovo Region of Siberia, of late Aptian age.

Phylogeny: Tritylodontidae::::::: *Stereognathus* + *.

Characters: buccal and labial cusps on the upper teeth form longitudinal crests.

Notes: This form is assigned to the tritylodonts on the basis of the two transverse rows of cusps on the cheek teeth. The buccal and labial cusps on the upper teeth form longitudinal crests. The same feature is developed to a lesser extent in the genus *Yunnanodon* from the Early Jurassic of southern China. However, I am somewhat skeptical of a specimen based only some isolated teeth. It *may* very well be a tritylodont (and if so it would be the youngest stratigraphic record of the family), or it may be an aberrant mammal. This little animal lived alongside dinosaurs (Psittacosauridae, Theropoda, and Sauropoda), crocodiles, turtles, fish, and the triconodont mammal *Gobiconodon borissiaki*. MAK010421.

Links: paleng4_99p422abs; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; RE: Details on SVP Thursday posters (Part 2). ATW031002.

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checked ATW031002

Cynodontia: Probainognathia

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         |  |--Pachygenelius
         |  `--Chaliminia
         `--MAMMALIFORMES
```

Contents

Taxa on This Page

1. *Chaliminia* X
2. *Pachygenelius* X
3. Probainognathia
4. Tritheledontidae X

The **Tritheledontids**, also and better known (especially in earlier literature) as the Ictidosaurs, were tinylatest Triassic to Early Jurassic cynodonts that neatly bridge the gap between advanced theriodonts and the primitive mammaliforms.

Although previously separated from other theriodonts as a distinct infraorder, the Ictidosauria, study of the type and only specimen of the genus the *Trithelodon* has determined its close affinities with the typical Ictidosaurs *Pachygenelus* and "*Diarthrognathus*". For this reason, Hopson & Kitching (1972) suggested using the family name Tritheledontidae Broom 1912 for all of the forms called "ictidosaurs", and included all these groups under the Cynodontia.

The Tritheledonts (Ictidosaurs) are thus very advanced, probably insectivorous, cynodonts of small size in which some incisors and in some species the upper and probably postcanines have a transversely-oriented cutting edge, in others the uppers have an oblique and the lowers a longitudinal cutting edge. These are features connected, as in the tritylodonts, with the more efficient chewing of food. As in the Chiniquodontidae the secondary palate is long (so the animal could eat and breathe at the same time, a mammalian feature) and the postorbital bar (the bar of bone behind the eyes) is absent, another feature found also in Tritylodonts and primitive mammals.

But what makes these animals unique is the new mammalian joint between the squamosal and dentary had come into functional being. Thus, the ictidosaur ***Pachygenelius*** (formerly known as *Diarthrognathus*) possesses both the reptilian quadrate-articular jaw joint and a newly developed mammalian squamosal-dentary jaw joint. Because of this Simpson (1959) suggested that it might better be classified as a mammal, but Hopson and Crompton retain it in the Therapsida. Although certain primitive features in the skull suggest a derivation from scaloposaurid bauriamorphs, indicating the posisbility that the mammalian condition may have evolved twoice (once from advanced therocephalians via the Ictidosaurs and once from cyndonts via Tritylodonts) But both the structure of the dentary and the braincase structure have independently confirm a cynodont ancestry, and the polyphyly of mammals is no longer considered a valid hypothesis.

Pachygenelius stands truly at the dividing line between cynodont and mammaliform in so far as this important diagnostic feature of jaw articulation is concerned. This is the only reason why the ictidosaurs are classified outside the mammaliformes. In the mammaliforms, the quadrate and articular bones have migrated from the articular region of the jaw to the middle ear where they have been transformed into two of the bones concerned with the transmission of vibrations from the eardrum to the inner ear. Because, in the ictidosaurs, this transformation of the quadrate and articular bones had not taken place, these animals are placed outside the Mammaliformes. MAK010421.

Probainognathia:

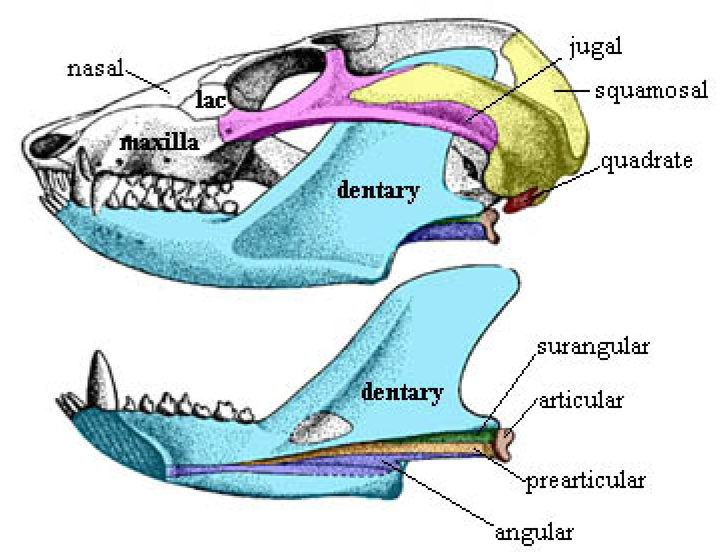
Range: from the Late Triassic?

Phylogeny: Eucynodontia: Cynognathia + *: Tritheledontidae + Mammaliformes.

Characters: **$** lack of pineal foramen [RS01]; **$** posteriorly elongated secondary palate [RS01]; **$** ribs (laterally?) expanded [RS01].

Links: Eucynodontia; Synapsida -- The Dinosauricon; Therapsida (all treating Probainognathia as a more inclusive clade).

References: Rubidge & Sidor (2001) [RS01]. ATW020601.



Probainognathus: skull and mandible in left lateral view. Modified from Carroll (1988)

Tritheledontidae: *Theioherpeton*, *Trithelodon*.

Range: Late Triassic to Early Jurassic of South Africa & South America.

Phylogeny: Probainognathia: Mammaliformes + *: *Pachygenelius* + *Chaliminia*.

Characters: Small (3-6cm skulls) carnivorous proto-mammals. cheek teeth broad, with prismatic enamel as in mammals; teeth may have been double-rooted; some teeth have transverse cutting edge, others the uppers have an oblique and the lowers a longitudinal cutting edge; probably squamosal-dentary jaw joint and quadrate-articular joint both functional, with masseter and opposing muscles holding jaw in "sling"; postorbital and prefrontal absent; frontal & palatine in contact; temporal opening confluent with orbit; postcranial skeleton said to be fully mammalian. ATW020223.

Comment: the alternative spelling Trithelodontidae is incorrect MAK121217

Links: Lecture 12 - Early Jurassic; therapsd.htm; CIENCIA HOY 32 - ARTÍCULO; traces; JawTransition; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory. Wikipedia

References: Luo *et al.* (2002) [L+02]

Image: "*Diarthrognathus"* from Argentine Museum of Natural Sciences.

Notes: [1] According to [L+02] the characters that support tritylodonts as the sister of mammaliforms are strongly localized to the orbital wall and sphenoid region. Characters of the jaw joint, mandible and palate point to tritheledonts. ATW020223.

Pachygenelius: *P. monus* Watson 1913; *P. broomi* Crompton 1958 (= *Diarthrognathus broomi*).

Range: Early Jurassic of South Africa, possibly North America. *P. monus:* Red Beds and Cave Sandstone (Middle and Upper Elliot Formation), Orange Free State, Red Beds and Cave Sandstone (Middle and Upper Elliot Formation), Orange Free State and Lesotho, South Africa, of Hettangian to Sinemurian age. *P. broomi*: Clarens Formation, Orange Free State, South Africa, of Sinemurian / early Pliensbachian age.

Phylogeny: Tritheledontidae: *Chaliminia* + *.

Image: *Pachygenelius* jaw (~2 cm), Parrsboro, Nova Scotia. From the Nova Scotia Museum Fossils of Nova Scotia Website. © 1998 Nova Scotia Museum and used by permission.

Links: parrs.htm; Tritheledont tooth; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; UNIVERSIDAD CAECE- Cursos y Seminarios.

Notes: [1] *Pachygenelius* ?*monus* has also been reported from the Early Jurassic of Nova Scotia. But while it is not unlikely that this jaw might belong to *Pachygenelius* (or a similiar form), a species attribution, or even an unambigious genus attribution, is very unlikely. **[2]** *Diarthrognathus broomi* is based on two juvenile specimens which are possibly, though not certainly, referable to *P. monus*. This then is either a synonym of the earlier *P. monus* or a distinct but closely related species, probably a descendent. Although a specific distinction may prove to be valid, it is doubtful that generic differences exist. MAK010421. ATW020601.

Chaliminia: *C. musteloides* Bonaparte 1978.

Range: Late Triassic to Early Jurassic of South America, Los Colorados Formation, Argentina, of late Norian to Hettangian age.

Phylogeny: Tritheledontidae: *Pachygenelius* + *.

Links: Tritheledont tooth; JURASSIC CYNODONTS; Tritylodontidae and Tritheledontidae, an internet directory; UNIVERSIDAD CAECE- Cursos y Seminarios.

Notes: The only known Triassic tritheledont, and part of a highly endemic fauna, which makes it difficult to correlate. However although the Los Colorados Formation is usually considered latest Triassic (Late Norian /Rhaetian), Jose Bonparte says somewhere (I can't find the exact passage...) that the fauna may not be isochronous. So it is possible that the upper part of the Los Colorados may be Hettangian (earliest Jurassic). That would fit in *Chaliminia* with the other tritheledonts. MAK010421. ATW020601.

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checked ATW021027, last modified MAK121217

Cynodontia: Dendrogram

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
```

Contents

```
THERAPSIDA
|
CYNODONTIA MH
|--Dvinia •X
`--+--Procynosuchidae X
   |  |--Nanocynodon •X
   |  |--Parathrinaxodon •X
   |  `--Procynosuchus •X
   `--Epicynodontia
      |--Galesauridae X
      |  |--Cynosaurus •X
      |  |--Nanictosaurus •X
      |  |--Galesaurus •X
      |  |--Platycraniellus •X
      |  `--Tribolodon •X
      `--+--Thrinaxodon •X
         `--Eucynodontia MH
            |--Cynognathia X
            |  |--Cynognathidae •X
            |  `--Tritylodontidae X MH
            |     |--Oligokyphus •X
            |     `--+--Tritylodon •X
            |        `--+--Bienotherium •X
            |           `--+--Kayentatherium •X
            |              `--+--+--Lufengia •X
            |                 |  `--Dianzhongia •X
            |                 `--+--Bocatherium •X
            |                    `--+--Yunnanodon •X
            |                       `--+--Stereognathus •X
            |                          `--Xenocretosuchus •X
            `--Probainognathia
               |--Tritheledontidae X
               |  |--Pachygenelius •X
               |  `--Chaliminia •X
               `--MAMMALIFORMES
```

Sources: Hopson & Kitching (2001) (in part)

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Cynodontia: References

Abbreviated Dendrogram

```
THERAPSIDA
|
CYNODONTIA
|--Procynosuchidae
`--+--Galesauridae
   `--Eucynodontia
      |--Cynognathia
      |  |--Cynognathidae
      |  `--Tritylodontidae
      `--Probainognathia
         |--Tritheledontidae
         `--MAMMALIFORMES
```

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Unit Back	Vertebrates Home	Vertebrate Dendrograms	Vertebrate References	Glossary	Unit Next

Mammaliformes: Overview

Mammaliformes Cladogram

```
CYNODONTIA
|
Mammaliformes
|--Allotheria
|  |--Haramiyida
|  `--Multituberculata
|     |--Paulchoffatiidae
|     `--+--Gondwanatheria
|        `--Cimolodonta
`--+--Morganucodontidae
   `--+--Docodonta
      |  |--Megazostrodontidae
      |  `--Docodontidae
      `--+--Hadrocodium
         `--Symmetrodonta
            |--Kuehneotheriidae
            |
            MAMMALIA
```

Contents

Introduction

The mammaliforms are, of course, the run-up to mammals. Not that they were "destined" to become us, or anything at all. The whole lineage could quite easily have disappeared during the Mesozoic without a trace. But, from our perspective, they're the group that produced us; so it is natural to wonder how that happened.

All of the early mammaliforms looked more or less like rodents and were about the same size as that most successful group of modern mammals. The mammaliform story is about internal, structural developments, many of which we have only begun to be able to study in the last decade. Understanding these changes unavoidably requires us to look at technical anatomical details. Some of the things to look for are these:

1) The dentary-squamosal jaw joint: All terrestrial vertebrates except mammaliforms form the jaw hinge between the articular and the quadrate. Mammaliforms form the joint between the dentary and the squamosal. This transition was well under way before mammaliforms got started.

