Dinosauria

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--PTEROSAURIA
   |
   `--DINOSAUROMORPHA
      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
            `--Dinosauria
               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
```

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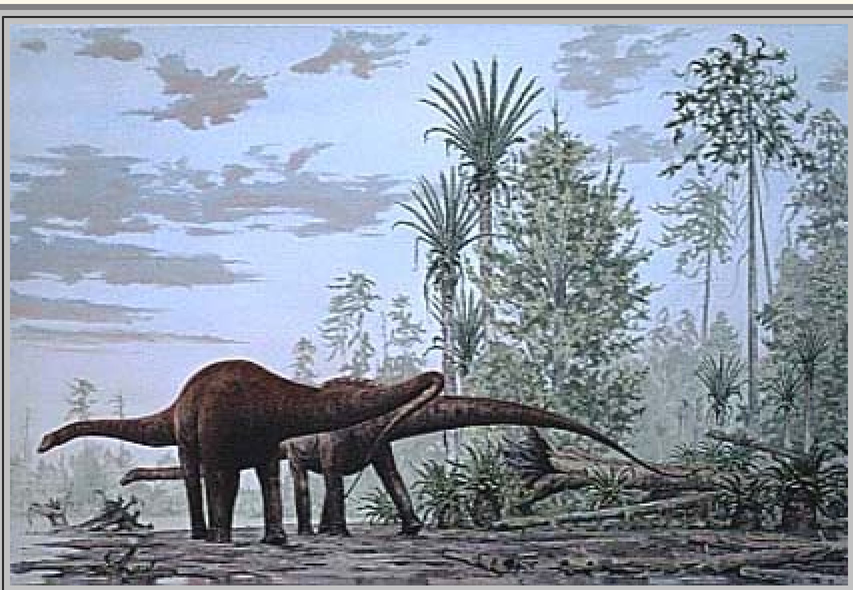
Introduction: Two Fossils from Patagonia

It wasn't more than a few years ago when all we knew of the protodinosaurs could, as with early hominine evolution, be housed in a single museum drawer. These scanty specimens belonged to two genera from the Middle Triassic of South America: *Lagerpeton* and *Marasuchus*. Six major phylogenetic groups (five clades and the basal archosauromorphs) converge here, revealing the density of the phylogenetic traffic at this crossroads. There are very few places like this in all of vertebrate phylospace. Two of the others are well-known landmarks: the radiations of the gnathostomes and the amniotes. Each of these represents some well-understood physiological transition which drove a radiation downstream from the first animals to achieve a particular set of (probably related) adaptations. We will make the case, largely based on the recent work of scientists like Hutchinson, Gatesy and Blob, that something almost as remarkable might have been at work in the re-engineering of the dinosauromorph hind limb. However, this seems simplistic. The pattern of cladogenesis is different here, perhaps more like the mammaliforms, which exhibited a kind of accellerating tendency to generate long-lived, rather unique groups of organisms over quite a long period of time, culminating in the Early Cenozoic radiation of the placental mammal (Eutherian) orders.

So much of this large-scale pattern-drawing could be an artifact of the spotty fossil record that it seems unwise to speculate much further. Still, there was something plainly remarkable going on. We can hope to gain some insight about that development by a more detailed study of these two fossil forms from Argentina. They are not so remarkable in themselves, but they do seem to be squarely at the epicenter of an evolutionary earthquake.

In the last few years however a number of exciting new discoveries have been made, which among other things have led to the naming of an entire new clade, the Silesauridae. As is typical in these situations, both further clarifies and further confuses (because the scrappy nature of some of the specimens) the situation. And the Triassic remains is one of those great unexplored wildernesses of tetrapod phylogeny. ATW020411, updated MAK120206

... and of course the Dinosaurs



Painting © Doug Henderson, reproduced with permission.

Probably no creatures that have lived upon this Earth have excited the imagination more than the Dinosauria. For some 150 million years they dominated ever medium to large to gigantic terrestrial vertebrate ecological niche, evolving into a wide range of forms and populating every continent.

Perhaps because they often had such bizarre forms, perhaps because they sometimes grew to such huge size, perhaps because after ruling this earth for so long they suddenly vanished, seemingly without a trace; all things add to the appeal of the Dinosauria in the popular -- and scientific! -- imagination.

As wonderful as the dinosaurs are, even these facts have to be qualified. True, many dinosaurs did have rather strange forms, but were they any stranger in appearance than, say, a giraffe or an elephant? True, many of them did grow to be quite large and even enormous, but no dinosaur ever rivalled even the smaller baleen whales in size. It would in fact be physiologically impossible for a land animal of more than 100 tonnes to exist (it's legs would have to be so massive they would touch, leaving no space for the body between!). So much for *Godzilla* and the dinosaurs of *One Million Years B.C.* (a cult film better known for a much smaller, but equally impressive, 60 kg and 180 cm Rachel Welch in a fur bikini) - such creatures belong to the realm of Hollywood fantasy. The majority of dinosaurs were actually medium-sized creatures, equivalent to modern medium to large mammals in size. Finally, as for dying out without a trace, this is also incorrect. One lineage of small insectivorous or /carnivorous dinosaurs did survive the great Mesozoic terminal extinction and are still with us today. They're called birds.

Some ecological niches the dinosaurs didn't invade. They never established themselves in the small terrestrial vertebrate niche (this was already taken over by mammals and lizards), nor (contrary to popular belief) did any of them ever adopt a marine or aquatic mode of life. They did however take over the air with style; and so successfully that their descendents are still the most numerous and diverse of the tetrapod (land-living vertebrates) even today. (MAK 010930)

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                     |==Herrerasauridae
                     |--SAUROPODOMORPHA
                     `--THEROPODA
```

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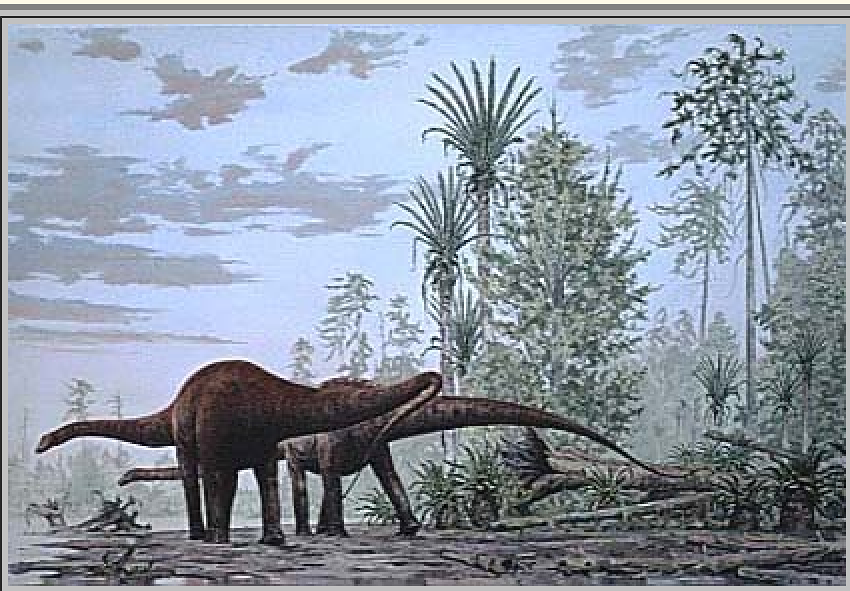
Introduction: The Dinosaurs



Painting © Doug Henderson, reproduced with permission.

Originally *Palaeos* had no dinosaur chapter as such, so the present admittedly brief unit was added as a place to introduce everyones' favorite multi-ton reptiles. Probably no creatures that have lived upon this Earth have excited the imagination more than the Dinosauria. For some 150 million years they dominated ever medium to large to gigantic terrestrial vertebrate ecological niche, evolving into a wide range of forms and populating every continent.

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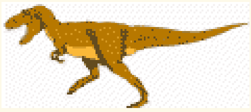
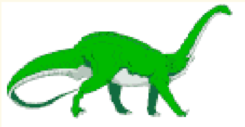
Dinosaur Groups

Traditionally, the dinosaurs were divided into two orders, depending on the structure of the hip bones. Those that had a reptilian-like pelvic bone were put in the Order Saurischia or "lizard-hips"; while the ones with a bird-like pelvic bone made up the Order Ornithischia or "bird-hips". (Paradoxically, it was from "lizard-hipped" and not the "bird-hipped" forms that birds evolved). This classification is still adhered to in some (especially older) popular and academic books, but has pretty much been rejected in favour of the cladistic interpretation.

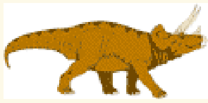
The earliest proto-dinosaurs **[1]** (basal Ornithodira) were a group of small early dinosaur-like archosaurs, known only from a few scrappy Argentinian fossils of Mid-Triassic age. These are neither saurischian nor ornithischian. These creatures, previously considered ornithosuchid thecodonts, are not even formally considered dinosaurs (although they are dinosauromorphs, which means dinosaurs and a few related forms more closely related to dinosaurs then to pterosaurs.). They are the stem forms from among which which the dinosaurs evolved. It has also for some years been felt that they are closely related to the Pterosaurs (flying reptiles). There is however a rival theory which derives the pterosaurs from prolacertiform "lizards," or perhaps even more distantly related stock.



The Saurischia or "lizard hipped" dinosaurs are those more closely related to birds than to *Triceratops*. Conventionally, they are divided in turn into two groups, one largely carnivorous, the other herbivorous. The first of these are the Theropoda, the bipedal carnivorous dinosaurs, with their bird-like legs and necks. Theropoda means "beast-feet", a rather inappropriate name; "bird(-like) feet" would have been better. Included in this huge and diverse group are both small forms (including the birds themselves) and large predators such as *Allosaurus* and *Tyrannosaurus*.



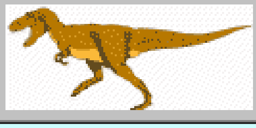
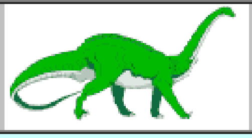
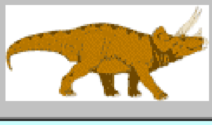
The other group of Saurischia, the Sauropodomorpha, were herbivores. There are two main subgroups, the Sauropoda (the inappropriately named "lizard-feet"), and their ancestors or uncles, the Prosauropoda ("before the sauropods"). Although the prosauropods were relatively small, the more advanced types, and all of the sauropods, were elephantine giants with tiny heads, very long necks and tails, massive bodies, and pillar-like legs. This group includes the famous "*Brontosaurus*" (or *Apatosaurus*) and its relatives. Like modern-day elephants, they relied on their great size as a defense against carnivores.



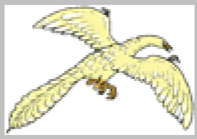
The Ornithischia ("bird hipped" dinosaurs), or Predentata (so called beacuse they posses a unique extra predentary bone in front of the jaw, which served as a sort of beak) were a more diverse group of herbivores. Being much smaller than the sauropods, they survived because they evolved various other means to avoid becoming fast food for their meat-eating theropod contemporaries. The ornithopods, for example, depended on fleetness of foot and acute sight and hearing. The Ceratopsian dinosaurs (*Triceratops*, etc) were the rhinoceroses of the dinosaur world, their formidable horns at least appear to be ample protection against even the largest and fiercest carnivores. There is a substantial body of opinion that these horns were more decorative than functional -- although we have probably not heard the end of this issue. The Stegosaurs and Ankylosaurs evolved armour plates, spikes, and tail-clubs as defensive and offensive weapons.

The Ornithischia -- unlike saurischian dinosaurs, reptiles and birds -- possessed mammal-like cheek muscles and cheek pouches to aid in chewing. In this respect they paralleled the mammalian form. Certainly, many Ornithischia filled ecological roles similar to those of the mammalian ungulates.

So we see among the dinosaurs the tendency towards both an *avimorphisation* or bird-form-tendency in the Theropods, and a *theromorphisation* or mammal-form-tendency) in the Ornithischia. The dinosaurs of the Mesozoic era in a sense presaged the birds and mammals of the Cenozoic era.

Dinosauromorpha	**Saurischia (Lizard Hipped dinosaurs)**		**Ornithischia (Bird Hipped dinosaurs)**
			
Lagosuchidae	**Theropoda**	**Sauropodomorpha**	**Predentata**

A word now about birds. Most palaeontologists and dino-enthusiasts today also consider the Birds to be a subgroup of dinosaurs. Cladistically (phylogenetically) speaking this is correct: birds evolved from dinosaurs, so if dinosaurs are to retain their monophyletic status they must include birds. MAK010930. Revised ATW050609.



Aves

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[1] The discussion here assumes a more or less conventional view of archosaur evolution. We are aware of unpublished work which might drastically alter this view. For both scientific and historical reasons, the data sets used to produce the present consensus tree of the archosaurs are weak. Some of those factors are discussed **elsewhere**. A complete restructuring of archosaur evolution, based on new data, is not at all out of the question.