2) The post dentary bones -- the articular and angular -- weren't lost. They, and the quadrate, became incorporated

into the middle ear as the auditory ossicles. In mammals they are called the malleus, incus and stapes.

3) The inner ear was also re-engineered. The otic capsule became somewhat separated from the rest of the braincase as a pair of *petrosals*. Within the petrosal, one of the organs of hearing (the maculae) became first enlarged, and then coiled.

4) The teeth of mammals are almost unique in a number of respects. Instead of having lots of simple teeth that were replaced frequently, mammals have only one set of adult teeth which meet (occlude) in a very precise fashion.

5) Most importantly, mammals developed separate, specialized molars. Molars not only have points (cusps) which shear past each other, but have a certain cusps which grind food on relatively flat regions of the opposite molar. This system seems to have evolved separately at least three times and probably more often. Since most mammaliform remains consist of teeth, we have a great many examples of tooth forms. Unfortunately, the degree of convergent dental evolution has also greatly confused the picture.

6) The brain itself, and the surrounding bone, seems to have undergone some profound reorganization. After hundreds of millions of years of gradual retreat, the anterior part of the old palatoquadrate (the epipterygoid of reptiles) makes a strong come-back in mammaliforms in vatious guises such as the alisphenoid and orbitosphenoid -- structures that provide central support for the anterior skull.

7) these changes in the organization of the skull are accompanied by soft tissue changes in the distribution of the cranial nerves and the major blood vessels. These transitions remain poorly understood.

8) Post-cranially, as in reptiles, the limbs tended to move under the body. Surprisingly, mammals seem to have been very slow to acquire a truly erect stance; and the fore- and hind-limbs seemed to have evolved erect postures almost independently.

Of course, a great many other things were going on at the same time: lactation, increased body metabolism, body hair, and so on. But these are almost impossible to study directly in the fossil record. They remain, for the most part, matters of speculation.

Phylogeny and Origins

Some time in the Middle Triassic, the mammaliforms derived from near one of two branches of the cynodont family: either the tritylodonts or the tritheledonts. *See* Rubidge & Sidor (2001) for a nice review. It is even possible that *both* statements are true. The Allotheria (multituberculates) are so different from anything else that one can almost imagine their deriviation from an entirely separate line of cynodonts.

The Mammali*a*formes, as current fashion spells it, are defined as: the last common ancestor of *Sinocodon* and modern mammals and all of its descendants. Luo *et al.* (2002). *Sinocodon* + *Smilodon* is one way to remember it. However, for our purposes, we have used a working definition anchored on *Haramiyavia*, assuming that the unknown intersection between multituberculates and modern mammals is the appropriate break point. This assumes that *Haramiyavia* really is a primitive allotherian, which is hotly debated.

Assuming all this -- quite a lot to swallow -- we can envision the Mammaliaformes as made up of three main groups: the Allotheria, the Docodonta and close relatives (e.g. *Morganucodon*), and the Symmetrodonta. The Allotheria consist largely of the multituberculates. They outlasted the dinosaurs and are the single longest lived branch of mammaliforms. The docodonts were relatively short-lived, but left us with a superb fossil record. The Symmetrodonts (*e.g. Kuehneotherium*) are no longer believed to be a separate branch at all, and include the living mammals. ATW020316.

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Mammaliformes

Allotheria

Mammaliformes Dendrogram

```
CYNODONTIA
|
Mammaliformes
|--Allotheria
|  |--Haramiyida
|  `--Multituberculata
|     |--Paulchoffatiidae
|     `--+--Gondwanatheria
|        `--Cimolodonta
`--+--Morganucodontidae
   `--+--Docodonta
      |  |--Megazostrodontidae
      |  `--Docodontidae
      `--+--Hadrocodium
         `--Symmetrodonta
            |--Kuehneotheriidae
            |
            MAMMALIA
```

Contents

Taxa on this Page

1. Allotheria X
2. Cimolodonta X
3. Gondwanatheria X
4. Haramiyida X
5. Mammaliformes
6. Multituberculata X
7. Paulchoffatiidae X

Multituberculates

Multituberculates are like that enormous 20-piece fondue set that Aunt Harriet gave you as a wedding present. Its very pretty and well made, but it doesn't go with anything and there's really no place to put it. Pieces of it get used for other things, and keep being lost and found, but no one knows how to assemble it -- and when was the last time you had everyone over for fondue, anyway?

At first glance, multis look like mammals. The skull structure is relatively familiar. They have differentiated teeth which occlude and have familiar-looking cusps. they have a one-piece dentary jaw, a normal mammalian middle ear, zygomatic arch, and are the right size and shape. However, the appearance is deceptive. Miao (1993) shows dramatically how few characters multituburculates share with mammals. In fact, he finds only two: absence of the septomaxilla and presence of the three otic ossicles. The molars -- if that's really what they are -- are nothing like the molars of mammals. In fact, multis didn't even chew the same way. There is essentially no transverse, grinding movement involved. That type of motion derives from *uni*lateral occlusion, where only one side of the jaw occludes at a time. Multuberculates always made contact on both sides of the jaw. Multis combined orthal chomping with a peculiar backstroke in which the cusps of the lower jaw were dragged posteriorly through the basins or along the sides of the upper teeth. Wall & Krause (1992). The multituberculate rostrum is also distinctly unmammalian. It is a box-like construction, more like a pelycosaur than a mammal, with the large flat maxillae forming the sides, the nasal the top, the the tall premaxilla at the rostral end. Compare the image of *Dimetrodon*. The zygomatic arch looks right, but the anterior portion is mostly maxilla, rather than jugal. The jugal is a minor element stuck in a little slot in the maxillary process. The squamosal never gets involved in the braincase, and the whole arrangement of the petrosal area is quite different from mammals.


Nemegtbataar, Ptilodus, and Lambdopsalis: reconstructed skulls. From Miao (1993).

The post-cranial skeleton is not very well known, but no multi is known which even approached a parasagital gait -- and the foot has been radically redesigned for an even more sprawling posture than a protomammal. Imagine a furry little defensive lineman or a mouse with the posture of a sumo wrestler. Perhaps this is a bit misleading. Kielan-Jaworowska has speculated that some multis may have been great jumpers, and this is easy to believe. It depends on the overall build, and most multis were small and gracile, so far as we know. It is only the posture that reminds us of something big and blocky. Multis are often called the "rodents of the Mesozoic," but it might be more apt to think of them as the "rabbits of the Mesozoic."

With all their strangeness, it would seem natural to put the multituberculates outside the mammals. However, despite every indication to the contrary, it is generally taught that they are just some lost tribe of mammal Isrealites with funny teeth. The problem here seems to be historical. As long ago as 1880, Marsh suggested a link between the multituberculates and "*Microcleptes*," later known as *Haramiya*, and erected the Allotheria to contain them. **[1]**. The haramiyids have a very spotty record. However, they do (mostly) have two parallel rows of cusps on their molariform teeth. Unfortunately, until very recently, that is *all* they had. *Haramiya* consisted only of a few teeth, as did every other genus of haramiyid. Thus, the argument for a *particular* pre-mammalian origin rested only on a few grams of tiny teeth, mostly from a single Late Triassic site in France. That wasn't too bad when the multis were just a tooth order as well, but the fossil record of multis kept improving, while the record of haramiyids did not. Thus, the connection between multituberculates and haramiyids was one of those issues like the dino-bird connection before the Chinese feather factory went into production: much debated, but with insufficient real evidence on either side.

To add to the difficulty, the definition of "mammal" is not generally agreed. The tendency is still to use a non-cladistic definition involving the posession of various "mammalian" character states. See for example, Pough et al. (1999). The discussion by those authors is excellent, but the fact remains that a non-cladistic definition invites problems with polyphyly. **[2]**. That is the reason that the definition of Mammalia in these Notes has recently been changed to include only crown group mammals, *i.e.* the last common ancestor of platypuses, possums & people and all of its descendants. Thus, under some definitions of "mammal", the multis would be mammals regardless of the haramiyid connection. However, that does not mean that they are more closely related to us than are echidnas.

In any case, the whole tree was shaken in 1997 with the description of *Haramiyavia* by Jenkins *et al.* (1997). Unlike every other haramiyid, *Haramiyavia* had jaws, and even bits and pieces of post-cranial skeleton. At last, haramiyid students had more than teeth to work on. Jenkins reconstructed *Haramiyavia* as having only an orthal jaw motion -- slash and gulp -- and other dental detail which appeared to be inconsistant with a multituberculate connection. "Available evidence," they concluded, "does not indicate a close relationship between the two groups."

This would appear to have killed off the Allotheria. However, the Allotheria still have a champion in Percy Butler, professor emeritus of the University of London, nor was he slow to answer from the barge. Professor Butler must be very nearly the oldest of the Old Guard, as he is now [July, 2001] almost 90. Although he claims that "I know no geology, and have never collected a fossil," he nonetheless managed to collect the Romer-Simpson Medal, the highest honor granted by the Society for Vertebrate Paleontology, back when he was a mere youth of age 82.

Prof. Butler may not know geology, but he certainly knows fossil teeth, which he has studied for some 65 years. In particular, he was one of the first to look at mammaliform teeth as products of ecological adaptation and developmental biology. Butler (2000) carefully compared the teeth of *Haramiyavia* and *Thomasia*. Neither Jenkins nor anyone else disputes that these forms are closely related. In addition, Butler was able to include data from a new haramiyid, *Eleutherodon*, which had not been available to Jenkins. Butler determined what the homologies were between the cusps in the various haramiyids. Using this information and some rather detailed dental modelling, Butler shows that there is a reasonable progression from orthal chomping, with a small degree of palinal motion in *Haramiyavia* to the fully palinal motion in multituberculates.

Of course, having a reasonable story to tell is not the same as evidence, but it does seem to *disprove* Jenkins' assertion that there is no possible relationship between haramiyids and multis. What is missing is a cladistic analysis. One suspects that it may not be possible to do this yet. As discussed elsewhere, it is critically important to get a good handle on the homologies *before* doing this analysis. Butler goes far in this direction, but we still lack enough bones from enough taxa to tell the difference between a reasonable conjecture and good working hypothesis.

In the mean time, the Allotheria remain the best guess about the relationships involved. Jenkins' identification of a groove in the jaw for the post-dentary bones confirms the suspicion that the haramyids cannot be mammals. All three living groups of mammals have the post-dentary elements fully incorporated in the middle ear. As Luo *et al.* (2001) have elegantly shown, this incorporation predates the crown group. Thus, just as Miao (1993) suggested, the superficial similarities between multituberculates and mammals are probably convergences **[3]**. ATW 010708

Note: Zhelestids were the first placentals to specialize in herbivory and may have have dominated the small herbivore niche in the upK of Central Asia, a semitropical lowland and coastal environment. At the same time, multituberculates occupied the same niche in the more arid, upland environment of Mongolia. [K+00]. **[1]** Marsh, OC (1880), *Notice on Jurassic mammals representing two new orders*, **Am. J. Sci. 3** 20: 235-239, *as stated in* Butler (2000). The work of Jenkins *et al.* (1997) confirmed suspicions that two haramiyids, *Haramiya* and *Thomasia*, were actually the upper and lower teeth of the same animal. Since *Thomasia* has seniority, there is no *Haramiya* any more -- although there are still haramiy*ids*. **[2]** This seems to be an odd trap that even the various best scientists fall into. Consider for example, the Arctometatarsalia of Holtz (1995) or the Myopterygia of Janvier. For an explanation of the problem, see Holtz (1996a). **[3]** Convergent development in this area may be particularly likely for reasons discussed elsewhere.

Descriptions

Mammaliformes: *Sinocodon* + living monotremes + living therians. [L+02].

Range: from the Late Triassic.

Phylogeny: Probainognathia: Tritheledontidae + *: Allotheria + (Morganucodontidae + (Docodonta + (*Hadrocodium* + Symmetrodonta))).

Characters: Primitively, very small (<100g); **$** fully developed dentary-squamosal jaw joint [L+02]; **$** petrosal promontorium develops at expense of ventrolateral wing of basisphenoid [L+02]; diphyodont teeth; **$** teeth double-rooted, with precise occlusion (permits true chewing, hence very fine oral food processing); **$** each post-canine tooth occludes with two teeth in opposite jaw; differentiated molars and pre-molars; fixed dental formula; prismatic enamel (very durable); dentary-squamosal jaw joint dominates; stapes very small; parietals fused; postorbital and prefrontal absent; brain enlarged; otic capsule (prootic + opisthotic) fused as petrosal; cerebellum folded; optic lobes divided; ring-shaped atlas; epiphyses on long bones; heart completely divided into four chambers; single aortic trunk; muscular diaphragm present; hair; sebaceous and/or sweat glands; endothermic (some exceptions known); typically viviparous; **$** lactation and suckling; primitively nocturnal insectivores.

Links: The Hall of Mammals; Class Mammalia; Mammal Directory; Skulls Unlimited International Inc.; Mammals - Introduction; The Structure and Classification of the Mammalia (1864); General Zoology - Subphylum Vertebrata, Class Mammalia (very basic); Taxonomy browser (Mammalia); The Origin of Mammals.

It is in fact hard to draw the line; and, after you have finally drawn a clear line, some inconsiderate field scientist will immediately find something new and make a mess of your system. *See*, for example, the hints of weird things to come (out of Brazil) from Barbarena & Bonaparte: NAPC Abstracts, Ar - Be. Thus, both "Mammalia" and "Mammaliformes" (or "Mammali**a**formes," although we deprecate that spelling) can and have been used in many different ways. Re- mammalian lineages (was Re- Cretaceous taeniodont). One of the problems with Mammaliformes is that some people, for various reasons, don't like the term. SeeRe- Cladospeak (Mammalia, Crurotarsi); and the glossary entries at Trevor Dykes' site. And, speaking of Trevor, probably the best coverage of the group (whose name he doesn't even like!) is at Trevor Dykes' MESOZOIC MAMMALS; Basal Mammaliaformes, Morganucodontidae ... page. Dr. Tom Holtz's notes, as usual, provide a good, short introduction to the characteristics of the group. Another good set of lecture notes (from Prof. Jon Baskin) can be found atBiology 4429 - Chapter 3. On specific organ systems, Dr. Luo Xhe-Zi provides a brief discussion of the evolution of the mammalian ear at CMNH Vertebrate Paleontology, while the text (no figures) of Christian Sidor's review of jaw changes can be found atEvolutionary trends and the origin of the mammalian lower jaw. Finally, Spotlight on Zoo Science- Lactating on Eggs - National Zoo| FONZ has an interesting, if a bit speculative, section on the evolution of lactation.

References: Luo *et al.* (2002) [L+02].

Note: Mammaliforms are unique among major taxa in that we have an enormous amount of information on one of the most basal species, *Morganucodon*. While this is obviously a Good Thing for scientists, it also makes it impossible to summarize "what makes a mammaliform" in a short paragraph. ATW050810.

Allotheria: *Eleutherodon*.

Range: upT-lwOc.

Phylogeny: Mammaliformes: (Morganucodontidae + (Docodonta + (*Hadrocodium* + Symmetrodonta))) + *: Haramiyida + Multituberculata.

Characters: Molariform teeth with two rows of cusps arranged longitudinally; buccal row of lower molariforms bites bilaterally between rows of uppers; orthal and palinal chewing only, with little or no transverse, grinding element.

Links: Allotheria; SistEspEvol (Portuguese); Main Page; Lecture 03 - Cont. Drift; Untitled Document; MESOZOIC MAMMALS; Haramiyida, an internet directory:; gatesy_pictures/11.JPEG;

References: Butler (2000), Miao (1993).

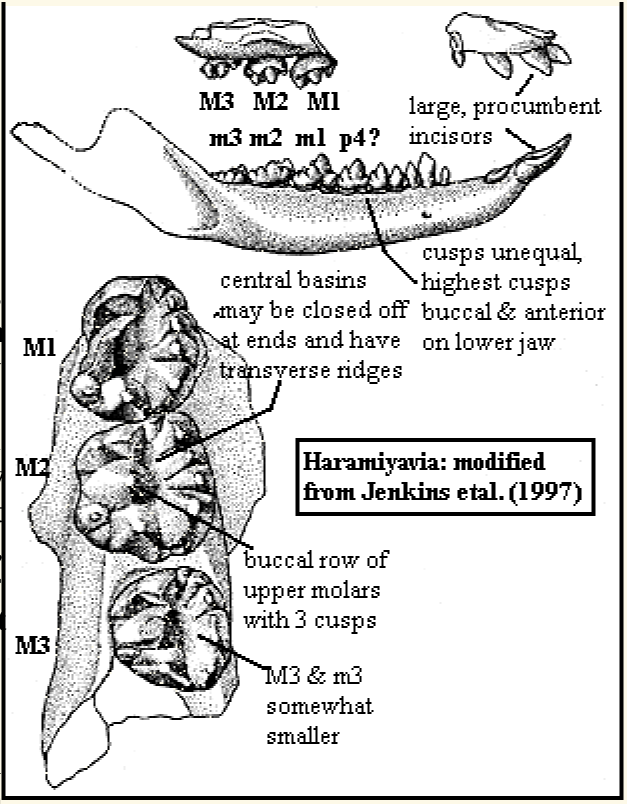
Note: supported by Miao basically by default as a place to put multis. 011202.

Haramiyida: *Eleutherodon*, *Haramiya*, *Haramiyavia*, *Theroteinus*, *Thomasia*.

Range: upT (Norian)-upJ of Eur, Greenland & Africa.

Phylogeny: Allotheria: Multituberculata + *.

Characters: Procumbent incisors (3/1-3); cheek teeth with 2+ roots;



Haramiyavia: modified from Jenkins etal. (1997)

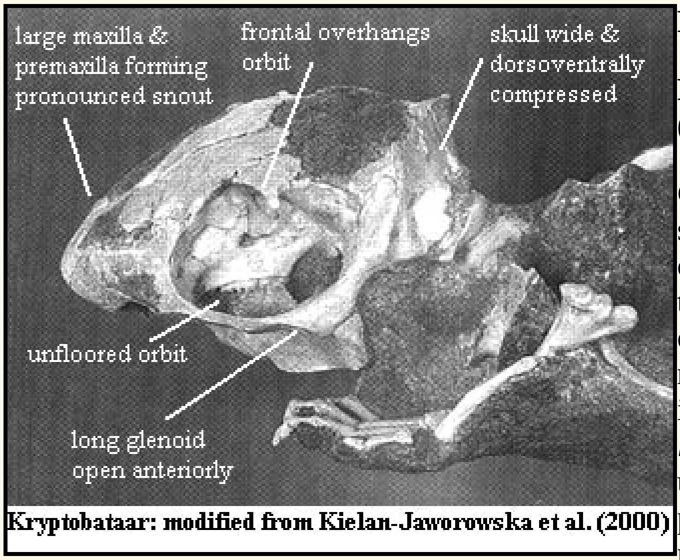
crown broad with cusps along margin, frequently in two parallel rows enclosing a central basin; 1st 2 molars of top and bottom larger than 3rd; at least one lower molar has central basin, rather than central row cusps; basins tend to be closed posteriorly, open anteriorly; molariform cusps of unequal height, with largest cusps anterior buccal on lower row, posterior or median lingual on upper row; buccal row of upper molariforms with 3 cusps, with middle cusp tallest (except *Eleutherodon*); occlusion pattern with cusps meeting opposing basins, usually the tallest upper lingual cusp in the basin of the lowers and/or the highest buccal lower in the basin of the uppers; jaw movement primarily or entirely orthal; dentary gracile & arcuate in *Haramiyavia* (looks a good deal like *Hadrocodium*, with coronoid a bit lower); sulcus for postdentary bones present; zygomatic arch originates above P3-P4 as in paulchoffatiids (actually "M3-M4" since these are all molari*forms*, rather than differentiated Ps & Ms); distal humerus with 2 condyles; well-developed olecranon process; gracile compared to *Morganucodon*, with longer jaw; humerus about same length as radius.

Links: Haramiyidae.

References: Butler (2000); Jenkins *et al.* (1997).

Note: May be mammaliform lineage unrelated to multituberculates or, alternatively, paraphyletic parent of multituberculates. Present majority view is probably that they are unrelated to multituberculates and represent an early mammaliform offshoot. The possibility exists that haramiyids are an early offshoot and that they *are* closely related to multituberculates. This is the position of Butler (2000) and is followed here. This approach does more to explain the weird primitiveness of multis. Per Jenkins et al. (1997), *Thomasia* is the lower dentition of *Haramiya*. 010701.

Multituberculata(= Plagiaulacoidea)**:** *Paulchoffatia* + Cimolodonta.

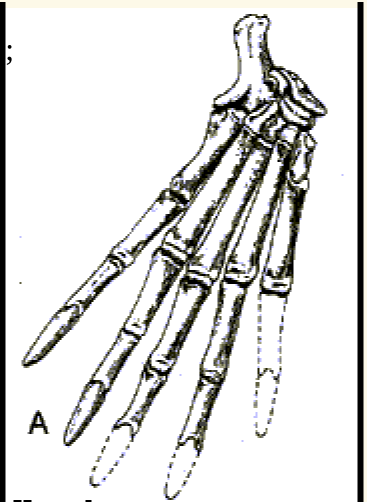


Kryptobataar: modified from Kielan-Jaworowska et al. (2000)

Range: upJ (mJ?)-lwOc of Eur, Asia, NAm, & SAm.

Phylogeny: Allotheria: Haramiyida + *: Paulchoffatiidae + (Gondwanatheria + Cimolodonta).

Characters: Mesozoic equivalent of rodents. Size 2-20 cm, up to several kg; herbivorous and omnivorous; skull low, broad & consolidated; large, strong jaw; angular process absent; no transverse jaw motion; dental formula 1-3/1, 0-1/0,1+/0+, 2+/1+; one pair of lower incisors enlarged & procumbent; opposite of rodents in that half-enameled lower incisors may exist independent of upper incisors (i.e. they may have gnawed with *lower* teeth!); mandibular symphysis not solid; no canines except upper in basal forms; large diastema; buccal cusps on lower premolars reduced or absent; large, blade-like premolars with multiple serrations; premolars clearly differentiated from molars; large multi-cusped molars with as many as three rows of cusps & 5-30 total cusps on a molar; cusps of roughly equal height; last upper molar is displaced lingually in relation to last lower; some dental specializations including blade-like forms; dentary "semicircular" and arcuate; jaw glenoid large, flat, tear-drop shaped & open anteriorly (allows propalinal motion); mandible brought posteriorly into articulation; choanae separated by



Kryptobataar: reconstructed right pes in dorsal view. From Kielan-Jawarowska et al. (2000).

vertical plate formed by vomers; most of posterior palate formed by palatines; ectopterygoids fused with pterygoid?; septomaxilla absent; **$** premaxilla large; maxilla large and forms most of lateral and ventral snout; maxilla usually with one infraorbital foramen; **$** nasal and nasal cavity large (not long) in most; nasal cavity with complex ventral ridge system (turbinates?); cribiform plate absent?; frontal overhangs orbit; palatine excluded from orbit (i.e., orbital process of palatine absent); orbits face laterally; orbits probably of moderate size and unfloored; orbits extended anteriorly; **$** postorbital process reduced or absent; postorbital process on parietal; **$** jugal reduced & zygomatic arch largely from squamosal and maxilla (jugal is internal to arch); squamosal small & contributes little to braincase; zygomatic arch stout, with jugal incorporated in medial wall; parietal extensive on skull roof but not significant otherwise; post-glenoid region short and wide; olfactory lobes large, with large, tall petrosal; supraglenoid foramen located on raised lateral wall of petrosal; 3 auditory ossicles as in therians; stapes not perforated and "columellaform"; stapes with round footplate; bone bulla absent; no bone external auditory meatus; promontorium narrow, straight & oriented anteromedially; cochlea nearly straight; vestibular apparatus differs radically in size among multis and may be greatly inflated; internal auditory meatus very small or absent; alisphenoid small (controversial); cerebrum smooth; no cerebellar hemispheres; cochlea uncoiled & ear relatively primitive; vertebrae with wide transverse and high spinous processes (thus jumper??); interclavicle present; scapula lacks supraspinous fossa; glenoid large, opening ventrally; pelvis very narrow (too narrow for shelled egg per Kielan-Jawarowska); "marsupial" bones present; acetabulum shallow & dorsal (from *Ptilodus*: may be arboreal adaptation rather than plesiomorphic); parafibula present in knee area as in monotremes; calcaneum contacts MtV; MtIII abducted ~30° from longitudinal axis (i.e. deeply sprawling posture); wide variety of ecological niches including arboreal form (*Ptilodus*) with reversed hallux and possible prehensile tail; also saltatorial and fossorial forms; possibly viviparous based on pelvic morphology. Longest lived mammalian lineage.

Links: Introduction to Multituberculates; pal1; mammevol.htm; kryptobataar; digital reslicing of kryptobataar; The first furry creatures; Main Page; Mesozoic mammals showcase; Literature - Mammalia; UTDMG - Kryptobaatar dashzevegi; Paleocene mammals of the world (**Best on the Web**); Stars of the Show (A to I); Untitled Document.

References: Butler (2000), Jenkins *et al.* (1997); Holtz (1995); Holtz (1996a); Kielan-Jaworowska *et al.* (2000); Luo *et al.* (2001); Miao (1993); Pough *et al*. (1999); Simmons (1993); Wall & Krause (1992). ATW 011128.

Paulchoffatiidae: *sensu* Simmons (1993), i.e. *Paulchoffatia* only.