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checked ATW030416

Dinosauromorpha

Abbreviated Dendrogram

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ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--PTEROSAURIA
   |
   `--DINOSAUROMORPHA
      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
            `--Dinosauria
               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
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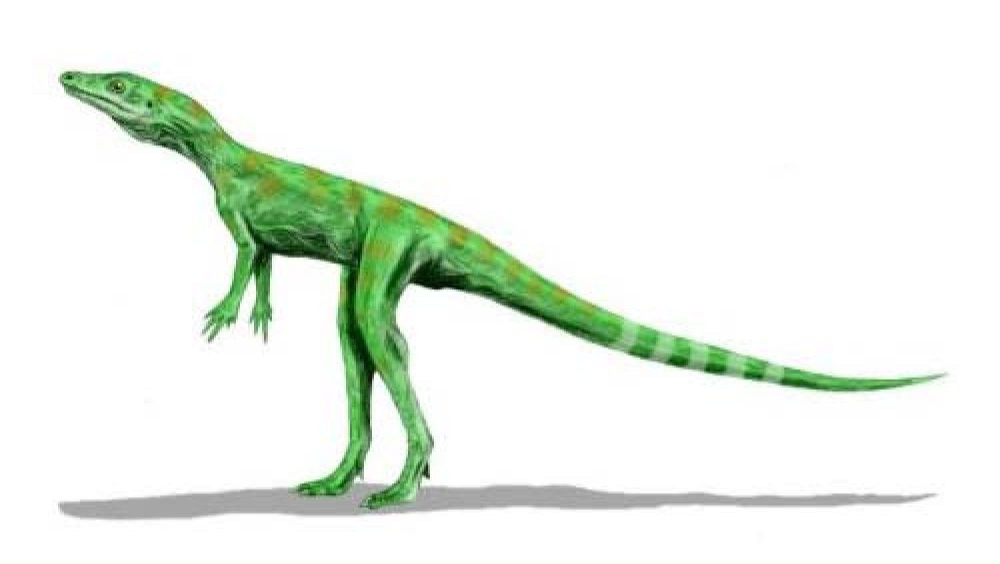
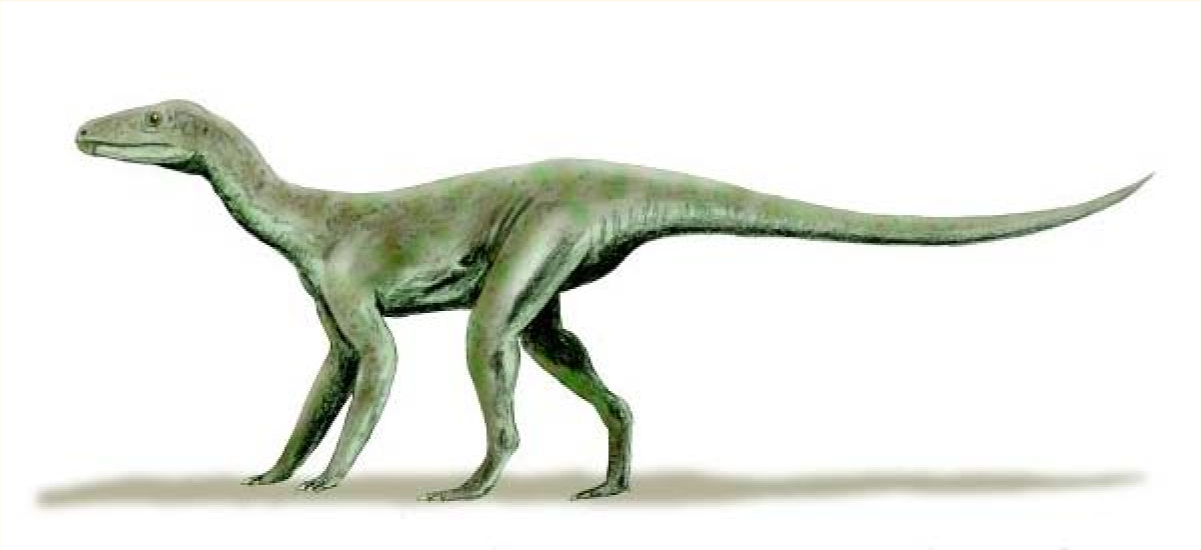
2. *Lagerpeton* X



Dromomeron romeri, a Lagerpetontid dinosauriform from the Late Triassic (Norian) of New Mexico. This animal, closely relate dto the earlier, South American

Lagerpeton, is one of a number of new discoveries that have shed light on the evolution of ornithodirans and the ancestry of dinosaurs
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike



The Silesaurid protodinosaur *Silesaurus oploensis*, from the Norian of Silesia, Poland. Length about 2.3 meters
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Evolution is an unbroken sequence. Bridging the divide between the thecodontian archosaurs and the first dinosaurs are a number of small, active, lightly built animals, the fossil remains of most of which have only come to light in the last few years. These are the protodinosaurs [1] or paleodinosaurs as Greg Paul refers to them in his early opus *Predatory Dinosaurs of the World* (although *Staurikosaurus* which he places in the paleodinosaurs is more properly included with the true dinosaurs). While very much playing second fiddle to their larger and more heavily built crurotarsan contemporaries, the little protodinosaurs would soon give rise to the true dinosaurs, and co-exist alongside them for at least ten million years or more. Their delicate bones would be less likely to be preserve than the heavy skeletons and armour plates of the large phytosaurs and aetosaurs, or the abundant remains of the traversodonts, dicynodonts, and replacing them, prosauropods. So it may well be that these little mesovertebrates were more common and diverse than they appear, and may have played an important role in Triassic terrestrial faunas. The fact that they flourished in a Norian world populated by herrerasaurid and coelophysid dinosaurs means that their extinction was not caused by competition with their very successful offspring, nor did they seme to have been discouriaged by sphenosuchid protocrocodiles, despite the latter being remarkably similar in size, build, and no doubt general appearance. It is more likely that were one of the many victims of the end-Triassic extinction event, although in view of the survival of sphenosuchians into the middle Mesozoic, it may well be that Jurassic protodinosaur remains may one day turn up. For now, these creatures remain one of the more intriguing of Triassic fuanas. MAK120206

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[1] Or, as they are more generally referred to, the dinosauriformes or dinosauromorphs. Technically these latter terms designate clades that include birds and dinosaurs *as well as* protodinosaurs. In order to emphasise the ancestral and transitional nature of these early animals, we have chosen to retain this paraphyletic term.

Descriptions

Dinosauromorpha: *Avipes*? Birds > pterosaurs.

Range: from the Middle Triassic.

Phylogeny: Ornithodira:: Pterosauria + *: *Lagerpeton* + Dinosauriformes.

Characters: Primitively, elongated rostrum & numerous small, serrated teeth; cervical column with a strong sigmoid curve; dermal scutes on dorsal midline; long legs (forelimb 50% or less hind limb length); hind-limb carried close to axis of body; inturned femoral head; advanced mesotarsal hinge with joint between astragalus-calcaneum unit and rest of foot; **$** astragalus with acute anteromedial corner; **$** articular surface of calcaneum for distal tarsals less than 35% of corresponding astragalar articular surface; **$** articular facet on distal tarsal 4 for metatarsal V reduced; "hooked" metatarsal V absent; **$** metatarsals I & V narrower than II-IV; probably habitually bipedal. **Note:** See image at Ornithodira. This image shows the ***primitive*** state. A dinosauromorph would lack the "hook" on metatarsal V, the calcaneum would be smaller relative to the astragalus, the astragalus would have a sharp corner on the lower left, and so on.

Links: dinosauromorpha; Reptilia.html; dinochar.htm; Marasuchus (formerly Lagosuchus); MEA 592D Dinosaur Osteology- Lecture 2; Selected characters for dinosaur groups discussed in this course ..; Dinosaur monophyly Fernando E. Novas, Journal of Vertebrate ..; Dinosaurier-Interesse - Glossar; GEOL 104 Lecture 14- The Origin of Dinosauria; アグノスフィティス·クロムハレンシス; Paleontologia de Argentina - Periodo Triasico. (**Best on the Web**).

Dinosauromorpha is a new site with considerable promise, but not much was posted when we visited (050828). The lecture notes at **Dinosaur Origins** and **MEA 592D Dinosaur Osteology- Lecture 2** have good, concise treatments of the ancestry and characters of the Dinosauromorpha; but no graphics. By contrast, **Microsoft PowerPoint - dinolec06.ppt** has all the slides, but no text to speak of. **Lec 6 Origin of Dinosauria** has a bit of both, but focuses on the Dinosauria, rather than their ancestors. **Wat is een dino I (moeilijk)** is a Dutch translation of an article I wrote a number of years ago focusing on mechanics. I think the English version has (fortunately) been lost. Most of the article was derived from the work of John Hutchison. This, and much more besides, can now be found directly at **Adductors, abductors, and the evolution of archosaur locomotion**, **The evolution of femoral osteology and soft tissues on the line to ...**, **The evolution of pelvic osteology and soft tissues on the line to ..**, and **PII- S1095-6433(02)00158-7**.

References: Arcucci (1997); Fastovsky & Weishampel (1996); Novas (1996); White (2001). ATW050828.

***Lagerpeton*:**

Range: mT of SAm.

Phylogeny: Dinosauromorpha: Dinosauriformes + *.

Characters: Small (<1m, ~500g), unspecialized ornithodire. Posterior dorsal vertebrae with anteriorly inclined spines; hip generally primitive, wide and short; ilium has wavy dorsal margin; large pubioischiadic "obturator"-type process; femur with square, flat anteromedial surface; astragalus with tongue-shaped posterior ascending process; astragalus and calcaneum co-ossified in adult; digits I & V strongly reduced; digit IV extends further than III; functionally didactyl foot (saltatorial?).

Links: **DinoData: Lagerpeton**; Lagerpeton -- The Dinosauricon; dinosauromorpha.

References: Arcucci (1997). 010324.