Range: upJ (Kimmeridgian) of Eur (Guimarota).

Phylogeny: Multituberculata: (Gondwanatheria + Cimolodonta) + *.

Characters: Dental formula 3/1, 1?/0, 5/3, 2/3; enamel evenly coats incisors;I3 on margin of palate, with multiple cusps; C1 present; P2-P4 double-rooted; P2 with 5-6 cusps; p3 & p4 have 3-5 cusps; p4 & m1 very short; p4 rectangular; lower premolars (p1-p3) not fully differentiated for shearing; M2 short, without lingual cusps; at least 1 molar (here **$** m2) with central basin instead of linear cusps (like haramiyids, so quite possibly plesiomorphic); incisive foramina small & round or oval; palatal vacuities absent; angle of coronoid >55° from tooth row; maxilla has two infraorbital foramina; no bone process (of frontal) over orbit; frontals pointed anteriorly & rounded posteriorly (?), postorbital process reduced or absent; nasal relatively compressed laterally; lacrimal present, large & extends to frontals; frontal-parietal suture V-shaped; zygomatic ridge weak or absent; zygomatic arch flares out & is not confluent with snout; base of zygomatic arch dorsal to P3-P4 embrasure; **$** nasal contacts parietal; **$?** condylar foramina (canal for XIIth [hypoglossal] nerve) paired .

Links: Plagiaulacoidea; MESOZOIC MAMMALS; Plagiaulacidae and Paulchoffatiidae, an internet directory:; SyrenCRL (French).

References: Kielan-Jawarowska & Hurum (1997); Simmons (1993).

Note: "Plagiaulacoidea" is clearly paraphyletic as confirmed by virtually all studies. As a result that taxon is not used here. Paulchoffatiids are the most basal known multis. 020228.

Gondwanatheria: *Ferugliotherium, Gondwanatherium, Lavanify, Sudamerica*.

Range: upK-lwPc of SAm, India, Mad & probably Antarctica.

Phylogeny: Multituberculata:: Cimolodonta + *

Characters: large, gnawing incisors; many with hypsodont dentition; characteristic microstructure of molar enamel, involving small circular prisms separated by sheets of matrix; molars curved along their height; molars with deep infundibulum; transverse ridges between molar cusps; p3 absent?; rectangular p4.

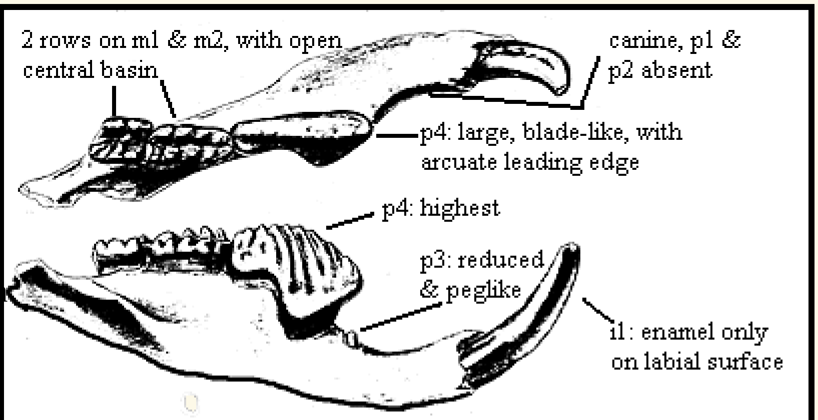
Links: scienceweek; Paleocene mammals of the world (**Best on the Web**); Untitled Document (questioning whether actually related to multis).

References: Kielan-Jaworowska & Hurum (1997); Krause *et al.* (1997). 010701.

Cimolodonta: *Cimexomys, Ptilodus*.

Range: upJ?-lwOc (mainly upK-upPc) of China & NAm.

Phylogeny: Multituberculata:: Gondwanatheria + *.



Cimexomys: right lower jaw in occlusal and lateral views. Modified from Montellano et al. (2000).

Characters: **$?** I1 absent; **$** enamel on i1 only on labial surface (?! -- see Wall & Krause (1992) on *Ptilodus*); **$?** I2 with <4 cusps; **$** I3 located medially; **$** no canines; **$** P0 absent; **$** p2 absent; p3 small & peg-like (*Cimexomys*); **$** p4 has arcuate leading edge; **$?** p4 monophyodont; **$?** M2 labial cusp row present; substantial incisive foramen in premaxilla; **$** palatal vacuities present; **$** snout length >50% of skull length; **$** 1 pair of infraorbital foramina; prenasal process of premaxilla forms internarial bar; **$?** lacrimal absent; **$?** frontal forms roof over anterior of orbit; **$** jugal fossa (on zygomatic arch?) large and deep; **$** strong zygomatic ridge; low condyle relative to occlusal plane maximized force at p4 (highest lower tooth) for crushing & slicing; probable omnivores with some degree of specialization for medium-large food objects; lacrimal present in one early group; vestibular apparatus may be enlarged; **$** single pair of condylar foramina; vertebrae dorso-ventrally compressed (*Cimexomys*).

Links: Cimolodonta.

References: Kielan-Jaworowska *et al.* (2000); Kielan-Jawarowska & Hurum (1997); Miao (1993); Montellano *et al.* (2000); Simmons (1993); Wall & Krause (1992).

Notes: **[1]** This clade is, obviously, *very* well supported. **[2]** The Djadochtatheria, Mongolian upK multis, were originally proposed to fall outside Cimolodonta. Kielan-Jawarowska & Hurum (1997). However, their cladogram actually places Djadochtatheria within Cimolodonta, and the group has accordingly been moved to this position. Kielan-Jaworowska *et al.* (2000). **[3]** In this general connection, the humble editor of these Notes would like to express his undying gratitude to Drs. Kielan-Jawarowska and Sigogneau-Russell for never co-authoring a paper. The world of early mammalian paleontology has been immeasurably enriched by the efforts of each scholar individually, but the small world of scientific commentary is made easier by not having to pronounce both formidable names in the same breath. **[4]** Wall & Krause (1992) analyze the jaw cycle in *Ptilodus* as: (a) jaw opened and moved forward on the glenoid (~2.5 mm); (b) orthal movement to either (i) pierce with incisors or (ii) crush and slice with the elaborate multituberculate p4; (c) retraction of the jaw with grinding along molar surfaces. Osteology suggests that posterior temporalis muscle was very strong and primarily responsible for adduction, masseter & temporalis for retraction. 010703.

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checked ATW050521

Mammaliformes: Docodonta

Morganucodontids & Docodonts

Abbreviated Dendrogram

```
CYNODONTIA
|
MAMMALIFORMES
|--Allotheria
|  |--Haramiyida
|  `--Multituberculata
|     |--Paulchoffatiidae
|     `--+--Gondwanatheria
|        `--Cimolodonta
`--+--Morganucodontidae
   `--+--Docodonta
      |  |--Megazostrodontidae
      |  `--Docodontidae
      `--+--Hadrocodium
         `--Symmetrodonta
            |--Kuehneotheriidae
            |
            MAMMALIA
```

Contents

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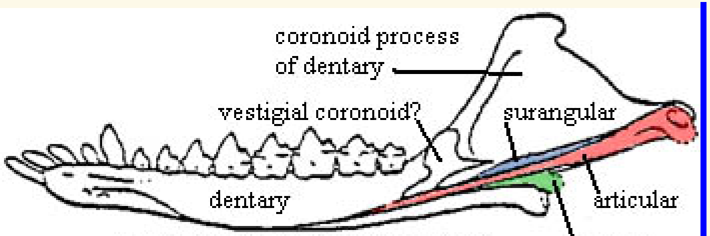
2. Docodontidae X
3. Megazostrodontidae X
4. Morganucodontidae X

Descriptions

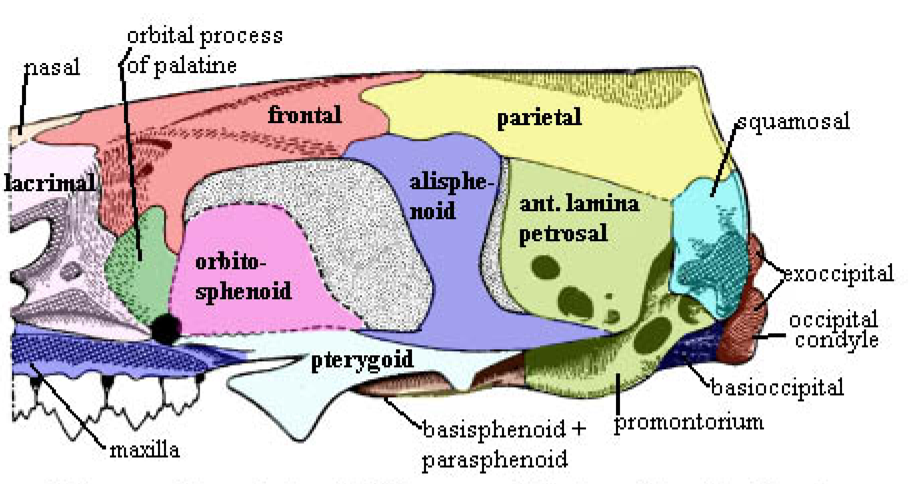
Morganucodontidae: *Brachyzostrodon*, *Morganucodon* (= *Eozostrodon*?)



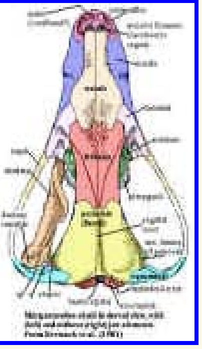
Morganucodon right jaw in medial view showing postdentary bones

Range: upT-mJ of Eur, China, Russia & NAm(?)

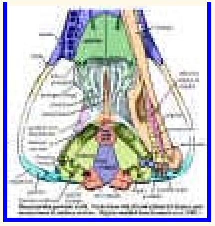
Phylogeny: Mammaliaformes:: (Docodonta + (*Hadrocodium* + Symmetrodonta)) + *.



Morganucodon posterior skull in parasagittal view, with quadratojugal, jugal and stapes omitted. From Kermack et al. (1981: 115 fig. 96).



Characters: ***General*** small, rat-like forms, ~10cm long; skull <3 cm, long & slender; ***Dentition*** dental formula 5/4, 1/1, 4/4, 4/4; well-differentiated, diphyodont molars; three cusps on the upper and lower molars; cusps were aligned anteroposteriorly with precise occlusion; ***Jaws*** slender jaw; dentary loosely attached at symphysis; post-dentary bones present in groove of dentary; post-dentary bones ~20% of jaw length (?); coronoid bone present at base of coronoid process of dentary; reflected lamina decreased to narrow ribbon-like horseshoe; both quadrate-articular and squamosal-dentary jaw joints; possible tympanic membrane in reflected lamina of angular; ***Palate*** hard palate from fused maxillae & fused palatines only; posterior palate shows ridges as in tritylodonts & multis; strong pterygoid flanges as in cynodonts (limited lateral motion in reptilian jaw); ectopterygoids may be present (primitive) no gap between palate & basicranium (change from cynodonts); ***Snout*** nares confluent (?); septomaxilla unknown but believed present; large nasal cavity above secondary palate, with ridges for turbinals (so clearly warm-blooded); narrow snout; probable vibrissae (from pattern of nerve & vessel foramina); maxilla large and tall (as multis); large nasal with fine grooves for circulation, suggesting fleshy snout; lacrimal large, forming anterior root of zygoma with maxilla; ***Orbit*** orbits large; no postorbital bar; temporal fenestra merged with eye socket; postorbital and prefrontal absent; anterior and dorsal margins from lacrimal & frontal, respectively; anteromedial surface from ascending process of palatine; medial surface from partial orbitosphenoid wall; ***Skull table*** frontal large, with circulation grooves as on nasal, frontals meeting dorsal process of palatine; frontal and parietal extend ventrolaterally over dorsal braincase; parietals fused, forming sagittal crest; transverse (lambdoid) crest formed by posterior parietals; pineal foramen absent; squamosal does not participate in braincase (like multis, unlike therians); ***Lateral skull*** zygomatic arch slender and dorsally arched but not much expanded laterally; most of anterior arch (except root) from thin jugal; posterior arch from squamosal; ***Jaw articulation*** both dentary-squamosal and articular-quadrate articulations present; jaw articulation far posterior (as therians) with little post-zygomatic skull; ***Occiput*** strong lambdoid crest from parietal & dorsal flange of squamosal; foramen magnum large; basioccipital has little occipital exposure; most of foramen magnum margin and all of occipital condyles from exoccipitals; condyles low compared to therians; posttemporal fenestra reduced to minor opening between dorsal & quadrate flanges of squamosal; jugular foramen present between exoccipitals & petrosal; tabulars and supraoccipital unknown but probably present; ***Braincase*** cribiform plate apparently present; orbitosphenoid partially (?) ossified within orbit; no contact with ascending process of alisphenoid; narrow, strap-like alisphenoid; ascending processes of alisphenoid on either side of sella turcica; petrosal lies behind alisphenoid (see **discussion** for details); basicranium triangular (primitive), dominated by basioccipital; lateral sides of triangle formed by strong *basipterygoid processes*, merging posteriorly with quadrate (posterior) rami of alisphenoid; internal corotid foramina on ventral surface of basisphenoid; basisphenoid lacks definitive dorsum sellae; basisphenoid sutured to pterygoids; parasphenoid (and vomer?) fused to pterygoid; lateral portion of basicranium from petrosal; enlarged cochlea with promontorium; cochlea not coiled; auditory bulla absent (developed to confine auditory ossicles when separated from lower jaw); stapes extends from inner ear capsule to quadrate; stapes still large; quadrate tiny; petrosal with large anterior lamina; cerebral hemispheres small and smooth, not overlying cerebellum; ***Axial*** cervival vertebrae with very large neural canal; mammalian pattern of posteriorly slanted neural spines on anterior vertebrae, reverse in posterior vertebrae; clearly differentiated lumbar area without ribs; lumbar zygapophyses tilted 35-45° to resist torsion; ~27 presacral



vertebrae; 2-3 sacrals; ~12 caudals; short tail; ***Appendicular*** limbs slender; procoracoid retained, but excluded from glenoid; no scapular spine; interclavicle and large clavicle retained; humerus broad, with ends twisted 50°; proximal head bent strongly dorsally; ectepicondylar foramen lost; entepicondylar foramen retained; pubes reduced; obturator foramen enlarged; short legs; femur essentially therian; 5-toed feet; ***Other*** probable fur (further extrapolation from vibrissae); insectivore(?).

Links: Morganucodon Printout- EnchantedLearning.com; Morganucodon oehleri (Norwegian); Stark-Verlag (German); Biological Principles, BI-120 Study Guide Page 20; Morganucodontidae after McKenna & Bell, 1997; Eozostrodon; Cuffey 2 - Mammal - Like Reptiles.

On The *Morganucodon* Petrosal -- and Lots of Tiny Little Holes with Big Names

We have often blundered into braincase anatomy in these Notes, usually to back out again as quickly as our injured dignity will allow. However, we can advance no further into the issues peculiar to mammalian evolution without delving somewhat more deeply into these minutiae. Such practical considerations aside, it is also futile to spend *all* of our time charging full-tilt through phylospace, looking for the Big Pictures. It is the nature of phylospace that each Big Picture is made up of a very large number of Little Pictures, each of which is not only made up of yet smaller images, but connects with other issues altogether; so that what might appear to be an eternal answer at one scale, is merely one aspect of an infinite question at another. This being the case, it is appropriate to stop periodically to look carefully at some randomly chosen detail in order to gain a sense for the way in which it is tied to the rest of phylospace.

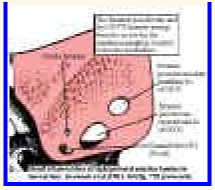
To be sure, the petrosal of *Morganucodon* could not fairly be described as "randomly chosen." Twenty years after the comprehensive work of Kermack *et al.* (1981), *Morganucodon* remains the world's best known mammaliform skull. The genus was originally known from one well-preserved and perfectly articulated skull. It was also discovered that various Paleozoic strata in Wales had been pierced by fissures in Early Jurassic times. These fissures had been filled by water-borne debris containing, among other things, hundreds of tiny, disarticulated bones from *Morganucodon*, many of which were in near-perfect condition. **[1]** The combination of a well-articulated and more or less complete skull *and* a broad sample of disarticulated bones allowed Kermack to reconstruct the head in unprecedented detail. Of all of the bones recovered by Kermack's group, the three, almost complete, petrosals are perhaps the most interesting for several reasons. First, the petrosal is the otic capsule: a fusion of (at least) the prootic and opisthotic bones. It is therefore the site of the crucial transfer of post-dentary bones from the jaw to the braincase to form the mammalian middle ear. This transfer had not yet occurred in *Morganucodon*; but it is supposed that the postdentary bones were already largely devoted to hearing. Second, the petrosal forms the lateral wall of most of the braincase, and thus reflects the path and position of many important cranial nerves and circulatory structures.

Study the first figure. If you are still searching for a Big Picture, this is it. The figure shows the petrosal in all of the usual orientations. Several arbitrary "regions" have been marked off as an aid to orientation and discussion, and the articular surfaces have been noted. For further assistance, you may wish to review the figure of the posterior skull in ventral view.

We might, to a very inaccurate first approximation, think of the petrosal as a sailing vessel, an old-fashioned gaff-rigged sloop, beating to windward against a stiff, posterolateral breeze, out through the occiput. The **anterior lamina** (in red) is the mainsail. The region of the **subarcuate fossa** (in blue) forms the foredeck and jib -- for the non-nautical, the little sail in front -- and the **promontorium** (green) marks the keel. The analogy breaks down when we try to describe the **lateral trough** (yellow), but, then, it wasn't much of an analogy in the first place.

The anterior lamina

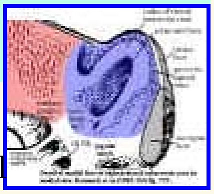
The anterior lamina (in red) might better be called the "lateral lamina." Its exact shape is a bit hard to



make out from Kermack's figures. One is tempted to guess that it may be a *crista prootica* gone berserk. It seems to serve much the same function in sheltering the numerous neural fossae in the lateral trough, although it is much larger and more vertically oriented than a conventional crista, and it articulates with the parietal along its dorsal ridge (this articulation is not shown in the figure). The anterior limit of the anterior lamina must have approached the ascending process of the alisphenoid, but the two were not in sutural contact.

In lateral view, the anterior lamina is pierced by two large foramina: the *foramen pseudorotundum* anteriorly and the *foramen pseudovalis* posteriorly. Kermack notes that this identification has been disputed, but we will follow his system for lack of any basis on which to disagree. The two foramina are the exits of the maxillary and mandibular branches of the trigeminal nerve (cranial nerve V), respectively. The large pit at the base of the medial face of the anterior lamina housed the semilunar (or trigeminal) ganglion -- the nerve center from which the trigeminal nerves arise. The two smaller foramina on the anterior lamina accommodate the facial (VII) nerve and one of its branches, the *chorda tympani*, which carries taste sensations. The main facial nerve passes through the more ventral (lower) of the two small foramina and emerges in the pit for the semilunar ganglion.

The subarcuate region



The **subarcuate region** (in blue) has been colored only on its medial face. The central feature of this region is the *subarcuate fossa*, probably so called because it is the area under the arch of the vertical semicircular canal. The foramen for the chorda tympani on the lateral face of the anterior lamina emerges inside the subarcuate fossa, and, in life, the fossa was probably filled with sensory nerves from the chorda tymapni, carrying taste information from the mouth.

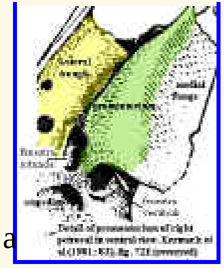
The small foramen just anteroventral to the subarcuate fossa is a branch of the endolymphatic system. Continuing in this direction, we find twin foramina which seem to approach obliquely from the anterior. The lower of the two is the auditory (VIIIth) nerve, and the upper is one of its branches, the *superior vestibular nerve*. The latter carries information about orientation and angular momentum from the lateral semicircular canal.

Immediately below (ventral) to the subarcuate fossa, the surface is somewhat recessed and the ventral edge of the petrosal is interrupted by a large, semi-circular notch, best seen in the dorsal view. This is the jugular notch, the petrosal half of the jugular foramen through which the internal jugular vein passes as it exits the cranium. The internal jugular then joins with the *vena capitis lateralis* **[2]** and drains into the neck to join the subclavian vein in the shoulder. The other half of the jugular foramen is formed by the exoccipital, the occipital, or the occipital portion of the temporal, depending on just how mammalian the organism is. The internal jugular drains the blood supply of the brain and originates from the sigmoid sinus. **[3]**. The jugular foramen also provides the exits for the glossopharyngeal (IXth) and vagus (Xth) cranial nerves. These mixed (*i.e.* motor and sensory) nerves are involved in brain interactions with the tongue and throat and with the viscera, respectively.

The lateral (uncolored) side of the subarcuate region is largely devoted to the articular surfaces for the squamosal and tabular. It projects a short way outward laterally. This lateral projection is all that remains of the opisthotic contribution to the paroccipital process in advanced mammaliforms. The exoccipital facet is perched on a small flange which extends a short ways out from the medial face. The entire articular region of the subarcuate area is fractured by vascular canals. The identity of the vessels is not completely clear. They certainly included the sigmoid sinus, which ran between the subarcuate fossa and the tabular facet, and the vena capitis lateralis, which may have been in the large canal almost directly opposite the subarcuate fossa on the lateral face.

The promontorium area

The promontorium is the portion of the petrosal which houses the cochlea. The cochlea, a specialized and elongate process of the lagena, is the primary organ of hearing in mammals. In modern mammals, the cochlea is strongly coiled, a state which seems to be correlated with a sophisticated ability to



discriminate among sounds. In mammaliforms, the cochlea is not coiled. The promontorium forms a sharp ridge anteriorly, but has a much more gradual curve toward the posterior end.

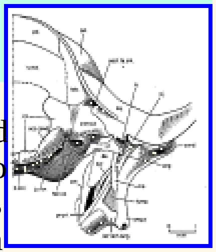
In ventral view, the promontorium ends posteriorly at the near-confluence of three large fenestrae: the fenestra rotunda, the fenestra vestibuli; and a pit which may have accommodated the body of the *m. levator hyoidei*. This muscle is a homologue of the mammalian stapedius muscle. Like the tensor tympani, the stapedius acts to damp excessively loud sounds -- in this case by restricting the movement of the stapes. The two middle ear fenestrate are discussed in connection with **The Ear**. Briefly, the footplate of the stapes fills the fenestra vestibuli and transmits sound to the inner ear. The fenestra rotundum simply moves in the opposite sense in order to relieve the pressure on the perilymphatic fluid in the inner ear caused by movement of the stapes.

Medial to the promontorium is a relatively featureless area, the medial flange. The edge of this flange provides the articular surfaces for the basisphenoid, anteriorly, and the basioccipital. Laterally, the promontorium forms the inner wall of the lateral trough.

The lateral trough

Most of the foramina in the lateral trough cannot be identifies with the kind of certainty which applies to other petrosal features discussed here, nor does Kermack provide us with a definitive image of the area. According to these authors, the area is also somewhat variable. Accordingly, we will omit a detailed consideration of the lateral trough at this point.

The beat of a different ear drum



Those who have been attempting to follow the ongoing struggle in these Notes to really understand braincase anatomy may be expecting that, at this point, we might finally have enough information to deal seriously with the development of the mammalian ear. That was, in fact, the original intent of this essay. Kermack *et al*. do provide their own vision of the pre-mammalian ear, involving a tympanum originally held by the angular and its reflected lamina distally, and by the manubrium (the retroarticular process of the articular), proximally. The difficulty is that the geometry and anatomy are simply not yet convincing.

The figure at right is that vision. Here are some of the problems. (1) Neither the reflected lamina of the angular nor the manubrium were fossilized, so that the entire critical structure is quite speculative. (2) The thing that is supposed to make the stapes vibrate appropriately is the quadrate. However, in *Morganucodon*, as in reptiles, the quadrate is still held in place by the quadratojugal which buffers it against stress with ligaments and soft tissues -- which would also seem certain to damp out sound vibrations imparted to the quadrate by the post-dentary bones. (3) As Kermack's group makes clear in another figure, the illustrated mechanism requires that at least the lower border of the tympanum be free. The physics of two-dimensional vibrating surfaces are quite complex **[4]**. However, *no* oscillator can operate with a free end or edge. How much music can you make with a guitar string if only one end is attached to the instrument? Essentially the same principle applies. (4) There is a reason why musical drums are round. Vibrations reaching the edge are reflected back and reinforce the vibrational node(s). The ear drum should work the same way. The trapezoidal to rectangular drum envisioned by Kermack can't work that way because the waves reflected from the edges will create a hash of rather randomly interfering signals. (5) Not to belabor the obvious, but is the space between the jaw and the skull really the best place to put an ear?