Dinosauriformes

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```
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      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
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               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
```

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1. Dinosauriformes
2. Lagosuchidae X

Lagosuchus talampayensis (= *Marasuchus*), Ladinian of South America,

reconstruction based on Bonaparte, 1975
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Descriptions

Dinosauriformes: *Lewisuchus* (= *Pseudolagosuchus*).

Range: fr mT.

Phylogeny: Dinosauromorpha: *Lagerpeton* + *: Lagosuchidae + (Silesauridae + Dinosauria).

Characters: shortened forelimbs; **$** at least partially perforated acetabulum (??); enlarged supraacetabular ridge; primitively, acetabulum remained relatively large compared to femoral head; **$** antitrochanter on posterior wall of acetabulum (primitively small); **$** extension of femoral articular surface under head of femur (?); **$** proximal femur with fossa trochanterica and trochanteric shelf; **$** anterior (lesser) trochanter on femur; **$** trochanteric shelf on proximal femur; **$** cnemial crest present on proximal tibia; **$** quadrangular distal tibia with lateral longitudinal groove; **$** posterior flange on the distal end of tibia.

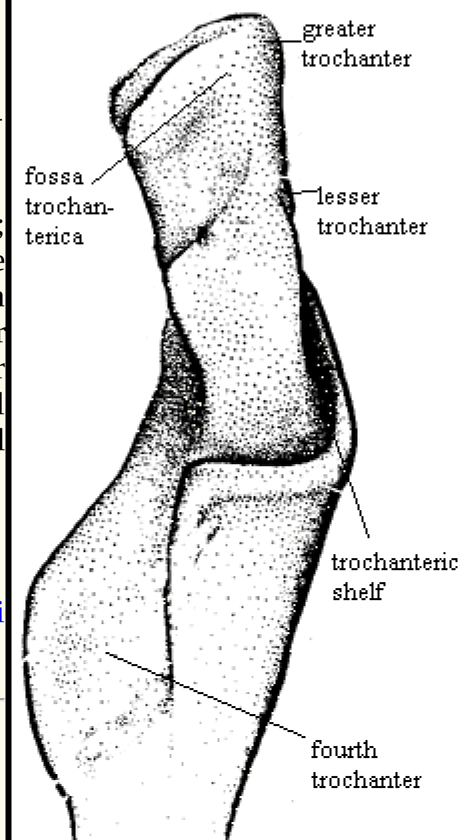


Figure 3. Marasuchus upper femur in posteromedial view.

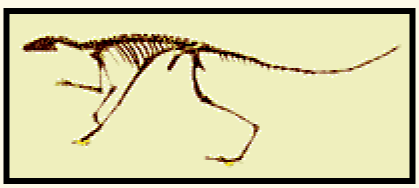
Links: Untitled Document; Dinosaur Monophyly; Dinosaurian Precursors.

References: Hutchinson & Gatesy (2000); Novas (1996); Sereno & Arcucci (1994). 010323.

Lagosuchidae: *Marasuchus* (= *Lagosuchus*).

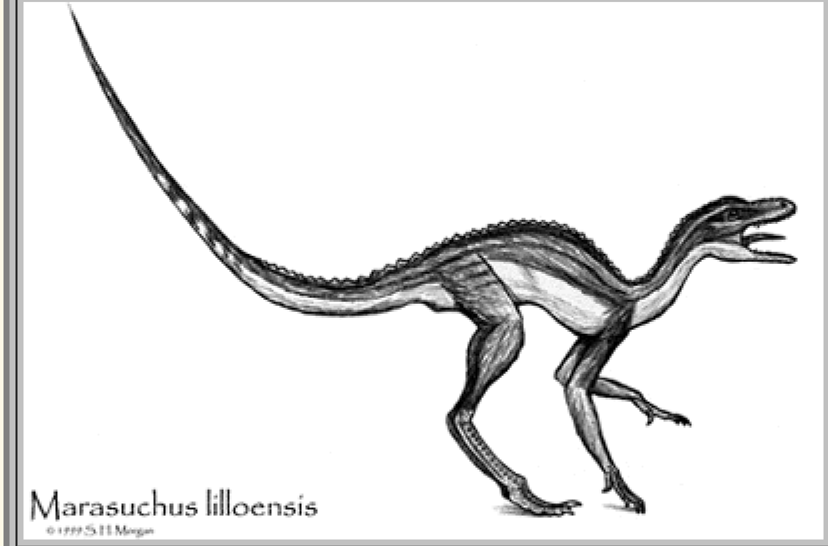
Range: mT of SAm.

Phylogeny: Dinosauriformes: (Dinosauria + Silesauridae) + *.



Characters: Small (<0.5m), gracile, bipedal proto-dinosaurs. Elongated snout with numerous, small teeth; long, S-shaped neck; vertebrae sharply regionalized (i.e. cervical, ant. dorsal, post. dorsal, & caudal); spines of dorsal vertebrae may incline anteriorly (said to be associated with saltatorial habit); acetabular fenestration minor or absent; posterior limbs much longer than anterior; tibia longer than femur; head of femur points toward midline, but femur may be somewhat sigmoid (*Lagerpeton*); fibula reduced sharply, limiting rotation at knee; calcaneum reduced relative to astragalus; calcaneal heel absent; dinosaur-like mesotarsal hinge between astragalus & calcaneum and between proximal and distal tarsals; but proximal tarsals not integrated with crus; metatarsals II-IV very long & closely appressed; 5th digit not hooked; fully erect posture; very likely obligate bipeds; may have line of dorsal scutes.

Discussion: The literal meaning of "lagosuchid" is, as Robert Bakker is fond of pointing out, "rabbit-croc." It would be interesting to know if they were actually saltorial, that is jumpers, like rabbits. The ability to use jumping as a routine means of locomotion leaves its mark on the skeleton, but the indications in the Lagosuchidae are ambiguous. Some common indications of a jumping animal are as follows:



Marasuchus lilloensis © 1999 by SH Morgan. Used by permission.

1) elongation and fusion of the phalanges (toe bones) and metatarsals (foot bones). Here, the toes and metatarsals are quite long, but there is no evidence of fusion.

2) hind limbs 2-4 times as long as front limbs. Lagosuchids are marginal.

3) center of gravity shifted posteriorly. Its hard to tell from skeletal remains alone. Perhaps the answer is "somewhat." The pelvis, in particular, suggests a design which maximizes the amount of posterior mass. However, this is not nearly the same degree of back-heaviness seen in a frog, rabbit, or kangaroo.

4) small head or stiffened or fused cervical spine. The head is not well known for any lagosuchid. *Marasuchus*, at least seems to have had a relatively small head and the cervical vertebrae are notably longer and deeper than the dorsal vertebrae, suggesting that the neck was less laterally flexible and may have been tightly bound with tendons. This impression is reinforced (as was the neck) by the presence of fairly long cervical ribs.

On the whole it seems likely that Lagosuchids were accomplished jumpers, although perhaps not as specialized for this locomotor style as rabbits. A reasonable speculation might be that they were ambush predators who used a leaping attack, but did not use repeated jumping in routine locomotion. The latter style is referred to as "ricochetal." The efficiency of ricochetal locomotion (which is very high) depends on the ability to store the kinetic energy of one leap and to use that energy to take off on the next leap. This is typically accomplished by stretching stiff tendons in the leg or foot on landing, or deforming bone, which "snaps back" to act as a propulsor on the next jump. There is no obvious sign that the lagosuchids possessed such a mechanism, although it might be very difficult to determine its presence or absence from skeletal remains alone. Given recent work on the origin of powered flight, the answers to these questions may be of more than casual interest. (ATW 000830)

Links: DinoData: Lagosuchidae; dinosauromorpha; Dinosaurian Precursors; Marasuchus -- The Dinosauricon.

References: Arcucci (1997); Carroll (1988); Garner *et al*. (1999); Padian (1997). 000829.

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checked ATW031023, page last modified MAK120206

Silesauridae

Abbreviated Dendrogram

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         |--Lagosuchidae
         `--+--Silesauridae
            |  |--Lewisuchus
            |  `--+--Asilisaurus
            |     `--+--Sacisaurus
            |        `--Silesaurus
            `--+--Silesauridae
               `--Dinosauria
                  |--ORNITHISCHIA
                  `--Saurischia
                     |--SAUROPODOMORPHA
                     `--THEROPODA
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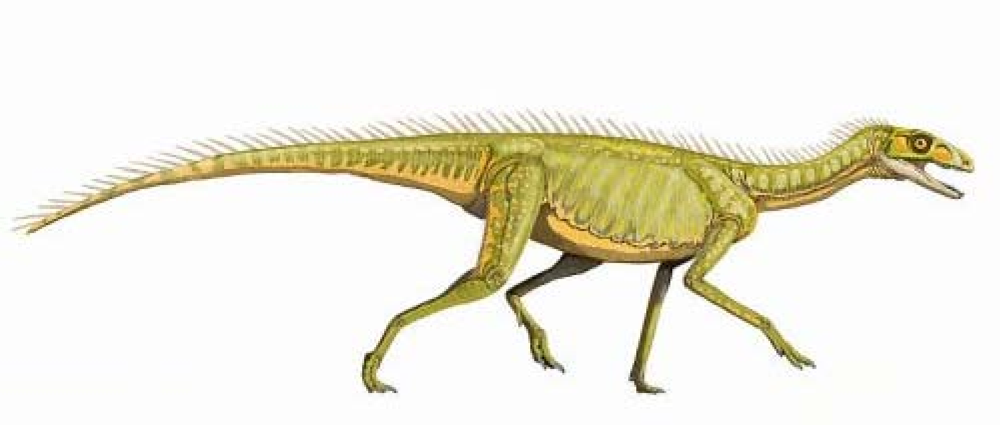
1. Silesauridae X

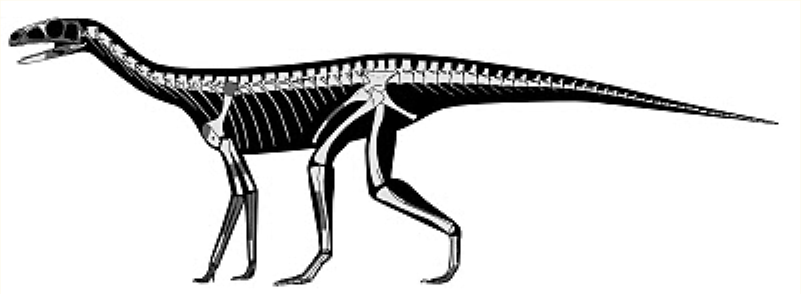


The protodinosaur *Silesaurus oploensis*, from the Norian of Silesia, Poland
Artwork by Dmitry Bogdanov, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

The Silesauridae are one of those groups that were unknown even just ten years ago, showing that paleontology, like science in general, is always full of new discoveries. They show that protodinosaurs were far more widespread and diverse than had previously been thought. The earliest, but not the most basal, of the silesaurids, *Asilisaurus*, lived as long ago as the Anisian (Nesbitt et al 2010). Some taxa previously included among the ornithischia, such as *Technosaurus*, have since been relocated here. Like other protodinosaurs, these were small, lightly built animals, about one and a half meters in length. They seem to have been mostly quadrapedal. Although considered the sister grpoup to dinosaurs, rather than actual ancestors, at least one genus, the herbivorous The well-preserved jaw indicates that *Sacisaurus* posesses a process at the tip that resembles the ornithischian predentary bone. Whether this is the result of homoplasy (convergence) or homology (common ancestry) will determine whether this taxon should be reassigned to the ornithischia, although in other respects it resembles Silesaurids such as *Diodorus* (Kammerer et al 2011). Alternatively, the ornithischian-saurischian split might be pushed back to the Silesauridae, which means the group itself might also be paraphyletic, or at least need redefining as several smaller monophyletic clades.

Descriptions

***Silesauridae*:** *Asilisaurus*, *Eucoelophysis*, *Silesaurus*, *Lewisuchus* (= *Pseudolagosuchus*), *Technosaurus*, and possibly *Diodorus* and *Sacisaurus*



Skeletal reconstruction of *Asilisaurus*, with missing bones in gray. Image by S. Nesbitt. Copied from Chinlea

Range: mT to lT (Anisian to Norian) of SAm, Afr, .

Phylogeny: Dinosauriformes **:** + Lagosuchidae + (Dinosauria + *.)

Comments: "Named in 2010 by paleontologist Max C. Langer and colleagues from Brazil and Argentina. They defined it as a branch-based clade of all archosaurs closer to Silesaurus opolensis than to either Heterodontosaurus tucki or Marasuchus lilloensis. At the same time, a second group of scientists independently named Silesauridae as a node-based clade consisting of Lewisuchus, Silesaurus, their common ancestor and all its descendants. (Nesbitt et al 2010) Currently, both definitions encompass the same group of animals." - Wikipedia.

References: Kammerer et al 2011, Langer et al 2010, Nesbitt et al., 2011.

Dinosauria

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--PTEROSAURIA
   |
   `--DINOSAUROMORPHA
      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
            `--Dinosauria
               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
```

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2. Saurischia

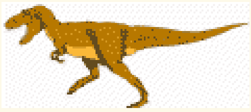
One of the most iconic and dramatic images of scenes from deep time ever produced; Charles R. Knight's painting of the face off between the elephant-sized horned *Triceratops horridus* and its nemesis, the apex predator *Tyrannosaurus rex*.
Image from The World of Charles R. Knight

One of the most successful lifeforms to inhabit the surface of the Earth, the dinosaurs dominated all medium to large terrestrial herbivore, omnivore, and carnivore niches and guilds for some 150 million years, were an important component of small terrestrial vertebrate fauna for the same period, as well as including the largest land animals ever to live, as well as being by far the most successful of the three clades of vertebrates that achieved powered flight and by far the most diverse and important aerial vertebrates for 130 odd million years. (yes,birds are dinosaurs, cladistically speaking!) MAK120206

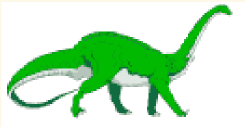
Dinosaur Groups

Traditionally, the dinosaurs were divided into two orders, depending on the structure of the hip bones. Those that had a reptilian-like pelvic bone were put in the Order Saurischia or "lizard-hips"; while the ones with a bird-like pelvic bone made up the Order Ornithischia or "bird-hips". (Paradoxically, it was from "lizard-hipped" and not the "bird-hipped" forms that birds evolved). This classification is still adhered to in some (especially older) popular and academic books, but has pretty much been rejected in favour of the cladistic interpretation.

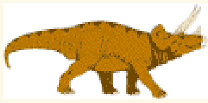
The earliest proto-dinosaurs **[1]** (basal Ornithodira) were a group of small early dinosaur-like archosaurs, known only from a few scrappy Argentinian fossils of Mid-Triassic age. These are neither saurischian nor ornithischian. These creatures, previously considered ornithosuchid thecodonts, are not even formally considered dinosaurs (although they are dinosauromorphs, which means dinosaurs and a few related forms more closely related to dinosaurs then to pterosaurs.). They are the stem forms from among which which the dinosaurs evolved. It has also for some years been felt that they are closely related to the Pterosaurs (flying reptiles). There is however a rival theory which derives the pterosaurs from prolacertiform "lizards," or perhaps even more distantly related stock.



The Saurischia or "lizard hipped" dinosaurs are those more closely related to birds than to *Triceratops*. Conventionally, they are divided in turn into two groups, one largely carnivorous, the other herbivorous. The first of these are the Theropoda, the bipedal carnivorous dinosaurs, with their bird-like legs and necks. Theropoda means "beast-feet", a rather inappropriate name; "bird(-like) feet" would have been better. Included in this huge and diverse group are both small forms (including the birds themselves) and large predators such as *Allosaurus* and *Tyrannosaurus*.



The other group of Saurischia, the Sauropodomorpha, were herbivores. There are two main subgroups, the Sauropoda (the inappropriately named "lizard-feet"), and their ancestors or uncles, the Prosauropoda ("before the sauropods"). Although the prosauropods were relatively small, the more advanced types, and all of the sauropods, were elephantine giants with tiny heads, very long necks and tails, massive bodies, and pillar-like legs. This group includes the famous "*Brontosaurus*" (or *Apatosaurus*) and its relatives. Like modern-day elephants, they relied on their great size as a defense against carnivores.

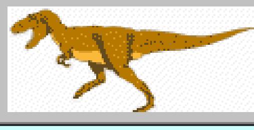
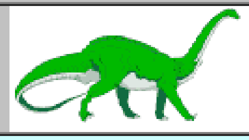
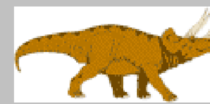


The Ornithischia ("bird hipped" dinosaurs), or Predentata (so called beacuse they posses a unique extra predentary bone in front of the jaw, which served as a sort of beak) were a more diverse group of herbivores. Being much smaller than the sauropods, they survived because they evolved various other means to avoid becoming fast food for their meat-eating theropod contemporaries. The ornithopods, for example, depended on fleetness of foot and acute sight and hearing. The Ceratopsian dinosaurs (*Triceratops*, etc) were the rhinoceroses of the dinosaur world, their formidable horns at least appear to be ample protection against even the largest and fiercest carnivores. There is a substantial body of opinion that these horns were more decorative than functional -- although we have probably not heard the end of this issue. The Stegosaurs and Ankylosaurs evolved armour plates, spikes, and tail-clubs as defensive and offensive weapons.

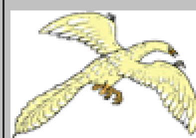
The Ornithischia -- unlike saurischian dinosaurs, reptiles and birds -- possessed mammal-like cheek muscles and cheek pouches to aid in chewing. In this respect they paralleled the mammalian form. Certainly, many Ornithischia filled ecological roles similar to those of the mammalian ungulates.

So we see among the dinosaurs the tendency towards both an *avimorphisation* or bird-form-tendency in the

Theropods, and a *theromorphisation* or mammal-form-tendency) in the Ornithischia. The dinosaurs of the Mesozoic era in a sense presaged the birds and mammals of the Cenozoic era.

Dinosauromorpha	Saurischia (Lizard Hipped dinosaurs)		Ornithischia (Bird Hipped dinosaurs)
			
Lagosuchidae	Theropoda	Sauropodomorpha	Predentata

A word now about birds. Most palaeontologists and dino-enthusiasts today also consider the Birds to be a subgroup of dinosaurs. Cladistically (phylogenetically) speaking this is correct: birds evolved from dinosaurs, so if dinosaurs are to retain their monophyletic status they must include birds. MAK010930. Revised ATW050609.



Aves

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[1] The discussion here assumes a more or less conventional view of archosaur evolution. We are aware of unpublished work which might drastically alter this view. For both scientific and historical reasons, the data sets used to produce the present consensus tree of the archosaurs are weak. Some of those factors are discussed **elsewhere**. A complete restructuring of archosaur evolution, based on new data, is not at all out of the question.

Descriptions

Dinosauria: *Eoraptor*. LCA birds & *Triceratops*.

Range: fr mT.

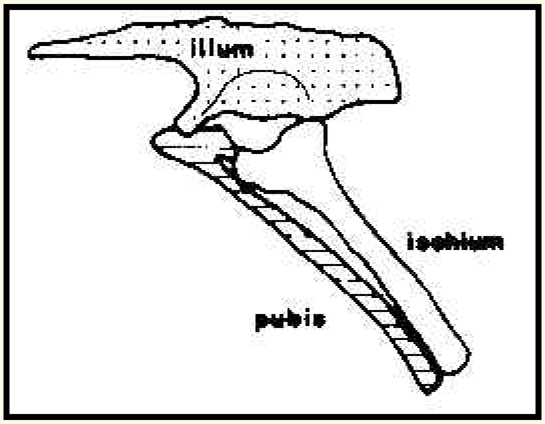
Phylogeny: Dinosauriformes: Lagosuchidae + (Silesauridae + *: Ornithischia + Saurischia.)

Characters: Ectopterygoid lateral to transverse flange of pterygoid; **$** postfrontal absent; **$** temporal muscles extend anteriorly onto skull roof; quadrate head laterally exposed; S-shaped neck; dorsal vertebrae shorter; **$** at least 3 fully incorporated sacral vertebrae (with 3rd incorporated from dorsal vertebrae); forelimb < 50% length of rear (reversals in several groups); deltopectoral crest extends further down humerus; **$** humerus with elongate deltopectoral crest; manus 4 with <4 phalanges; claws on 1-3 only; semi-perforate (usually fully perforated) acetabulum with buttress; brevis shelf on ilium; ischium with obturator process restricted to anterior 1/3rd; **$** femur with ball-like head; medial tuberosity of femur reduced; shaft of femur straight or bowed anteriorly; femur vertical; femur has greater, lesser & 4^{th} trochanters; **$** tibia with cnemial crest; **$** well-developed ascending process of astragalus on anterior face of tibia; **$** calcaneum with concave surface for articulation of fibula; metatarsals elongate and function as part of pes.

Links: **DINODATA**; The Dinosauria; Dinosaur Links (links to many significant sites); Dinosaur Paleontology (more); The Dinosauricon; Dinosauria On-Line; Dinosauria; National Museum of Natural History - Dinosaur Exhibits; Dino Russ's Lair; Paul Sereno's Dinosaur Web Site; Dinosaur evolution title page; Dinorama @ nationalgeographic.com; The Unnatural Museum - Dinosaur Safari (a good, often overlooked, site); Discovery Channel: Walking With Dinosaurs; New Scientist | The Rex Files | Everything you wanted to know about dinosaurs; Zoom Dinosaurs - EnchantedLearning.com; Dann's Dinosaur Reconstructions; Dinosauri - by MediaSoft; Royal Tyrrell Museum Tour: The Origin of Dinosaurs; Archives of the DINOSAUR Mailing List.

Discussion: The limiting factor is that muscles contract only about 30% of their length. Increasing muscle length therefore increases motion of the bone.

Tetrapod Model: Simple, tri-radiate structure. Pubis, ileum & ischium meet at Y-shaped junction. Acetabulum located at the junction, and head of femur extends outward at 90° along its long axis. *Protraction*: Pubis extends antero-ventrally. Muscles insert on femur (pubofemoral) and protract (forward) it . *Retraction*: Tail (and/or ischium?) extends posteriorly and retract femur (caudofemoral). *Abduction*: Ileum extends posteriorly and muscles inserting on femur abduct it towards mid-line. Basic Tetrapod pelvis is plate-like. Extensions of pelvic bones are relatively small, and ileum articulates with only 1-2 vertebrae in sacrum. Muscles to pubis and ischium extend ventrally, countered to some extend by iliofemoral muscles.



The Problem: As the femur rotated downwards to become more vertical, the length of the muscle running from the pubis and ischium shortened relative to the length of the femur.

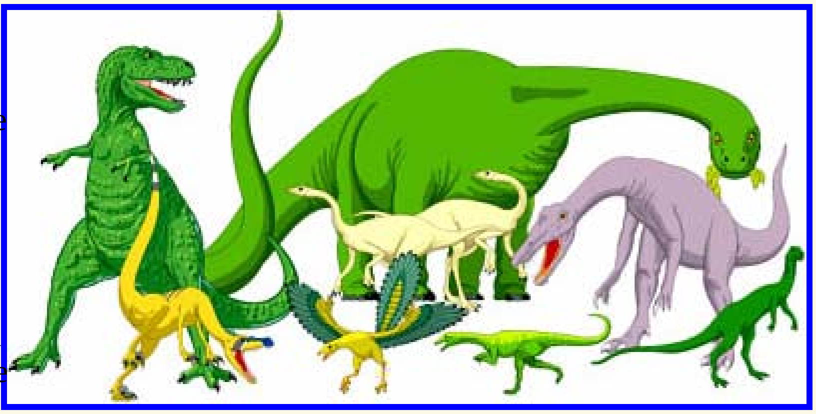
The Solutions: Open acetabulum with bracing dorsally. *Saurischians*: extended pubis & ischium and rotated pubis antero-dorsally. Early ornithischians retroverted pubis (parallel to ischium) and protracted femur by attachment to anterior extension of ileum (see image). Later ornithischians secondarily developed an anterior projection of the pubis, as well as retaining the retroverted shaft.

References: Benton (1997); Hutchinson & Gatesy (2000); Novas (1996); White (2001). 010324.

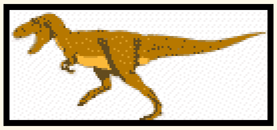
Saurischia: All dinosaurs closer to birds than to *Triceratops*.

Range: from Middle Triassic.

Phylogeny: Dinosauria: Ornithischia + *: Sauropodomorpha + Theropoda.



Introduction: The Saurischia or "lizard hipped" dinosaurs are conventionally divided in turn into two groups, one carnivorous, the other herbivorous. The first of these are the Theropoda, the bipedal carnivorous dinosaurs, with their bird-like legs and necks. Theropoda means "beast-feet", a rather inappropriate name; "bird(-like) feet" would have been better. Included in this huge and diverse group are both small forms (among them the ancestors of birds) and large predators such as *Allosaurus* and *Tyrannosaurus*.



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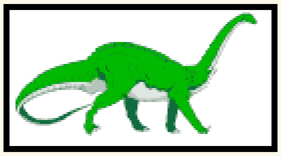

Characters: No contact between maxillary process of premaxilla and nares; **$** subnarial foramen; antorbital fenestrae; **$** forked post process of jugal; **$** jugal overlaps laterally onto lacrimal; temporal musculature extends into frontals; neck elongated & S-shaped; posterior cervical vertebrae elongated; **$** axial postzygapophyses lateral to prezygapophyses; trunk vertebrae have accessory articulations; enlarged manus I; metacarpal I short, robust, & has 2 asymmetrical distal condyles so that digit is set off at an angle (the "grasping hand"); manus III longest (hand characters would exclude Herrerasauridae); **$** ischium with rod-like shaft; pubis points forward (propubic); wedge-shaped ascending process of astragalus.

Links: anatomy; The Saurischia; Saurischian Dinosaurs - Enchanted Learning Software. 010708.

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Dinosauria: Dendrogram

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--PTEROSAURIA
   |
   `--DINOSAUROMORPHA
      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
            `--Dinosauria
               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
```

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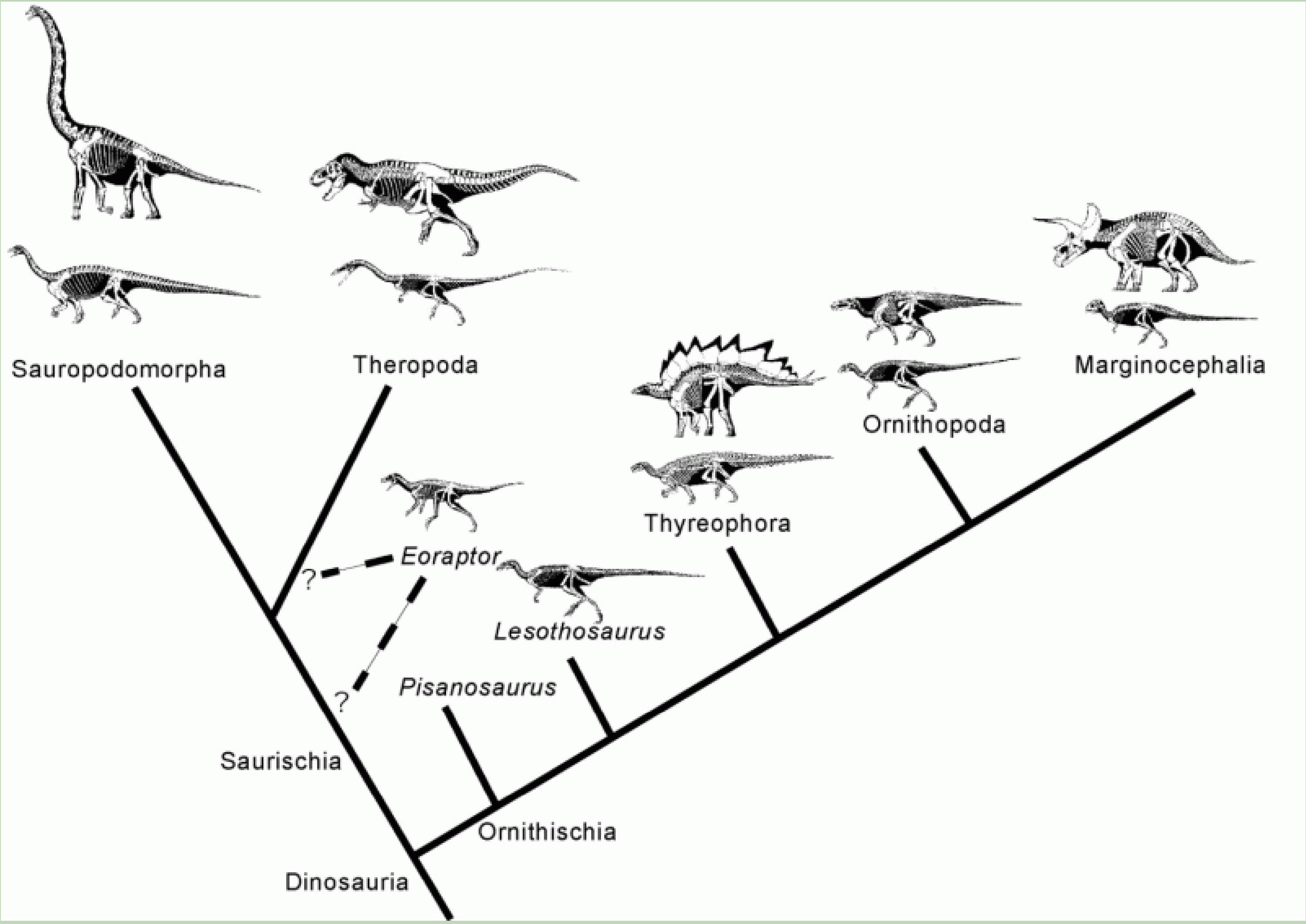
Dendrogram



Cladistics would probably have remained an obscure scientific methodology had it not been for its appropriation by dinosaur-loving paleo geeks the world (and world wide web) over. A simple google image search will return hundreds of hits. Historically, dinosaur cladistics derives from a seminal paper by Jacques Gauthier (Gauthier (1986)); more recently, other professional paleontolgists such as Tom Holtz have helped popularise and explain the subject.

Here we also need to distinguish between cladograms proper, which are diagrammatic representations of phylogenetic hypotheses, in which each terminal node represents a species, and dendrograms which are more generic tree-like diagrams, in which terminals include supra-specific taxa, species and higher ranks are combined, and/or a number of cladograms are mashed together. Unfortunately, these two terms are almost always conflated, even by professionals.

The above dendrogram shows the cladistic relationship of the dinosaurs, from Holtz's GEOL 104 Dinosaurs: A Natural History course notes (see Rise of the Dinosaurs). Each of the major clades are also illustrated by one or two silouettes and skeletal illustrations a la Greg Paul (where two illustrations are shown, the lower one is the more basal). The phylogenetic position of *Eoraptor* (and the Herrerasaurs) is uncertain; we have suggested here that the Herrerasaurs constitute a paraphyletic assemblage of early forms. See also UK Dinosaurs for a dinosaur supertree, dated 2001, thus predating the first peer review published supertree (Pisani et al (2002)). There uis also an updated version in both circular and stratigraphic format.

Mickey Mortimer (The Theropod Database) has created an amateur a giant ascii dendrogram of the theropods and a somewhat smaller one of the Sauropodomorpha, inspired by Mike Keesey's much missed Dinosauricon site. while the the Open Dinosaur Project gives a 2010 cladogram of selected basal archosaurs, dinosauromorphs (protodinosaurs), basal saurischia, and ornithischia. General comments, with hyperlinked taxa, can be found on Wikipedia (along with a basic bubble diagram version). MAK120206

Dinosauria: References

Abbreviated Dendrogram

```
ARCHOSAURIA
|--CROCODYLOMORPHA
`--+--PTEROSAURIA
   |
   `--DINOSAUROMORPHA
      |--Lagerpeton
      `--Dinosauriformes
         |--Lagosuchidae
         `--+--Silesauridae
            `--Dinosauria
               |--ORNITHISCHIA
               `--Saurischia
                  |--SAUROPODOMORPHA
                  `--THEROPODA
```

Contents

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Dinosauromorpha, *Lagerpeton*, Lagosuchidae.

Benton, MJ (1997), *Origin and early evolution of Dinosaurs,* in JO Farlow & MK Brett-Surman, **The Complete Dinosaur**. Indiana Univ. Press, pp. 204-215.
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Dinosauria; Dinosauriformes.

Christian F. Kammerer, Sterling J. Nesbitt, and Neil H. Shubin (2011) The first basal dinosauriform (Silesauridae) from the Late Triassic of Morocco. Acta Palaeontologica Polonica (in press) doi:10.4202/app.2011.0015
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Dinosauria, Dinosauromorpha.

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Ornithischia: Overview

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Fabrosauridae
`--+--Thyreophora
   |  |--Stegosauria
   |  `--Ankylosauria
   `--Cerapoda
       |--Ornithopoda
       |  |==Hypsilophodontidae
       |  `--Hadrosauridae
       `--+--Heterodontosauridae
          `--Marginocephalia
             |--Pachycephalosauria
             `--Ceratopsia
```

Contents

The Predentata or Ornithischia are a very diverse group of dinosaurs distinguished by their bird-like hip bones and the presence of an extra bone (the *predentary*) in the front of the low jaw (hence the two names for them - "Ornithischia" is the older name). Many types evolved ungulate (hoofed) mammal-like features like elaborate batteries of chewing teeth, and horns and other types of crests and head ornaments (used not so much against predators as in intra-specific rivalry - competition for mates, etc).