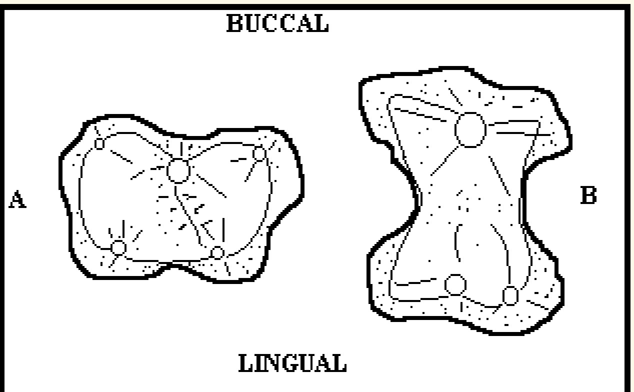
There may well be answers to these questions. For one thing, I am not certain that the tympanum really needs to have the properties of a harmonic oscillator, which would eliminate most of concerns (3), (4), and perhaps (2). Other answers are not obvious from our current level of understanding; nor do any alternatives immediately suggest themselves. Accordingly, we will once again have to leave this issue without a really satisfactory ending to the story. -

-ATW 011111

Notes: **[1]** The average cranial bone of *Morganucodon* is perhaps 2mm in maximum dimension. **[2]** That is, the "vein of the side of the head." The reader will not be stunned to learn that this vein drains the side of the head. **[3]** The sigmoid sinus itself resides in the mastoid process, a structure that will not be discussed here. **[4]** The reader may be aware that the famous Schrödinger wave functions are based on the equations describing standing waves in three-dimensional harmonic oscillators. For a graphic, see the link. The two-dimensional case is not really a heck of a lot simpler. See this link. I believe **Scientific American** ran an article on Chinese gongs about ten or fifteen years ago that touched on some of the math, but I lack the citation.

References: Kermack *et al.* (1981) [K+81]. 011102.

Docodonta: *Dinnetherium*.



Docodont cheek teeth (A) lower and (B) upper.

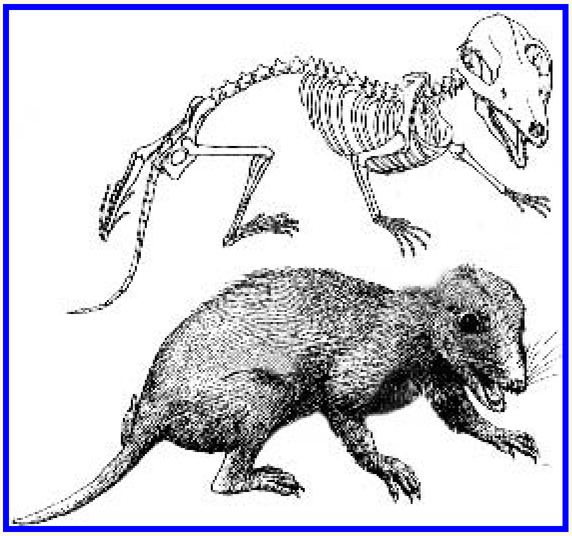
Range: mJ-upK of Eur, NAm & SAm.

Phylogeny: Mammaliformes::: (*Hadrocodium* + Symmetrodonta) + *: Megazostrodontidae + Docodontidae.

Characters: mouse-sized; snout & jaws elongate; probably retained some articular-quadrate contact with jaw; angular process of dentary directed ventrally; some species with as many as eight molars per jaw; lower molars rectangular and elongate; outer cusps taller than inner (derived from cingulum?), with ridge connecting buccal and lingual sides; upper molars expanded laterally with waisted central portion.

Links: Mesozoic Mammals; Docodonta and Triconodonta, an internet directory.

Megazostrodontidae: *Megazostrodon*.



Range: upT to lwJ of Afr.

Phylogeny: Docodonta: Docodontidae + *.

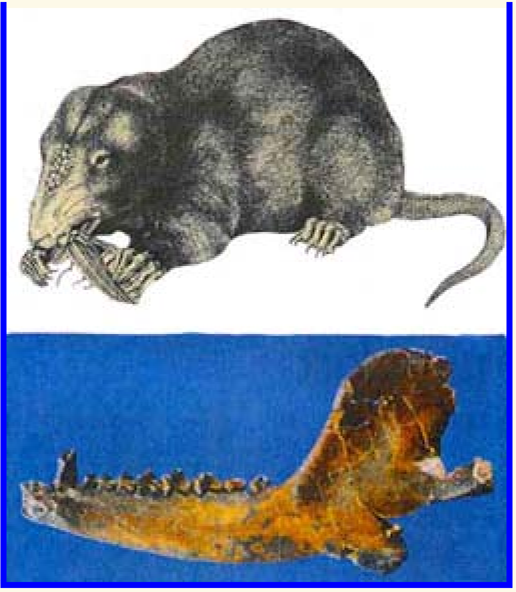
Characters: ~10cm; dental formula 5/4,1/1,4/4,4/4; cheek teeth differentiated into premolars and molars; occlusal pattern in which upper teeth alternate with the lower teeth; dentary - squamosal functional jaw joint; articular & quadrate retained in jaw and skull base, respectively; brain with relatively large olfactory & auditory areas; relative brain size 3-4x cynodonts; and it had a flexible backbone with clear division into thoracic & lumbar regions; probable nocturnal insectivores.

Links: Paleontology and Geology Glossary: Me; Megazostrodon, Drawing Nature Studio; Megazostrodon; South African Museum - Fossil Reptiles of the South African Karoo; Evol.Page to Print: Clado Pic.Sinoconodon & Megazostrodon; first mammals appear; Biology 356; Mesozoic Mammals; Docodonta and Triconodonta, an internet directory; JURÁSSICO mamíferos (Spanish).

Image: *Megazostrodon*, substantially altered from Notes for Lecture 11. Auditory pinnae have been removed (can you imagine an external ear on the jawbone?), a small parietal crest added, the jaw gape is increased, the posture of all limbs made slightly more primitive, some superfluous shading removed, and body contour made leaner.

Docodontidae: *Docodon*, *Haldanodon*, *Reigitherium*.

Range: mJ-upJ of Eur. & NAm.



Phylogeny: Docodonta: Megazostrodontidae + *.

Characters: wear surfaces on mesiolingual part of lower molars, including basined crushing surface in some (reverse of normal mammal pattern in which talonid is posterior to to trigonid) [L+02]; omnivores(?).

Links: The Fossil Mammal Hall; Guimarota - A Jurassic Ecosystem (German); Pascual et al..

References: Luo *et al.* (2002) [L+02].

Image: *Haldanodon*, life reconstruction and left jaw in medial view. 020223.

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Mammaliformes: Symmetrodonta

Hadrocodium & Kuehneotheriids

Abbreviated Dendrogram

```
CYNODONTIA
|
MAMMALIFORMES
|--Allotheria
|  |--Haramiyida
|  `--Multituberculata
|     |--Paulchoffatiidae
|     `--+--Gondwanatheria
|        `--Cimolodonta
`--+--Morganucodontidae
   `--+--Docodonta
      |  |--Megazostrodontidae
      |  `--Docodontidae
      `--+--Hadrocodium
         `--Symmetrodonta
            |--Kuehneotheriidae
            |
            MAMMALIA
```

Contents

Taxa on this Page

1. *Hadrocodium* X
2. Kuehneotheriidae X
3. Symmetrodonta X

Descriptions

Hadrocodium: a Miniscule Mammaliform

Luo Zhe-Xi is the master of mammaliforms. **[1]** His papers over the last few years have transformed our understanding of the key transitions in the mid-Mesozoic which made us the hairy niusances we are today. *Jeholodens*, *Zhangheotherium*, and now *Hadrocodium* have all been described by Dr. Luo and his associates at the IVPP in Beijing and the Carnegie Museum in Pittsburgh. Hu *et al.* (1997); Qiang *et al*. (1999); Luo *et al*. (2001). There are, however, two trivial matters about his scientific output that are somewhat difficult to deal with. The first is that Dr. Luo is from the PRC. Consequently, his name (along with other researchers from China) has been Westernized in a number of different ways. As it turns out, LZ Xi, L Zhexi, Z-X Luo, and so forth are all the same Dr. Luo, although each scientific persona has probably published enough important papers to satisfy most workers.

The other matter has less to do with persons than economics. Luo publishes some of his best material in **Science**. This is a Good Thing, since more people see it this way. However, the page limitations in **Science** are severe. When Luo's *Zhangheotherium* paper came out, there was a certain amount of professional grumbling that the authors had actually revealed very little, particularly about the all-important teeth. Possibly in reaction, the *Hadrocodium* paper almost goes to an opposite extreme. It pushes the envelope on length at 5½ pages. More importantly, in an effort to shoehorn the maximum amount of data per column-centimeter, the paper is more densely written than an annotated edition of Joyce's *Ulysses*. The cryptically abbreviated labels on the figures are in so fine a font that one has to enlist neighborhood children with good eyesight to decipher them. In addition, the paper comes with an on-line addendum of about 100 pages, although this is unfigured and largely concerns the cladistic analysis. For most readers of these Notes, it would be best to set aside a full day -- with a 200 watt bulb and a good magnifying glass – to tackle this work.

Nevertheless, Luo *et al*. (2001) is a fine paper, or really two fine papers. The first part is the description of *Hadrocodium* -- an isolated skull -- and its mammalian adaptations. The second part is the mandatory cladogram. Both are worth careful study. However, for the purposes of this Note, we will restrict our attention to the first section. The object here is simply to unpack this part of the article a little and make the incredibly dense Figures 1 and 2 a bit more accessible.

Hadrocodium is tiny by any measure. It is fully adult but Luo *et al*. estimate the mass of the creature at 2g -- as small as the very smallest modern mammals. This may be significant. If one is looking for the source of major morphological innovations, one might expect to see more of them in a small organism with a very high rate of reproduction. Each individual represents a trivial investment of gestation time and food energy from the standpoint of the species, and genetic drift should be higher in species with (a) short generation times and (b) populations which are easily separated by physical barriers. Thus selection against mutation may be relaxed, and those that occur are more likely to become entrenched in some meaningful number of individuals. The implication is that *Hadrocodium* may not simply be the sister of all mammals, but something very close to an actual ancestral form.

Luo *et al.* describe *Hadrocodium* as having four suites of mammalian apomorphies. The first two are quite simple. The third and fourth are interrelated and quite complex.

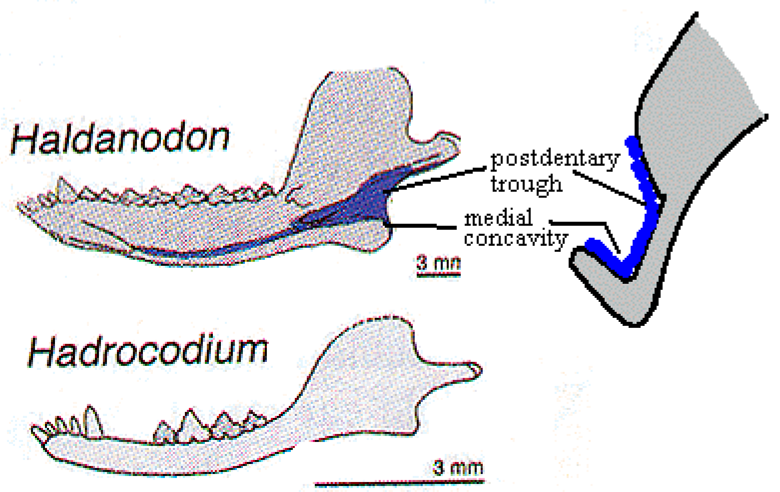


Figure 1. Haldanodon: right mandible in medial and posterior views. Hadrocodium right mandible in medial view. Modified from Luo et al. (2001), Fig. 3.

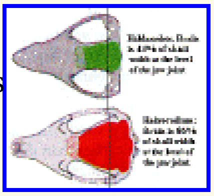
1. Inside the Jaw

This series of changes is fairly straightforward. As we will discuss at great length below, the original postdentary bones in the ancestral synapsids were the angular, surangular and articular. The jaw joint was formed by an articulation between the articular and the quadrate. Between the Carboniferous pelycosaurs and the first Jurassic mammals, the jaw articulation changed. These post-dentary bones became increasingly small and less relevant to prey capture and eating. By the Middle Jurassic, Docodonts, such as *Haldanodon*, relied exclusively on a "new" dentary-squamosal jaw joint.

However, the lower jaw was also involved in sound reception, and it was advantageous to have small bones in this area. Through a series of transformations which need not be detailed here, the dentary overgrew the old postdentary elements. These, in turn, formed a small trough and concavity at the posterior end of the jaw, on its medial (inside) surface. This space supported the tympanic membrane on the tympanum (angular) as well as the auditory ossicles of the middle ear: the incus (quadrate), malleus (articular) and stapes.

Crown group mammals have all lost this portion of the jaw, and the entire assemblage has been transferred to the cranium. The key observation here is that *Hadrocodium* has no trough or concavity. The conclusion is that the middle ear machinery had already been moved to the cranium. As we will see, this supposition is supported by other anatomical observations. Interestingly, the dentary retains an odd, inflected curve that both mammals and other mammaliforms lack. The implication is that the loss of the postdentary elements from the jaw had perhaps been *very* recent, so that the dentary retained the odd curvature which would be left by simply subtracting out the portion formerly related to the postdentary bones. **[2]**.