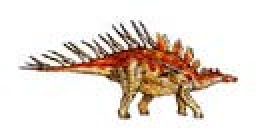
Originally only four suborders were distinguished - Ornithopoda, Stegosauria, Ankylosauria, and Ceratopsia. More recently some of these groups have been shown to be related and hence united under larger sub-ordinal groups, while new groups are also required by modern discoveries.

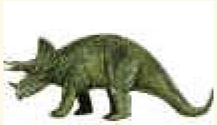
The base of the Ornithischia, like the base of many other big groups, is a mess of poorly known specimens which are impossible to classify with much accuracy. In the case of the Ornithischia, this group is known collectively as the Fabrosauridae. In addition, the three main (large) clades of Ornithischian (Predentata) dinosaurs are the:

1) Thyreophora or armoured dinosaurs, including stegosaurs and ankylosaurs.
2) Ornithopoda or mostly bipedal, typical plant-eaters: hypsilophodonts, iguanodonts and hadrosaurs.
3) Marginocephalia or horned and bone-head forms: pachycephalosaurs, psittacosaurs and ceratopsians.

Here is another, slightly more detailed breakdown, in the form of a cladogram with some synapomorphies (unique characters) of each group:

Ornithischia





```
|--"Fabrosaurs"  paraphyletic: no synapomorphies
`--Genasauria  cheeks
   |--Thyreophora  armor
   |  |--Stegosauria   armor as plates covering back
   |  `--Ankylosauria  armor as spikes or plates
   `--Cerapoda  uneven enamel
      &|--Ornithopoda  jaw
joint below tooth row
      |   |--Heterodontosaurus
elongate hands
      |   `--+-
-Hypsilophodontidae  ridge on
teeth
      |      `--+--Iguanodontidae  thumbs spike-like
      |         `--Hadrosauridae laterally expanded distal rostrum ("duck bill")
      `--Marginocephalia  back part of skull makes shelf
         |--Pachycephalosauria  domed head
         `--Ceratopsia  rostral bone
            |--Psittacosauridae reduced hands
            `--Neoceratopsia "frill"
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We will discuss the fabrosaurs and each of the principle groups in more detail below. MAK000117.

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Ornithischia

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--SAUROPODOMORPHA
|  `--THEROPODA
|
ORNITHISCHIA
|--Pisanosaurus
`--+--Eocursor
   |--Fabrosauridae (Lesothosaurus)
   `--Genasauria
      |--Thyreophora
      |  |--Stegosauria
      |  `--Ankylosauria
      `--Agilisaurus
         `--+--Cerapoda
            |--Ornithopoda
            |  |==Hypsilophodontidae
            |  `--Hadrosauridae
            `--+--Heterodontosauridae
               `--Marginocephalia
                  |--Pachycephalosauria
                  `--Ceratopsia
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2. *Eocursor* X
3. Fabrosauridae (*Lesothosaurus*) X
4. Genasauria X
5. Ornithischia X

Pisanosaurus

"Fabrosauridae" and Other Basal Ornithischians

The cladistic paradigm has meant these early types have been stuck as "outgroups" with no Linnean status beyond family level. Since these early groups differ at least as much as the later ones I decided to take matters into my own hands and christen a new suborder [Stanley Friesen's Dinosaur classification follows a similar tack].

Fabrosauria - small early ancestral forms - active fast-running lightly-built bipeds, paraphyletic and ancestral to all other Ornithischian lineages, Late Triassic to Early Jurassic - length about a metre. This isn't shown on our cladogram for the obvious reason that it isn't a clade. It collectively refers to things like *Lesothosaurus* and *Agilisaurus*. These actually may form a monophyletic group, the Fabrosauridae. In addition, it would include the South American *Pisanosaurus*, which is probably not a fabrosaurid. (MAK000117 & ATW020420)

The most basal, generally recognized clade is **Genasauria**. Genasauria is defined as the last common ancestor of Thyreophora and Cerapoda and all of its descendants. The thyreophorans are the armored ornithischians: the stegosaurs and ankylosaurs. The cerapods include both the hadrosaur-like forms and the line which includes both *Triceratops* and the bone-headed Pachycephalosauria. In short, Genasauria includes all of the major Ornithischian groups.

The most important unique characteristic of the group is the inset tooth row. That is, the teeth are not located in the same plane as the sides of the skull. Instead, they are moved in close together, toward the center line. The functional significance of this structure is the advantage it gives to a plant-eater. Herbivores on the model of a sauropod, or even an aetosaur, gulp masses of vegetation. However, leaves, stems and seeds are tough stuff, and chemically hard to digest. This kind of herbivory requires an enormous amount of internal processing, which means carrying around grinding stones in the gut (gastroliths) and a big fermentation vat for chemical decomposition. The simple adaptation involved in putting the teeth close together, combined with more teeth and articulating dentition (teeth which are in contact when the mouth is closed and thus cut or crush food between opposing jaws) allows the animal to cut plant food up into tiny bits and crush the juices out of leaves and fruit. This, in turn allows it to do without gastroliths (intestinal rocks for cutting up bulk vegetation), and also to reduce the size of the fermentation area for chemical digestion. Since the pieces swallowed are small, they have a greater surface area per unit volume and can be attacked more quickly by digestive enzymes. This huge gain in efficiency translates into an ability to be more selective about food, to move faster or to carry armor, to spend more time on mate selection or in rearing young. Quite possibly, this simple anatomical change was ultimately responsible for the worldwide relative decline of the sauropods and the extinction of the prosauropods by the Late Jurassic.

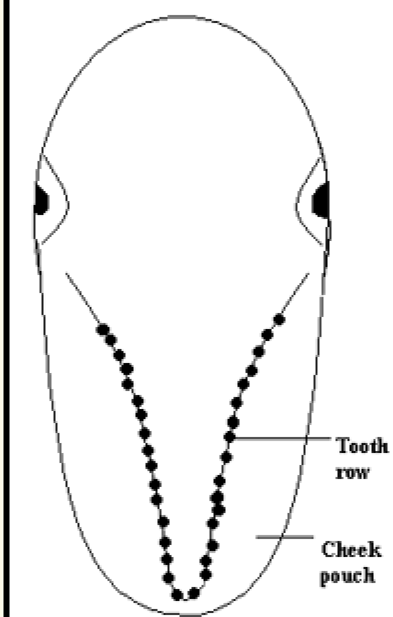

Fig. 1 Generalized genosaur skull in palatal view, showing inset tooth row.

Of course, narrow jaws are not enough. Other changes were important. For example, if the teeth were merely moved inward, plant material might simply fall out the sides as the dinosaur chewed -- hugely wasteful as well as frustrating. The narrowing of the jaw gives an advantage to an animal with cheeks to keep the food in. Thus, the evolution of genasaurs required cheeks as well as jaw structure innovations. But cheeks, in turn, allow further changes: improvements in jaw musculature, the ability to use salivary enzymes to start chemical digestion in the mouth (not to mention the improved etiquette of chewing with the mouth closed!), reduced water loss by evaporation from the mouth, and so on.

In this connection, it might be useful to examine the details of a basal genasaur. It might – if there were any to examine. As it turns out, there are probably none. The only form that comes reasonably close is*Echinodon*. Unfortunately, *Echinodon* is a Late Jurassic (or even later) species, and most of the relevant developments are presumed to have taken place in the Triassic. Worse, there are few remains. The best *Echinodon* material is still a handful of disarticulated jaw parts from England originally described by Owen in 1861 and more recently by Galton (1978). Other than this, there is almost nothing. A single tooth from Spain has been referred to the genus. Estes & deAvalle (1982). Callison & Quimby (1984) have discussed post-cranial material from an unnamed and undescribed "fabrosaur" from the Jurassic of Colorado. Olshevsky (1994) and others have suggested that this, and accompanying jaw material, is *Echinodon*. However, without any attempt by anyone at formal publication of the fossils, it seems pointless to speculate.

As if to emphasize the ambiguity of these bits and pieces, there has been little agreement on the position of *Echinodon*. Galton (1978) assigns it to the Fabrosauridae. Sereno (1991) disputes a number of important details of Galton's re-description, disputes the very existence of the Fabrosauridae, and suggests that *Echinodon* is a heterodontosaur. Olshevsky (1994) agrees (more or less), but his conclusions about the phylogenetic place of heterodontosaurs are markedly different from those of Sereno. Coombs *et al*.. (1990) have an entirely different understanding, and place *Echinodon* near *Scutellosaurus* in the Thyreophora, based partly on the association of the English fossils with dermal scutes of uncertain provenance. Perhaps Sereno would now agree. Sereno (1999) currently places virtually all of the fabrosaur material in the basal Thyreophora, although he omits any discussion of *Echinodon* itself in the most recent study. We, also, treat *Echinodon* as a thyreophoran; but the choice is rather arbitrary. Much of the debate centers on the "canine" heterodont teeth of the English fossils; but, based on the photographs in Galton's paper, it is not at all certain that the fossil even has such teeth. There are negative casts which *might* reflect caniniform teeth. In addition, one specimen bears a disarticulated caniniform tooth which *might* have belonged to *Echinodon*, but could also have been left by a scavenger. The Fruita specimen is said to have unambiguous fangs, but the specimen remains undescribed.

This is obviously an unsatisfactory state of affairs. In the last analysis, it appears that *Echinodon* is simply another one of those fossils "whose charm exceeds their scientific merit." Feduccia (1999), quoting Storrs Olsen. It is particularly discouraging that acute and experienced observers such as Sereno and Galton cannot even agree on a description of the known material, much less on its interpretation. All things considered, this is a genus best tucked back into the deep recesses of the British Museum until something more informative comes along. ATW000514.

Descriptions

Ornithischia:*Pisanosaurus*. All Dinosaurs closer to *Triceratops* than to birds.

Range: Late Triassic to Late Cretaceous

Phylogeny: Dinosauria: Saurischia+ * **:** *Pisanosaurus* + (*Eocursor* + (Fabrosauridae+ Genasauria.))

Characters: Cheek teeth with low, subtriangular crowns; teeth foliate with constricted roots; predentary; toothless & rugose snout (probable horn beak); jaw joint below upper tooth row; palpebral; 3 to 5 sacral vertebrae; retroverted pubis; ossified tendons above sacrum; pes V reduced to splint. All had cheeks, horny beaks and were herbivorous. Great variety of "defensive" ornamentation.

Links: ; link

Pisanosaurus mertii Casamiquela, 1967

Horizon: Ischigualasto Formation (Late Carnian) of Argentina.

Phylogeny: basal Ornithischia

Comments: Based on a single, fragmentary skeleton, this is the oldest known, and also the most primitive, ornithischian. The sacrum and orientation of the pubis are not certain, but seem to be propubic, like classic saurischians (Thescelosaurus). The animal when alive was about a meter long MAK120309

Eocursor parvus Butler, Smith, and Norman, 2007

Horizon: Lower Elliot Formation (Norian) of Orange Free State, South Africa.

Phylogeny: Ornithischia : *Pisanosaurus* + ((Fabrosauridae /*Lesothosaurus* + Genasauria) + *)

Comments: Apart from *Pisanosaurus*

this is the oldest known ornithischian. Known from a single specimen comprising substantial cranial and postcranial material, it is also the only Triassic ornithischian known from reasonably complete remains. This was a small lightly built long-legged bipedal dinosaur about 1 meter in length, similar in appearance to early Jurassic ornithischians such as *Lesothosaurus* and *Scutellosaurus*. The tibia is significantly longer than the femur, indicating highly cursorial (fast running) ability. The hands are large and resemble those of the Heterodontosauridae. Providing the earliest evidence for the acquisition of many key ornithischian postcranial characters, including an opisthopubic pelvis. Triangular iguana-like teeth suggest a herbivorous or partially herbivorous diet. Extraordinarily, phylogenetic analysis places *Eocursor* above the heterodontosaurs, which are here placed near the base of Ornithischia, but below fabrosaurs, and forming a sister taxon to the the Genasauria. The implication is that a large grasping hand is a primitive (plesiomorphic) ornithischian characteristic (Butler et al. 2007). On the other hand, analysis of the basal ceratopsian *Yinlong* shows the heterodontosaurs to be sister clade to the Marginocephalia (Xu et al. 2006). Assuming the latter (and large manus and other features hared with heterodontosaurs as convergences due to a similar foraging lifestyle), *Pisanosaurus*, *Eocursor*, *Lesothosaurus* represent the fundamental ornithischian condition, from which heterodontosaurs, scelidosaurs, and hypsilophodonts evolved and radiated out from during the early to mid Jurassic. MAK120308

Image: Life reconstruction of *Eocursor parvus*. Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

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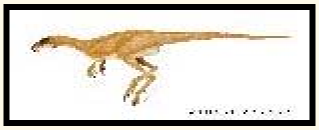