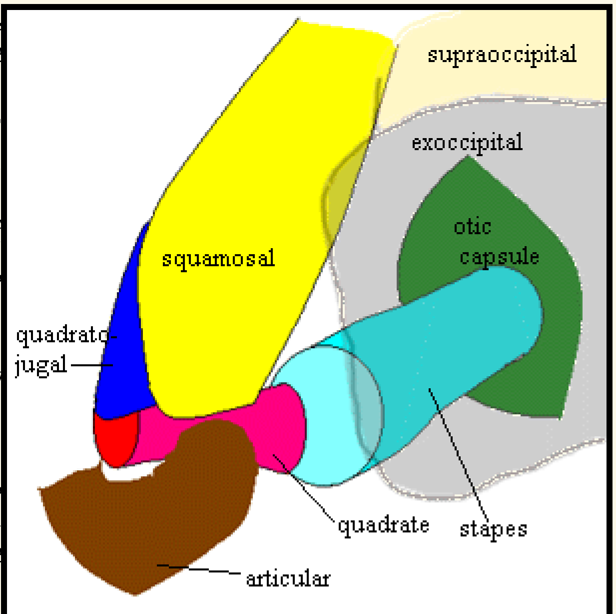
2. The Brain



Mammal brains are bigger. This is one that everyone knows. Many steps were involved in this development, but the step represented by *Hadrocodium* seems to have been a large one. In mammaliforms below the level of *Hadrocodium*, the occiput, the jaw joint, and the transverse part of the zygomatic arch were all at more or less the same level of the skull. The squamosal portion of the arch flared out widely to accomodate the bulging jaw musculature. However, the muscles driving the jaw still took up a great deal of room.

In *Hadrocodium*, jaw articulation is moved anteriorly, so that the jaw musculature is spread forward as well, leaving more room for the brain cavity in the posterior half of the skull. The reason for this is very likely the separation of of hearing from eating. The jaw was able to move forward only because it was freed from its connection with the otic capsule. Even more important for later mammals, it became possible to expand the brain cavity posteriorly and dorsally, since the otic capsules could be moved away from the jaw articulation. We can see that this process has already begun in *Hadrocodium*. In addition, it is likely that the existence of the tympanum on the lower jaw imposed constraints on the muscle attachments to the jaw. Although we cannot know what these constraints were, it is certain that they were removed by the shift of the tympanum to the cranium.

3. The Jaw Joint and the Mammalian Ear



Basal amniote: schematic posterior view of lower left occiput

Here's where things get a bit complex. We must begin with a long digressive journey. As with many complex journeys in osteology, we start by paying a visit to our friend Bob, the Basal Amniote. Bob, as usual, has the Standard Condition. Looking closely at the lower corner of the back of Bob's head, we see that the quadrate is a key player. It braces the stapes, which supports the braincase through the otic capsule. Most importantly for our purposes, it forms the cranial part of the craniomandibular joint -- the jaw joint. It acts as a kind of spool, and the articular bone, at the very back of the lower jaw, hooks around it. All this tension and torsion is stabilized by the squamosal (which attaches to the occipital bones and the skull table further up) and by the the quadratojugal (which is anchored on the jugal and maxilla).

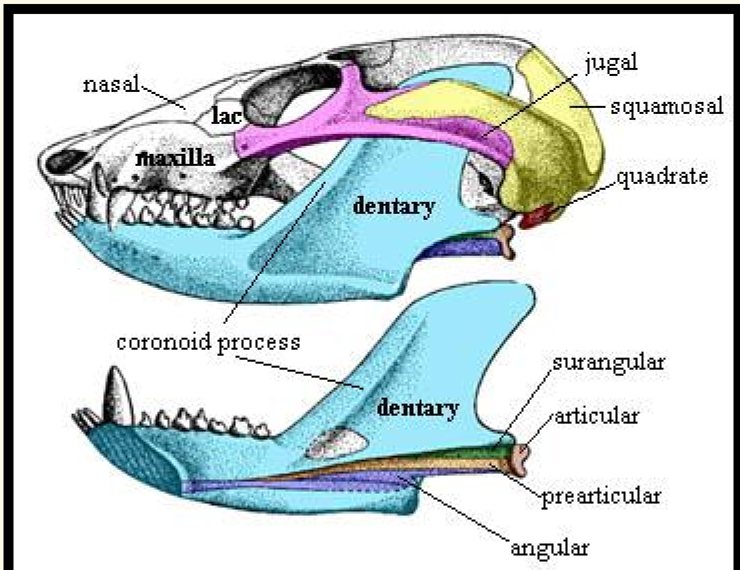
This is a fine arrangement for blockheaded basal amniotes. However, when evolution started knocking holes in the skull, the squamosal and quadratojugal became less dependable supports. At the same time, the formerly robust stapes evolved into a more gracile bone devoted to hearing. These developments, in the Sauria, both allowed and required the quadrate to become more massive and self-supporting. Eventually, as in lizards and dinosaurs, the quadrates took over from the squamosals and became pillars of the osteological community, graciously supporting the posterior corners of the skull. **[3]**.

Among the synapsids, things took a very different turn. The skull table remains solid, as there is no upper temporal fenestra. However, squamosal is sternly barred from the skull table by the intervening supratemporal, and the back of the skull is frequently slanted. As a result, the posterior of the skull tends to be held together transversely by the occipital bones, rather than vertically.

The effect on the jaw attachment is dramatic. As shown in the *Dimetrodon* at right, the squamosal

has grown down almost over the quadrate and become a plate-like, lateral element. The jugal has undergone a similar transformation, while the quadratojugal has disappeared. In the lower jaw, the post-dentary elements (angular, surangular, prearticular and articular) have rotated down to met the quadrate, while the dentary itself remains relatively straight -- as it must in order for the teeth to close simultaneously. The result is that the post-dentary bones have almost become*sub*-dentary bones. Finally, the angular has effectively been doubled, or folded (the"reflected lamina" of the angular), creating a sort of hollow tube below the jaw.

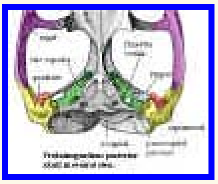
There is not a great deal of solid information on what all this sculpturing in the lower jaw was supposed to accomplish. Much later, it becomes intimately connected with hearing. However, many textbooks notwithstanding, its a real stretch to imagine an ear drum the size of an Olympic gold medal on the lower jaw communicating vibrational information (how?!) with the stapes, which is hidden behind the quadrate. **[4]**. Any noise loud and/or low enough to cause this tympanum to vibrate in a coordinate fashion would probably be detectable by other means – such as by observing landslides and seismic fissuring.



Probainognathus: skull and mandible in left lateral view. Modified from Carroll (1988)

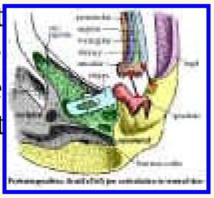
Whatever the answer, we must now press on about 50 My to the Middle Triassic and the eucynodont *Probainognathus*. Not by coincidence, *Probainognathus* is the outgroup used by Luo's group to root the phylogenetic analysis of *Hadrocodium*. At first glance, *Probainognathus* looks quite different from *Dimetrodon*. In reality, the changes are more matters of proportion than design. The temporal fenestra has become huge, dominating the greatly lengthened postorbital skull. The lateral skull is still composed of the squamosal and jugal, which bow outwards to form the zygomatic arch. In the lower jaw, the dentary has not only overgrown all of the other mandibular bones, but has formed its own, very large coronoid process. The coronoid *bone* has been reduced to a small, ovoid element on the medial face of the dentary. The splenial has vanished entirely. The dentary has also encroached on the postdentary bones ventrally, wrapping around them and leaving only long, thin remnants. These remnants include an angular, still with its miniature reflected lamina, forming a long concavity along the midline of the internal surface of the jaw. Despite the mass of the structure, the jaw still articulates through a small articular, which rotates on the quadrate, just as in *Dimetrodon*.

It seems unreasonable for a jaw of this size to rotate about so small an articulation. *Probainognathus* was not a large animal -- about 10 cm overall -- but the coronoid process is huge for the size of the jaw and the space available for the jaw adductors is enormous. To make things worse, the articular is not braced on the solid frame of the dentary, but on the feeble splinters of the surangular and prearticular. The system clearly worked, or these Notes would have been authored by something with scales and a muscular tail. But *how* it worked is a difficult matter. The engineering is usually explained by the decreasing importance of the jaw adductors and their gradual functional replacement by the masseter muscles, an evolutionary develoment which largely replaced slash-and-gulp eating with chewing – so important to the development of civilized etiquette. Be that as it may, *Probainognathus* looks as if it posessed massive adductors and minimal table manners, so the issue is still incompletely resolved.



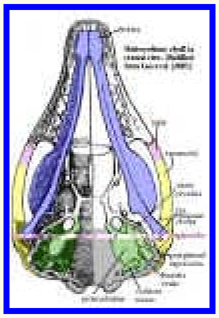
Since we will be comparing *Probainognathus* to *Hadrocodium*, let us take a closer look -- first at the base of the skull and then at the jaw articulation itself. The quadrate and stapes are now both small elements. Although their size has changed, their relative position has not. The stapes clearly has no remaining significance in the structural support of the braincase. The stapes terminates at a well-defined fenestra ovalis, suggesting that the stapes was specialized for hearing. The otic capsule is otherwise relatively flat and featureless. The occiput has already fused to become a single ossification.

With these landmarks in mind, examine a detail of the articular region. Two things should be apparant. First, when the articular contacts the quadrate, a corner of the dentary will contact the squamosal directly. Thus, even at the level of *Probainognathus*, we see the beginnings of the mammalian dentary-squamosal jaw joint.



Second, the post-dentary bones are now inevitably going to have an impact on hearing. anything that shakes the articular will be carried through the quadrate to the stapes to the oval window and on to the inner ear. The thing *most* likely to set the articular vibrating is the long, thin surangular or its probable homologue in later forms, the retroarticular process of the articular. This stretches back (it wouldn't have far to go) to the point where the angular and its reflected lamina could now plausibly maintain a tympanic membrane of reasonable size.

The rest, as they say, is history. The selection pressures which brought about the condition in *Probainognathus* are not really clear and took some 50 My to operate -- suggesting that these pressures were not particularly strong. However *Probainognathus* is only a few steps from the mammalian jaw and ear. The advantages of separate, specialized structures for chewing and hearing do not require much explanation. In fact, it is a little surprising that the mammalian condition took as long as 20-30 My more to develop. Perhaps this was due to a combination of two factors: (a) the rather more urgent matter of surviving the rise of dinosaurs in the Late Triassic and (b) the complex topological transformation needed to free the post-dentary bones from the dentary.



Now, at last, we are ready to return to *Hadrocodium*. The changes from *Probainognathus* to *Hadrocodium* are more subtle, but in many ways more fundamental than the changes between *Dimetrodon* and *Probainognathus*. The postdentary bones have disappeared from the jaw without a trace. The mandible is now composed entirely of the dentary. The dentary articulates only with the squamosal through a fully developed glenoid. The quadrate is no longer in contact with the jaw, or even visible.

All of these missing postdentary elements have presumably been incorporated into a very modern looking ear complex. The old otic capsule has been replaced by a much more complex structure, the petrosal, formed by fusion of the prootic, opisthotic, and incorporation of the postdentary elements. The paroccipital process has wrapped around the petrosal as a containing crista prootica. The tympanum is, of course, not preserved. However, the epitympanic recess is easily recognizable. Within this recess we would find the curved remnants of the angular (the tympanic) which actually form the tympanic annulus. The retroarticular process of the articular persists only as the tiny manubrium which remains in contact with the tympanic membrane as it presumably did in *Probainognathus*. The ancient articular - quadrate - stapes link is likewise preserved, but as the malleus - incus - stapes chain of ossicles in the mammalian middle ear. The entire assembly has been completely divorced from the jaw and is contained within the petrosal. Significantly, the *inner* ear has also expanded greatly and is easily observed as a large bulge, the promontorium. Finally, the promontorium bears a distinctive conical process for the cochlea, the signature organ of hearing in mammals.