Fabrosauridae: *Lesothosaurus* (= *Fabrosaurus*), *Agilisaurus*, and assorted taxa

Range: Late Triassic to Late Jurassic, possibly later.

Phylogeny: Ornithischia : *Pisanosaurus* + (*Eocursor* + (Genasauria + *)) (for *Lesothosaurus*)

Characters: Generally 1-2 m; very lightly built & clearly bipedal; triangular skull; small antorbital fenestra partially occluded by maxilla (primitive); very large orbits & palpebral; lacrimal inserts into slot in maxilla; premaxillary teeth small, laterally compressed, leaf-shaped incisiforms; dentary and maxillary dentition marginal (primitive); single wear facets on teeth (vertical tooth action) (primitive); upper and lower teeth occlude alternately; teeth with enamel on medial & lateral surfaces; supra-acetabular buttress over anterior half of acetabulum; femur with head not strongly inturned; femoral shaft slightly bowed anteriorly; fourth trochanter long (caudofemoralis attachment); tibia longer than femur; fibula is reduced to narrow splint; astralagus & calcaneum strongly integrated into tibia and fibula function as part of crus; distal tarsals separate but closely associated with heads of metatarsals; pes tridactyl, with fifth digit lost & first reduced with a slight turn to the rear.

Notes: This likely not a clade, but a paraphyletic collection of very basal ornithischians. The description above largely relates to *Fabrosaurus* and should not be taken too seriously. ATW

Comment: *Fabrosaurus* and *Stormbergia* would seem to be synonyms of *Lesothosaurus*. A number of poorly-known forms have bene assigned to the Fabrosauridae, including *Alocodon, Gongbusaurus, Lufengocephalus, Nanosaurus, Technosaurus*, and *Xiaosaurus.* have been assigned to this group. Some of these, such as *Technosaurus*, aren't even dinosaurs; others could belong anywhere at around the base or even further up the ornithischian family tree. Middle or

Late Jurassic Chinese forms such as *Agilisaurus* and *Gongubusaurus* are "fabrosaurs" that represent an advance over *Lesothosaurus* MAK120308

Links: Literature - Basal Ornithischians & Fabrosaurids; Lesothosaurus - Enchanted Learning Software; Ornithischian dinosaurs: Fabrosaurids; Camptosaurus Nanum (??); Camptosaurus Nanum (view 2); Xiaosaurus - Enchanted Learning Software; FPDM : Agilisaurus louderbacki. ATW020901.

Genasauria: Definition: Thyreophora + Cerapoda.

Range: Early Jurassic to Late Cretaceous

Phylogeny: Ornithischia **:** *Pisanosaurus* + (*Eocursor* + (*Lesothosaurus* + * **:** Thyreophora + (*Agilisaurus* + Cerapoda)))

Characters: Tooth rows offset medially, from which existence of muscular cheeks is inferred; mandibular foramen reduced and spout-shaped.

Links: **DinoData: Genasauria;** Lectures 19-20: Late Cretaceous (cladogram); NEW STUDIES; columbia 12; ornithischia; Lecture 19- Late Cretaceous I; ornithischia cladogram; Dinosauria Translation and Pronunciation Guide G. ATW021129.

Agilisaurus louderbacki Peng, 1990

Horizon: Lower Shaximiao Formation of Sichuan, China (Bathonian/Callovian)

Phylogeny: Genasauria **:** Thyreophora + (*Agilisaurus* + Cerapoda + *)))

Comments: A small, lightly built, cursorial ornithischian of a typically fabrosaur mould. A single complete skeleton is known, making it one of the most complete small ornithischians. agility suggested by its lightweight skeleton and long legs. Its tibia (lower leg bone) was longer than its femur (upper leg bone), which indicates that it was an extremely fast bipedal runner (Wikipedia). The contemporary *Hexinlusaurus* is similar, although, with a longer tibia relative to its femur, would have been even more agile Thescelosaurus Comparisons between the scleral rings of *Agilisaurus* and modern birds and reptiles suggest that it may have been diurnal, unlike larger herbivorous dinosaurs that were inferred to be cathemeral, active throughout the day at short intervals (Schmitz & Motani 2011, via wikipedia). Despite the completeness of its remains, *Agilisaurus*' phylogenetic position is uncertain. Cladistic analyses by Weishampel et al.. 2003; Norman et al.. 2004) found it to be the most basal member of the group Euornithopoda (all ornithopods more derived than Heterodontosauridae). More recent analysis by Zheng et al. 2009 Butler et al. 2011 place *Agilisaurus* and *Hexinlusaurus* as stem Cerapoda, an interpretation we have followed here until something better comes along. Regardless of where they belong on the ornithischian family tree, These small and active animals clearly represneted an important element of the small herbivore niche, before being supplanted by hypsilophodonts in the late Jurassic. MAK120308

Image *Agilisaurus louderbacki*, skeleton reconstruction, photo © from Dinosaur Catalogue and Fossil and Mineral World

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Ornithischia: Thyreophora

Abbreviated Dendrogram

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DINOSAUROMORPHA
|--+--SAUROPODOMORPHA
|  `--THEROPODA
|
ORNITHISCHIA
|==Fabrosauridae
`--Genasauria
   |--Thyreophora
   |  |--Scutellosaurus
   |  `--+--Emausaurus
   |     `--Eurypoda
   |        |--Stegosauria
   |        `--Ankylosauromorpha
   |           |--Scelidosauridae
   |           `--Ankylosauria
   `--Cerapoda
      |--Ornithopoda
      |  |==Hypsilophodontidae
      |  `--Hadrosauridae
      `--+--Heterodontosauridae
         `--Marginocephalia
            |--Pachycephalosauria
            `--Ceratopsia
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Thyreophora

These are small to large specialized quadrupedal armoured forms - Early Jurassic to Late Cretaceous - length one to ten metres. There are three traditional subgroups: the primitive ancestral scelidosaurs, the unusual stegosaurs, and the heavily armoured ankylosaurs. It has been suggested that the Stegosaurs are actually more closely related to the ornithopods, but generally the following three lineages are grouped together, with the scelidosaurs as the basal (paraphyletic) grade from which the other two clades developed.

Thyreophorans as a model of Evolutionary Radiation

Writing about popular dinosaurs is a daunting proposition. So many have written so much and so well that little remains but to be repetitious or wrong. Given the choice between ennui and error, we will choose a little of both by discussing choices -- lineage splitting -- and how these dinosaurs made them.

The armored dinosaurs are an interesting opportunity to study radiations. The earliest dinosaurs all looked rather alike: barrel-bodied, with long necks, long, smallish heads like truncated cones, powerful hind limbs and tails, and surprisingly agile-looking forelimbs with prodigious claws. Examples of this general body plan include *Herrerasaurus*, *Saturnalia*, *Thescelosaurus*, and even *Scelidosaurus*. These forms represent all of the major groups of the first, Triassic, dinosaurian radiation: Sauropodomorpha, Theropoda, Cerapoda, and Thyreophora, respectively. These transitions can be readily understood -- if at the cost of considerable oversimplification -- as diversification into large-bodied guilds of carnivores, and of high, medium, and low browsers, respectively. It appears that either the dinosaurs possessed overwhelming selective advantages, or they were radiating into an ecological vacuum, since they managed to dominate all of these guilds by the earliest Jurassic without greatly elaborating on the basic dinosaur body plan.

At that point, however, the dynamics of dinosaur evolution began to change. Perhaps this occurred because the only serious competition left was from other dinosaurs. In any case, by the Middle Jurassic, the dinosaurs evolved many new and peculiar body forms which differed radically from the original dinosaur *bauplan*. These included the big-headed, bipedal tetanurans, the classic long-necked sauropods, the posturally enigmatic, short-bodied, stiff-tailed iguanodonts and their early hadrosaur and marginocephalian relatives, the heavily armored eurypods (ankylosaurs and stegosaurs), and perhaps minor forms we know nothing about as yet. The Jurassic was a poor time for fossils and we are still missing large parts of that story.

The eurypod part of the tale is the part that concerns us. Here, two lineages split: the stegosaurs and the ankylosaurs. Both were elephantine, armored, low-level browsers with wide bodies presumably accommodating a powerful digestive fermentation system. Both groups are relatively uncommon dinosaurs, but both are cosmopolitan in distribution. Unlike the original radiation, these forms do not appear to have split along the fault lines of easily identified ecological guilds. The question (which it has taken us rather long to get to) is "why?" *Scelidosaurus* suggests that the first thyreophorans looked more or less like every other early dinosaur, with the addition of some osteoscute armor and a wedge-shaped skull. It is understandable that some lineage would diverge into armored, elephantine herbivory. But why two such bizarre and divergent forms?

The question is complicated by the fact that stegosaurs and ankylosaurs flourished at different times. Stegosaurs are known from the Cretaceous, but are primarily creatures of the Jurassic. The opposite is true of the ankylosaurs. However, there is little doubt that the split occurred in the early Jurassic. The ankylosaurs were simply less successful. The possible reasons for this may fall into one or more of the following categories: (1) some environmental condition(s) disfavored the ankylosaurian form, (2) ankylosaurs did not evolve their typical mid-Cretaceous body form for a very long time, or (3) ankylosaurs were marginalized by competition from the stegosaurs.

Reason (1) seems unlikely. Absent conditions amounting to a general mass extinction, it would be hard to imagine a case which would encourage the diversification of stegosaurs, while suppressing the ankylosaurs worldwide, for 100My or so. Condition (2) can also be eliminated. We know almost nothing about Jurassic, or even Early Cretaceous, ankylosaurs. However, it takes only one exception to disprove this hypothesis, and at least two exceptions appear to exist. *Dracopelta* and *Tianchiasaurus* are well-enough known to state that both definitive nodosaurids and ankylosaurids, respectively, existed in widely divergent locations during the Jurassic. Therefore, we can conclude that the most important condition limiting the success of the ankylosaurs was most probably competition from their cousins and fellow low-browsers, the stegosaurs.

Based on this somewhat attenuated chain of reasoning, as well as the earlier history of the thyreophoran radiation, we can tentatively identify three stages of a major radiation (or, more cynically, we are going to shoehorn the eurypods into the following theoretical framework):

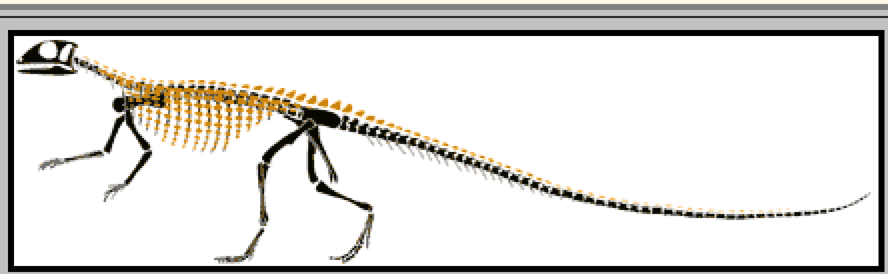
1. Geographical dispersal: A fairly generalized form radiates geographically without much anatomical change. The innovations introduced by this form, or perhaps some pre-existing mass extinction, creates an environment in which there is little competition. The main constraints are (a) environmental limitations and (b) some rather basic anatomical choices. Thus the dinosaurs radiated without much variation from the basic form, except the marginal exception of certain prosauropods, for much of the Middle and Late Triassic. Their anatomy restricted them from marine environments and probably dictated a basic election between carnivorous and herbivorous habits. However, there were few constraints other than such fundamental anatomical and environmental conditions. Note that, so long as the group is expanding its range, selection will tend to disfavor specialization and favor generalist pioneers.

2. Diversification into Guilds: Following consolidation of their position in an ecosystem, the principle constraints become internal to the group. The advantage shifts from highly generalized pioneers to guild specialists who can take advantage of one particular type of environmental resource or lifestyle more efficiently than other members of the group. Like Darwin's finches, this does not require gross changes in body form. Rather the same basic body form is retained, with the development of specific guild-related tools. In the case of dinosaurs, this involved, over the course of the Latest Triassic and Early Jurassic: top predators with larger heads and jaws, high browsers with long necks, middle browsers with considerable range of head motion and specialized dentition, low-browsers with armor and elephantine quadrupedalism -- all retaining the basic dinosaurian body plan.

3. Intra-guild Competition: At some point, particularly with organisms much larger than finches, further guild specialization is not possible. Finches can continue to subdivide ecospace according to seed types almost indefinitely. By contrast, a dinosaur runs out of any specialized resource, within a reasonable geographical range, fairly quickly. This limits the degree of anatomically "easy" specialization possible, unless the beast has very high mobility and access to other geographical pockets with the specialized resource. Arguably, the iguanodont - hadrosaur - marginocephalian group, the Cerapoda, was capable of more specialization (and hence more coexisting similar forms) because of greater mobility. The thyreophorans, burdened by armor, greater weight, and simple graviportal posture, lacked this option. This ecological trap created the conditions for the intense adaptive pressures (and perhaps geographical fragmentation) necessary for major re-engineering of the body plan. That is, further subspecialization could be achieved only by major anatomical changes because of greater size and limited mobility. Hence the basic thyreophoran body types diverged earlier than the corresponding cerapod types. The same could be said of the sauropodomorphs by contrast to the theropods, and for much the same reasons.

Clearly, if one of the new body plans is sufficiently flexible, and conditions are right, this may start a whole new radiation. The radiation of birds from the theropod stem may be an example of this sort of thing. However, for the most part, only a few, increasingly aberrant and specialized forms will survive -- until the specialization becomes so extreme that a change in environment extinguishes the entire line. ATW 011216

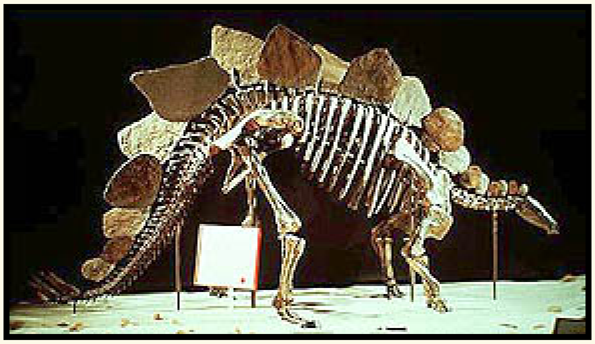
Although the closely related *Scelidosaurus* is sometimes regarded as a primitive ankylosauromorph, and the family is treated in that fashion here. However, *Scutellosaurus dawleri*, another traditional scelidosaur, probably is truly basal and pre-dates the split between stegosaurs and ankylosaurs. *Scutellosaurus* was a small lightly built ancestral armoured type. It was a fast sprinter, relying on agility to escape predators, with a light covering of armour plates (scutes) as well. It was originally classified with the fabrosaurs, from which it is no doubt descended. *Echinodon becklessi*, discussed above, may be another member of this group. MAK990714 & ATW020419.



Scutellosaurus dawleri **Owen (1868) from the Pliensbachian (Early Jurassic) of Arizona. About 120 cm and 10 kg.**

Descriptions

Thyreophora: Definition: (stegosaurs, ankylosaurs) > Cerapoda. [C97].



Range: Early Jurassic to Late Cretaceous.

Phylogeny: Genasauria **:** (*Agilisaurus* + Cerapoda) + * **:** *Echinodon* + (*Scutellosaurus* + Eurypoda).

Characters: fairly weak coronoid process [R56]; **$** postorbital process of jugal expanded transversely; broadened pelvis; **$** keeled scutes on dorsal surface in parallel rows.

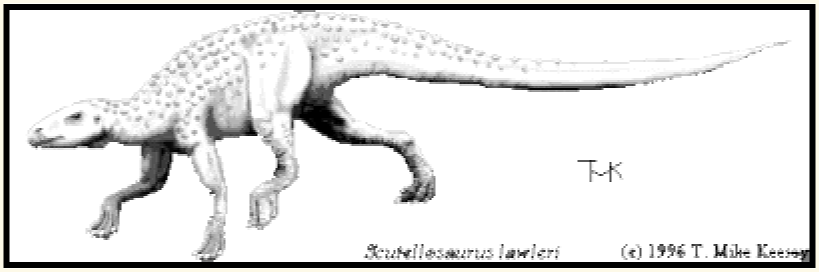
Notes: *Scutellosaurus* is the most basal form known from reasonably good remains[C97]. It looks more or less like any other advanced dinosauriform, i.e. somewhat bipedal, long necked and long-tailed, but stouter and with the beginnings of armor. ATW011201. Another extremely primitive form, and not so well-known, is *Tatisaurus oehleri* Simmons 1965. *Tatisaurus* is an isolated dentary from the Dark Red Beds, Lower Lufeng Series, Yunnan, China, and is probably of Late Hettangian- or Early Sinemurian age (Earliest Jurassic). *Tatisaurus* is the earliest known member of the Thyreophora It is still not very far removed from its fabrosaur-like ancestors, but within a few million years *Tatisaurus*, or a form like it, evolved into large armoured quadrupeds, the scelidosaurs. MAK990714.

Image: *Stegosaurus*.

Links: **DinoData: Thyreophora**; Prehistoric World Images Dilophosaurus & Scutellosaurus; Thyreophora - EnchantedLearning.com; Britannica.com; New Page 5; Introduction to the Thyreophora; GEOL 104 Lecture 18- Thyreophora- Defense! Defense! Defense!; Witmer's Lab Dinosaur Skull Collection- Thyreophora; The Armored Dinosaurs by Kenneth Carpenter (ed.); Chapter 14 Links (links).

References: Carpenter (1997a) [C97]; Romer (1956) [R56]. ATW030717

***Scutellosaurus*:**



Range: Late Jurassic (Tithonian) of North America.

Phylogeny: Thyreophora:: Eurypoda + *.

A bigger (120cm), heavier version of *Echinodon*.

***Emausaurus*:**

Range: Early Jurassic (Toarcian) of Europe

Phylogeny: Thyreophora **:** Eurypoda + *.

This animal has been compared to a miniature version of *Huayangosaurus*, the skull of which is very similiar. MAK990724.

Eurypoda: defined as *Stegosaurus* + *Ankylosaurus*

Range: Middle Jurassic to Late Cretaceous. Cosmopolitan.

Phylogeny: Thyreophora **::** *Scutellosaurus* + * **:** Stegosauria + Ankylosauromorpha

Characters: skull width very broad with intraorbital width at the supraorbitals widest portion of the skull; **$** reduced or absent antorbital fenestra and fossa; **$** three palpebrals ("supraorbitals") form dorsal rim of orbit [G90]; **$** supraorbital horns; **$** quadrate with shaft and pterygoid ramus in same plane (??) and no distinct lateral ramus [G90]; **$** quadrate with articular surface directed ventrolaterally [G90]; **$** no ("otic") notch between paroccipital process and quadrate [G90]; **$** exoccipital ventral portion around foramen magnum recessed and overhung by dorsal part and supraoccipital [G90]; **$** deep median keel on hard palate (may have supported soft secondary palate) from vomers & pterygoids [G90]; **$** ossified epipterygoid; **$** atlas neural arches fused to atlas intercentrum [G90]; parascapular spines present; **$** scapular blade of roughly constant width [G90]; robust ulna with convex external margin and huge olecranal expanse; **$** short metacarpals with hoof-like unguals (also on pes) [G90]; **$** laterally tilted, dorsoventrally compressed preacetabular blade (of ilium, presumably); **$** ilium anterior process diverges at least 35° laterally from midline [G90]; ilia broad and overhang entire pelvic area; **$** ilium posterior process very short, with antitrochanter (*sensu* Romer) [G90]; **$** partially closed acetabulum (plesiomorphic?); femur neckless, with head almost terminal [G90]; **$** enlarged greater trochanter confluent with femoral head; femur with reduction of the fourth trochanter; **$** pendent fourth trochanter (?!); mediolaterally expanded tibia with width about equal to craniocaudal length of proximal end; **$** proximal tarsals tend to fuse with epipodials in adults [G90]; mediolaterally expanded calcaneum; metapodials short & robust; **$** metatarsals short and arranged for spreading, elephantine stance (vs. compact) [G90] [S99]; **$** cervical dermal rings (not sure what this means); **$** cranial dermal ossicles; parasagittal arrangement of armor.

Links: DinoData: Eurypoda.

References: Galton (1990) [G90]; Sereno (1999) [S99]. 011130.

Ankylosauromorpha: *Ankylosaurus* > *Stegosaurus*? But see Ankylosauromorpha (*Scelidosaurus* + Ankylosauria).

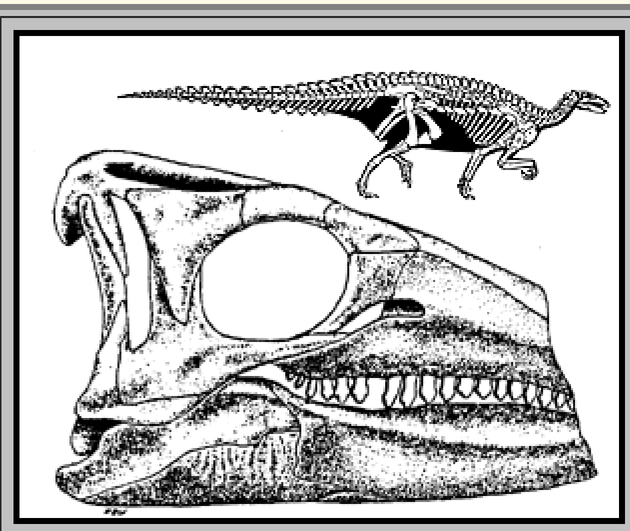
Range: Early Jurassic to Late Cretaceous

Phylogeny: Eurypoda: Stegosauria + * **:** Scelidosauridae + (*Minmi* + Ankylosauria).

Characters: skull surface extensively modified by reworking bone surface by overlying scales, or by fusion of armor; body very wide (probable hindgut fermentation); 7-8 cervicals, ~16 dorsals, 3-4 sacrals, 40+ caudals; neck short; trunk very long; caudals typically short near hip & elongated near middle of tail; quadrupedal; ilium expanded horizontally & angled away from midline (allows wide hip to accommodate gut); pubes rotated to at least partially close acetabulum; armor over whole body; armor embedded in skin; armor of projecting spines, large narrower spikes, thin walled cone-like plates, keeled nearly flat plates, solid, keeled scutes, with small rounded ossicles on ventral surface & filling gaps; armor in species-specific pattern.

Links: Ankylosauromorpha.

Scelidosauridae: *Bienosaurus*, *Scelidosaurus*. Early, ankylosaur(-like?) Thyreophorans



***Scelidosaurus* skull and skeletal reconstruction from Coombs *et al.*. (1990), figs. 20.1a & 20.2a. Skeletal reconstruction by Greg Paul.**

Range: Early Jurassic, possibly surviving to Late Jurassic of England.

Phylogeny: Ankylosauromorpha **:** (*Minmi* + Ankylosauria) + *.

Characters: Characters: Skull tall posteriorly, but tapering anteriorly to form wedge-shaped lateral profile [C+90]; skull also tapers slightly laterally [C+90]; skull retains all 5 pairs of fenestrae, unlike ankylosaurs; premaxilla with teeth [C+90]; maxilla triangular [C+90]; maxilla with shelf lateral to tooth row [C+90]; nasal long [C+90]; lacrimal rectangular, forming most of anterior orbit [C+90]; nasal-maxillary suture continuous with prefrontal-lacrimal suture [C+90]; additional osteoderm incorporated into orbital rim; jugal and postorbital with extensive overlap, forming broad pillar between orbit and lower temporal fenestra [C+90]; lower temporal fenestra very narrow [C+90]; rugose areas for osteoderms on skull roof, jaws; parietals hour-glass shaped, with narrow waist between upper temporal fenestrae [C+90]; squamosal forms posterior & lateral borders of circular upper temporal fenestrae [C+90]; quadrate vertical, with jaw articulation ventral to tooth row [C+90]; mandibular symphysis broad, rugose & inclined anteriorly (probably a small beak) [C+90]; "cropping beak" of ankylosaurs absent (selective feeder?); predentary unknown or absent [C+90]; mandibular symphysis absent

[C+90]; surangular large and forms posterior half of coronoid process [C+90]; spliner-like splenial on ventral margin of jaw [C+90]; teeth with symmetrical enamel [C+90]; tooth roots long and straight [C+90]; vertebral count 6-7 cervicals, 17 dorsals, 4 sacrals, 35 caudals [C+90]; axis centrum fused to atlas [C+90]; neural spines laterally compressed & short [C+90]; parapophyses shift dorsally down the spine, so that last few ribs have single head articulating distally on the transverse process [C+90]; scapular blade short & wide [C+90]; humerus straight, with large, long deltopectoral crest [C+90]; broadening of pelvis; pubes thin & distal pubes curve ventrally away from ischium [C+90]; ilium long post-acetabular region; reversion to quadrupedalism; femur straight to slightly curved [C+90]; femoral head displaced medially, but without a neck [C+90]; lesser trochanter prominent & separated from greater by groove; 4th trochanter large, pendent and placed at mid-length [C+90]; tibia slightly longer than femur [C+90]; large cnemial crest [C+90]; large, free astragalus, large calcaneum and (at least?) 2 other tarsals [C+90]; 4 massive metatarsals & vestigial V [C+90]; phalanges short & flat with blunt, flat unguals [C+90]; phalangeal formula 23450 [C+90]; three rows of plates on each side of body; four rows on each side of the tail; unique 3-pointed plates just behind skull (shoulder spines?) [C+90].

Links: DinoData Classification Scelidosauridae; STEGOSAURS, ANKYLOSAURS (October 8); Scelidosaurus; Lecture 12 - Early Jurassic; dinocountup01.html (see entry for *Bienosaurus*); Scelidosaurus The Natural History Museum's Dino Directory; _Bienosaurus_ questions.

References: Coombs *et al*. (1990) [C+90]. ATW030606.

Ornithischia: Ankylosauria

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauromorpha
|     |--Scelidosauridae
|     `--+--Minmi
|        `--Ankylosauria
|           |--Ankylosauridae
|           `--Nodosauridae
|
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
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2. Ankylosauridae X
3. *Minmi* X
4. Nodosauridae X

Ankylosauria

The ankylosaurs were heavily armoured dinosaurs, 2 to 10 meters long, quadrupedal, slow moving, and fed on swampy soft vegetation. They are largely known from the Cretaceous. These creatures were equipped with bony plates, studs, spikes, and, in the case of one lineage, a bony tail-club. Despite their formidable defenses, they are never very common in the fossil record, although a large number of different species are known.

Traditionally, there were two families of ankylosaurs: the **Nodosauridae** and the

Ankylosauridae. This picture has been somewhat obscured by the suggestion that *Scelidosaurus* is an ankylosaur, and the discovery of *Minmi paravertebrata* (shown at right), a small, long-legged running ankylosaur from the mid Cretaceous of south-east Gondwanaland. To avoid -- or perhaps create -- confusion, the term **Ankylosauromorpha** is used to describe all "ankylosaurs," *i.e.* everything closer to *Ankylosaurus* then to *Stegosaurus*. The term **Ankylosauria** is reserved for the traditional ankylosaurs: the last common ancestor of *Ankylosaurus* and *Nodosaurus* and all of its descendants.

The Nodosaurids appeared as small forms in the Jurassic of Europe, spreading to North America and Asia (Laurasia) during the early and middle Cretaceous. They had more extensive armoring then the Scelidosaurs, and often whole patches of external bone were fused into plates. The head was small, equipped with peg-like teeth. Nodosaurids differ from the contemporary ankylosaurids in the presence of side spines and absence of a tail club.