This set of developments is really what sets *Hadrocodium* and mammals apart from all that came before. The separation of the jaw and ear freed the posterior skull from a significant restraint. Since the otic capsule was no longer under selective pressure to remain in exact coordination with the craniomandibular joint, the skull was free to expand posteriorly and laterally. The jaw, in turn, was freed to adopt configurations suited to take maximum advantage of precise dental articulations. That is, it was the separation of hearing and chewing that indirectly permitted the explosion of dental specializations which characterize evolution among the crown group mammals. --ATW 010616

Notes: **[1]** Luo refers to the taxon as "Mammali**a**formes." This is probably incorrect. The members of Mammaliformes are not morphologically similar to Mammalia, which is a clade. They are morphologically similar to *mammals*. Thus, it is appropriate to use the combining form for the critters themselves, rather than their taxon. **[2]** The absence of the groove and re-engineering of the lower jaw should also result in repositioning the Meckelian cartilage. As we have seen elsewhere, this can result in novelties in dentition and jaw function which might be related to the evolution of the tribosphenic molar. **[3]** See, for example, the discussion at Hadrosauridae or the sumptuous illustrations in Fairman (1999). **[4]** At this point, the hopelessly compulsive may wish to review where this is all going by visiting The Ear.

References: Fairman (1999); Hu *et al.* (1997); Luo *et al*. (2001); Qiang *et al*. (1999); Wang *et al*. (2001).

***Hadrocodium*:**

Range: lwJ of China.

Phylogeny: Mammaliformes:::: Symmetrodonta + *.

Characters: Post-dentary foramen absent; post-dentary bones completely disassociated from jaw; fully functional temporomandibular joint; zygomatic arch does oriented anteriorly (does not swing laterally); cranial process of squamosal anterior to fenestra vestibuli; post -glenoid depression on squamosal between cranial & zygomatic processes; large promontorium (housing of cochlea) present on petrosal; epitympanic recess (attachment for incus) present; brain expanded laterally to mammalian proportions.

Image: *Hadrocodium wui*. Modified from a reconstruction by Mark Klinger. Length without tail: about 3 cm. Changes similar to those made to *Morganucodon*: outline leaner, slight crest added, shape of rostrum changed, pinnae reshaped and moved, vibrissae further de-emphasized. Possibly, the eyes could be more lateral. Klinger's original appears on the cover of **Science** for May 25, 2001. Since he is with the Carnegie and had the opportunity to work with Luo, his work is more accurate. The point here is simply to show an alternative.

Notes: Wang *et al*. (2001) regard *Hadrocodium* as a probable juvenile. ATW 010610.

Links: Flash Hadrocodium (Greek); Tiny Animal May Be Mammals' Ancestor.

References: Fairman (1999); Hu *et al.* (1997); Luo *et al*. (2001); Qiang *et al*. (1999); Wang *et al*. (2001).

Symmetrodonta: (= Holotheria? = *Kuehneotherium* + Prof. Kuehn) *Kotatherium* (family *i.s.*)

Range: upT-upK.

Phylogeny: Mammaliformes:::: *Hadrocodium* + *: Kuehneotheriidae + Mammalia.

Characters: Tiny, very unspecialized mammals; ***cranial:*** auditory meatus may be present; cochlea primitively uncoiled; no angular process; loss or reduction of Meckelian groove and coronoid bone in derived forms; jaw action with some transverse and proplinal elements (?); primitively post-dentary bones in slot (?!!), but advanced forms converge on mammalian condition; **$** molars with basic reversed triangles pattern [L+01]; molars fit into embrasures of teeth in opposite jaw; occlusal surfaces formed developmentally, rather than by wear; molars with two roots; cristae may bear complex pattern of cuspules; external (i.e. buccal) cingulum well-developed and may bear cusps [SE98]; ***upper teeth:*** buccal cingulum frequently absent [SE98]; upper molars with tall, lingual A/paracone [SE98]; mesiobuccal B/stylocone [SE98]; one or more buccodistal cusps including C/metacone, with or without a more distal 'c' conule [SE98]; ***lower teeth:*** **$** buccal curvature of lower molar more bulging on primary a/protoconid than on cusps b/paraconid and c/metaconid [L+01]; **$** lingual curvature of a/protoconid is far less convex than on b/paraconid c/metaconid [L+01]; **$** hypoconid present [L+01]; may have small talonid, but talonid has probably been derived independently in different lines [L+01], is anterior in one case, and may or may not be homologous with mammalian (some derived forms have no talonid); **$** posterior talonid is incipient, or with a cingulid or cingulid cuspule [L+01]; **$** b/paraconid c/metaconid support single wear facet [L+01]; **$** lingual cingulid present, at least distally [L+01] [SE98]; lower molar roots of equal size [SE98]; ***axial:*** cervical vertebrae not fused; thoracic ribs robust and antero-posteriorly compressed; ***appendicular:*** interclavicle primitively present, but allows clavicle to pivot shoulder blade; forelimb posture sprawling, but clavicles move broadly and independently; epipubics present; pelvic girdle slight & not deep; acetabulum with dorsal ridge; ankle spurs as in monotremes.

Links: Cifelli & Madsen; Sigogneau-Russell; Transitional Vertebrate Fossils FAQ: Part 1B; Evol.Page to Print: Clado Key: Team Assignments and Traits; Mammal origins; mammif_chinois.pdf; SyrenCRL (French -- useful despite the lack of the figures it describes).

Discussion: To judge by the literature, symmetrodonts were a group of vaguely triangular, free-range molars that roamed the world unencumbered by either bodies or synapomorphies for almost 150My. In fact, until 1997 there was not a single symmetrodont bone known other than the occasional partial dentary. Many symmetrodont species exist only as tiny, isolated molars and, except for *Zhangheotherium*, the entire world's production of symmetrodont remains could probably fit into a beer mug.

To this day there is no satisfactory understanding of what a symmetrodont is. Much of the early work was done on *Kuehneotherium*. This genus was founded on a number of teeth and lower jaws found in association with fissure fillings of the basal mammal *Morganucodon*, whose teeth are frankly not very different. It was therefore supposed that *Kuehneotherium* looked pretty much like *Morganucodon*. The eventual discovery of virtually complete remains from the advanced, Early Cretaceous *Zhangheotherium* (Hu et al. (1997)) suggests that this wild guess was not far off. Certainly, *Zhangheotherium* has many interesting features, some of which are startlingly advanced. However, it *looks* pretty much like every other Mesozoic mammal.

Worse, as Sigogneau-Russell & Ensom (1998) note, there are no real and unequivocal synapomorphies which allow us to say what is symmetrodont and what isn't. Again, all symmetrodont species consist entirely of teeth and the odd dentary fragment, except for *Zhangheotherium*. For the latter, the teeth have yet to be described in meaningful detail. By definition, symmetrodont molars have the ancestral tricuspid configuration. The homologies between this molar type and the tribosphenic molar of Theria are not understood, and the nomenclature and description of these teeth is confused and inconsistent. For example, Fox's (1985) taxonomy seems **[3]** to refer to the primary cusp of the lower molars as both "paraconid" and "protoconid" on the same page. Because of these difficulties, as well as the persistent mammalian problem of convergences, Sigogneau-Russell and Ensom were unable to perform a cladistic analysis. It remains entirely possible that we are dealing, not with a discrete phylogenetic category, but with a series of intermediates between triconodonts, an the one hand, and dryolestoids and therians, on the other.

As a result, some phylogenies have essentially abandoned the whole idea of the symmetrodonts as a separate branch of the mammalian radiation. Instead, the various symmetrodont families are arranged as separate branches, or even paraphyletic grades, around the main trunk of mammalian evolution. There is nothing inherently wrong with such an arrangement. It might also help to explain some biogeographical anomalies in which similar new dental species show up more or less simultaneously on opposite shores of the Tethys and Labrador Seas. See, e.g., Sigogneau-Russell & Ensom (1998) (Tethys); Cifelli & Madsen (Labrador). Unfortunately, in most cases, treating the symmetrodonts as paraphyletic only makes matters worse. Land bridges may be a better explanation. However, Luo *et al*. (2001a) present powerful evidence that the symmetrodonts are simply the stem lineage of all mammals, and that the tribosphenic molar evolved twice (at least!) in this group.

Truthfully, there is not enough evidence for fully informed consent to either course at the moment. Since we do not know what species are correctly described as symmetrodont, it is difficult to make a rational choice. There does seem to be a core group of forms which originally developed a talonid of sorts, but subsequently minimized and lost this dental tool. Instead, they evolved in the direction of complex and poorly understood stylar interconnections between adjacent teeth, with the elaboration of stylar cuspules and ridges. These elements probably worked together to create very precise articulations between molars and the embrasures between teeth on the opposite jaw. It is also noteworthy that the incisors of symmetrodonts, where they are known, tend to show substantial specialization. One might speculate that, like rodents, the advanced symmetrodonts, particularly Spalacotheroidea, had at least two possible types of articulation depending on what set of teeth were being used.

However, this is all supposition. For the time being, symmetrodonts will be treated here as the stem lineage of mammalian evolution which diverged from other mammaliforms sometime in the Late Triassic or Early Jurassic. When *Zhangheotherium* is fully described, and, with luck, something other than a tooth is found in North America or Europe, we may see a very different picture. ATW 001230. Revised 011221.

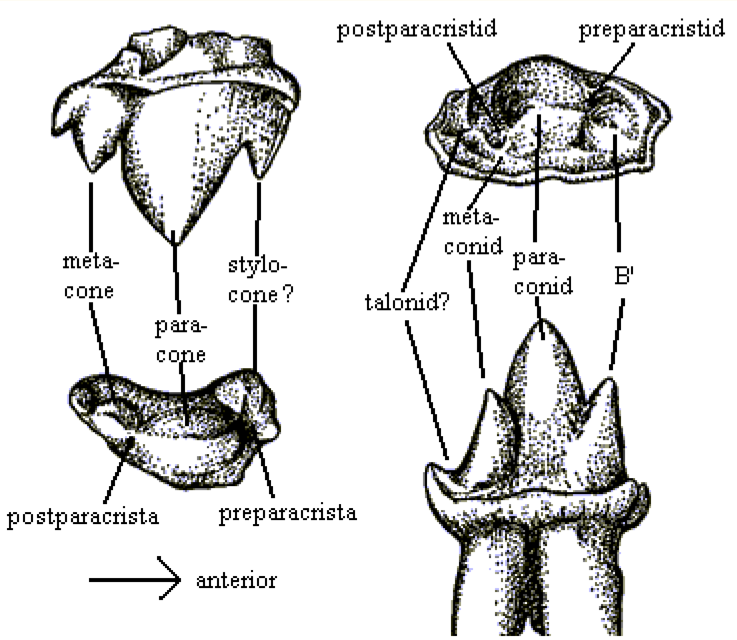
Note: **[1]** a third, African, radiation of Symmetrodonts may also be present in the Late Mesozoic. **[2]** For dental terminology in symmetrodonts, see images at Kuehneotheriidae and Spalacotheroidea. **[3]** **I am unable to rule out the possibility that I completely misunderstand what Fox is saying.**

References: Ensom & Sigogneau-Russell (2000); Fox (1985); Hu *et al.* (1997); Luo *et al*. (2001a) [L+01]; Sigogneau-Russell & Ensom (1998) [SE98]. 020218.

Kuehneotheriidae: **"Obtuse-angle symmetrodonts."**
Kuehneotherium, Woutersia??

Range: mT-lwJ of Eur.

Phylogeny: Symmetrodonta: Mammalia + *.



Left upper and lower molars of Kuehneotherium in lingual and occlusal views, generally following the nomenclature of Fox (1985). Modified from Carroll (1988).

Characters: Retain some trough for post-dentary bones [L+02]; both upper and lower molars have well-developed trigon and molar is triangular in cross-section, with three roots; angle formed by three principal molar cusps is generally >90°, with angle decreasing on posterior molars; paracone highest and most lingual on uppers; complete cingulum present [SE98]; cingulum without cuspules [SE98]; lower molars with a/protoconid (sometimes referred to as paraconid) largest and most buccal; small talonid present [SE98]; metaconid small (questioned by [SE98]); postparacristid shorter and more transverse than preparacristid; strong cingulids lingually & mesially, otherwise weak or absent [SE98]; believed to have had some degree of transverse jaw movement.

Links: mammalogy1.html; augtwoe; MESOZOIC MAMMALS; KUEHNEOTHERIIDAE and Co & "AMPHIDONTIDAE" (Best on the Web); Mammals (very basic); SyrenCRL; (French); volume_2_3-4; Untitled (brief explanation of traditional take on this taxon).

References: Fox (1985); Luo *et al.* (2002) [L+02]; Sigogneau-Russell & Ensom (1998) [SE98]. ATW030101.

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Mammaliformes: References

Abbreviated Dendrogram

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CYNODONTIA
|
MAMMALIFORMES
|--Allotheria
|  |--Haramiyida
|  `--Multituberculata
|     |--Paulchoffatiidae
|     `--+--Gondwanatheria
|        `--Cimolodonta
`--+--Morganucodontidae
   `--+--Docodonta
      |  |--Megazostrodontidae
      |  `--Docodontidae
      `--+--Hadrocodium
         `--Symmetrodonta
            |--Kuehneotheriidae
            |
            MAMMALIA
```

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