The ankylosaurids were the last of the armoured dinosaurs to evolve. They are distinguished by the heavy club-like tails, presumably used as a defensive weapon against predators. The primitive polacanthine group had small tail clubs, and was originally included under the Nodosauridae. (mostly MAK990512)

Descriptions

Minmi**:** *M. paravertebrata* Molnar, 1980.

Range: middle Cretaceous of Australia (and perhaps New Zealand)

Phylogeny: Ankylosauromorpha :: Ankylosauria + *.

Characters: 2-3m; snout arches higher than the roof of the skull (as nodosaurs); vertebrae with bony projections along side the neural spines (*paravertebrae*), probably similar to ossified tendons in ornithopods; tail club probably absent; forelimbs about as long as hindlimbs; legs unusually long for ankylosaur; long post-acetabular region of the ilium; femur round in cross-section (plesiomorphic & unlike ankylosaurs); armor of large & small body scutes, large scutes on limbs, plates around neck, tear-drop shaped spiked plates behind hips, and triangular plates & large scutes along the tail; armor present as small scutes embedded in skin on ventral surface.

Notes: Widely speculated, on the basis of the long, unspecialized limbs and paravertebrae, that *Minmi* was adapted to running despite heavy armor. The only ankylosauromorph known from Gondwana.

Image: *Minmi paravertebrata* from the **Queensland Museum**.

Links: **DinoData: *Minmi***; Dann's Dinosaur Info: MINMI (with refs & photos); Minmi; Minmi; Minmi - Dinosaur - Enchanted Learning Software; Minmi (Australian Museum site); MINMI; Minmi (brief essay in Spanish); OZ fossils - The Age of Reptiles - Northern Region - Minmi (with life reconstruction). ATW031217.

Ankylosauria: Definition: Ankylosaurs + Nodosaurs

Range: (possibly Early or) Middle Jurassic to Late Cretaceous of Laurasia. Most common in middle and Late Cretaceous.

Phylogeny: Ankylosauromorpha **::** *Minmi* + * **:** Ankylosauridae + Nodosauridae.

Introduction: These squat, broad, heavily armoured creatures were equipped with bony plates, studs, and either spikes or a bone tail-club. Despite their amazing protection they were never very common in terms of individuals, although a large number of different species are known.

The Ankylosauria are conventionally divided into two families, the spiked Nodosauridae and the club-tailed Ankylosauridae, but there are also a few forms that don't fit in either category and would seem to constitute independent evolutionary lineages, outside the Ankylosauria, like the Australian *Minmi*.

The teeth are small and weak, indicating a diet of soft vegetation, and the massive limb bones are supported by particularly strong shoulder and pelvic girdles, presumably to carry the weight of the armour.

Ankylosaurian armored scutes are rectangular to oval bony plates organized in rows along the back and tail, giving them the appearance of giant dinosaurian armadillos. Smaller bony nodules fill the spaces between the large plates. The addition of spines and a solid bone tail club in some forms make these squat animals a prickly target for any carnivores. (MAK990512)

Characters: usually large (2.5-8m), heavy & broad [T00]; ***skull:*** skull flat and broad [CM90]; posterior skull wider than tall [CM90]; skull covered with armor [CM90]; cranial armor from remodeling of bone surface (= ornamentation, not fused osteoscutes); premaxilla broadly expanded on undersurface of snout [R56]; maxilla with deep, dorsally arched cheek emargination [CM90]; nares moderately large to very large, near terminal & facing laterally [R56]; sometimes with complex air passages [C97]; most fenestrae (groups differ) closed by dermal bone [T00] [C97]; orbit large and circular to elliptical [C97]; orbit walled in by supraorbitals, "postocular shelf" (from postorbital & jugal), ventral jugal extension of shelf, lacrimal shelf & "accessory bones of uncertain homology" [CM90]; extra supraorbitals (modified palpebrals) present [C97]; skull roof sutures obliterated in adults [CM90]; quadratojugal contacts postorbital [CM90]; quadrate slants forward ventrally below squamosal [CM90] [R56]; quadrate pterygoid process dorsoventrally short [CM90]; rectangular occiput [T00]; occipital condyle faces ventrally [R56]; palatal bones extensively fused [CM90]; premaxillae may have foramina for vomeronasal organ [CM90]; palate with strong central keel made up of vomers, pterygoids, premaxillae, nasals, and/or ethmoids [CM90]; keel extends to skull roof bones [CM90]; palate largely closed by pterygoids & palatines [CM90]; but secondary palate not primitive and derived separately in derived groups [CM90]; quadrate process of pterygoid laterally directed [R56]; lower jaw with co-ossified keeled plate along ventrolateral margin (like some pareiasaurs!) [CM90]; predentary small and symphysis narrow [CM90]; teeth primitive, small, laterally compressed, foliate, denticulate & non-interlocking [CM90] [C97]; primitively, premaxillary teeth present; dentary tooth row medial to maxillary teeth [CM90]; strong hyoids suggest large, mobile tongue [C97]; ***axial:*** vertebral column with 7-8 cervicals, ~16 dorsals (3-6 fused to presacral rod), 2-4 sacrals, and 20-40 caudals (1-3 fused to sacral rod) [C97] [CM90]; atlas with complete neural arch with elongate postzygapophyses ~40% of axis arch [CM90]; axis with massive odontoid and neural arch with short spine [CM90]; atlas and axis are fused in some forms [CM90]; short neck with shortened cervicals [C97]; posterior cervicals with anterior & posterior centra at different height [CM90] [T00]; cervical diapophyses horizontal or slightly ventral [CM90]; dorsal centra amphicoelous to amphiplatyan with similar length & diameter [CM90] [R56]; long & broad torso with elongated dorsal vertebrae [C97]; rib facets (diapophyses) angled upward 30-50° to give broad, barrel-shaped dorsal surface [C97]; posterior dorsal ribs tend to fuse with centra & transverse processes [CM90]; 3-6 dorsals fused with sacrum to form rigid synsacral rod, preventing rotation of the pelvis about the vertebral column [C97] [CM90]; diapophyses in sacrum + sacral rod are relatively flat [CM90]; presacral rod neural spines form continuous blade-like ridge [CM90]; sacral neural arches low & broad [CM90]; tail as long as body [CM90]; caudals are typically short near pelvis & 1-2 may fuse to sacrum; caudals rapidly elongate; neural & hemal spines of distal caudals elongated along axis of tail [CM90]; ***appendicular:*** limbs short [C97]; limb bones stout [CM90]; acromion (pseudoacromion?) typically a thickened area along dorsal border of scapula; scapula & coracoid may be co-ossified [T00]; forelimbs shorter (length 65-75% length of hind limbs) [CM90] [T00]; humerus broad, with strongly developed deltopectoral crest [C97]; ulna with very tall, long olecranon for extensor muscle (triceps?) attachment [C97]; manus short & broad, with 4-5 digits [C97]; pelvis wide, with ilium rotated into long, nearly horizontal structure that angles away from the midline, with attachment scars of retractor muscles [C97]; ilium with long anterior, short posterior processes [CM90]; ilium anterior process distally curves ventromedially [CM90]; ilium pubic peduncle absent [CM90]; ischium bent to project ventrally [C97]; pubes much reduced [C97]; anterior pubic process absent [CM90]; pubes posterior process short [CM90]; pubes almost excluded from acetabulum [CM90]; acetabulum cup-like & closed [CM90]; most of body weight carried over the hind legs; femur straight and pillar-like [CM90] [C97]; femoral neck absent [CM90]; femoral trochanters and cnemial crest poorly developed [R56]; lesser trochanter frequently absent [CM90]; 4th trochanter ridge-like [CM90]; tibia and fibula short and stout; proximal tarsals not fused to epipodials [R56]; metatarsals more slender & less spreading than metacarpals [CM90]; massive pes with 3-4 digits [C97]; ***other:* $** armor covers dorsal surface; most of body armor plates of bone embedded as rows in the skin in species-specific pattern (so sexual selection?); plates oval to rectangular with longitudinal keel; plates commonly arranged in longitudinal rows [CM90]; gaps and limbs have small rounded osteoscutes; supplemented with spines; perhaps insectivorous as well as herbivorous [T00]; tracks show limbs close to midline, with elbow bent [CM90].

Note: **[1]** The majority opinion is probably now that *Scelidosaurus* is probably a basal ankylosaurian or ankylosaurid rather than a stem thyreophoran. **[2]** Very wide bodies combined with relatively weak dentition suggest highly-developed internal fermentation system. ankylosauria. **[3]** cranial bones poorly known because of extensive fusion and armor. [CM90].

Links: **DinoData: Ankylosauria**; Thyreophora: Stegosauria and Ankylosauria - EnchantedLearning.com; ankylosauria cladogram; FPDM : Ankylosauria; Ankylosauria; ankylosauria; Ankylosauria (Spanish); Ankylosauria (Japanese - models); Literature - Ankylosauria; Toyama 2000-11-6 (footprints); The Natural History Museum's Dino Directory.

References: Carpenter (1997b) [C97], Coombs & Maryanska (1990) [CM90], Romer (1956) [R56], Tumanova (2000) [T00]. ATW011130.

Ankylosauridae: *Ankylosaurus, Cedarpelta, Euoplocephalus, Gargoyleosaurus, Mymoorapelta.*

Range: Late Jurassic to Late Cretaceous of North America, Asia, Australia?

Phylogeny: Ankylosauria **:** Nodosauridae + *.

Introduction: The ankylosaurids are the last of the armoured dinosaurs to evolve. They are distinguished by the heavy club-like tails, presumably used as a defensive weapon against predators, but lack the long spines ofthe nodosaurs. The primitive Polacanthine group were first classified as nodosaurids. They only had small tail clubs.

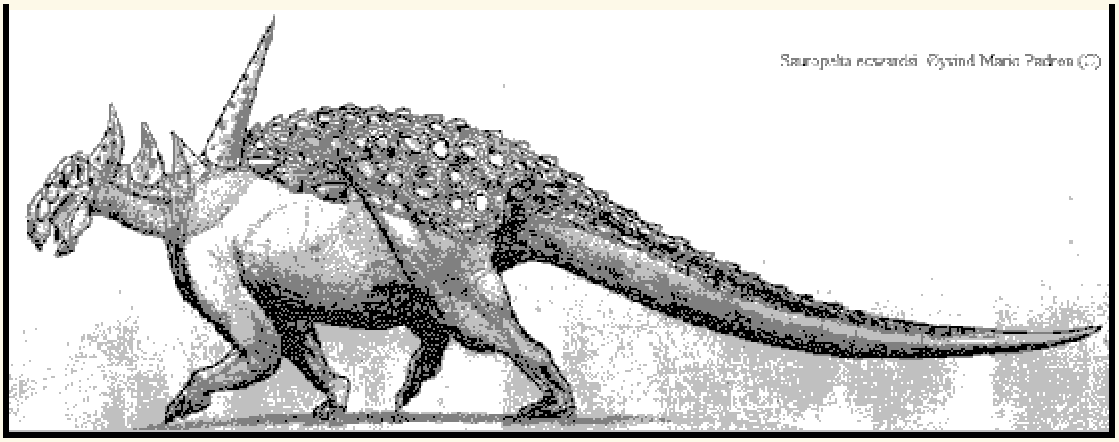
The ankylosaurid skull is heavy and re-enforced, and in comparison to the nodosaurids, wider and triangular with small horns at upper and lower corners and a mosaic of small armour plates over the skull. The beak is also wider, indicating a non-selective grazing or cropping of low vegetation, so it is clear that these animals had different feeding strategies than the contemporary nodosaurs.

In all ankylosaurids the armour is arranged in transverse bands of bony plates along the neck, back and tail.

Characters: Low, wide (75% of length or more), triangular skull, usually covered in bony plates, even eyelid (1spp); beak usually wide (non-selective cropper) but primitively longer than wide; nares usually forward; usually complex air passage includes loop; large postorbital "horns"; jugal large; lateral temporal fenestra closed by posterior expansion of postorbital; coronoid process of dentary low; small teeth with wide base (except *Gargoyleosaurus)*, bulging base in derived species; neural spines low; 3-4 dorsals fused with sacrals & ilium = synsacrum; some other fusions; distal caudal vertebrae are stiffened with chevrons and zygapophyses; also stiffened with ossified tendons; typically distal 50% of caudal vertebrae fused; caudal bone club formed from fusion of 2 large & several small bone plates surrounding fused vertebrae; pectoral girdle massive; prominent knob at scapula- coracoid junction; deltopectoral crest not strongly projecting forward (??); "the distal condyles of the humerus are in nearly the same vertical plane as the deltopectoral crest" (Ankylosauridae); massive olecranon process on ulna (elbows flexed & close to body?); large preacetabular ilium (iliotibialis protractor?); ischium long, oriented dorsally; femur 4th trochanter distal to midpoint; distal tibia has large fibular process (prevents movement between tibia & fibula); 3-4 functional toes (primitively 4); keeled bone plates (per Ankylosauridae "thin-walled scutes"); spines & spikes absent from shoulder & neck; neck has 2nd layer of bone (?); skull surface ornamented (scales); cranial sculpturing increases with age.

Links: **DinoData: Ankylosauridae**; Saichania; Ankylosauridae after Carpenter, 2001; Ankylosauridae (**Best on the Web**); DINOBASE, Sibbick's dinosaur pictures; Figure 2 (somewhat heterodox today); Biologybase: Checklist of the Non-Avian Dinosaurs; Ankylosaurs Dinosaurs - Enchanted Learning Software; Lecture6 GLY137.ppt; Skull of a Jurassic ankylosaur (Dinosauria); 13; Ankylosaurier gevonden in Frankrijk (Dutch); Gargoyleosaurus - Dinosaur - Enchanted Learning Software; GEOL 104 Lecture 18- Thyreophora- Defense! Defense! Defense!; ATW021029.

Nodosauridae: *Amantarx, Anoplosaurus, Edmontonia, Niobrarasaurus, Nodosaurus, Panoplosaurus, Pawpawsaurus, Pricodon, Sauropelta, Silvisaurus, Stegopelta, Struthiosaurus, Texasetes.*



Range: Middle Jurassic to Late Cretaceous of Laurasia, South America & Antarctica. "Definitive" nodosaurs from the Early Cretaceous II (Aptian).

Phylogeny: Ankylosauria **:** Ankylosauridae + *.

Introduction: The nodosaurids appeared as small forms in the Jurassic of Europe, spreading to North America and Asia during the Early and mid Cretaceous. They had more extensive armoring then the scelidosaurs, and often whole patches of external bone were fused into plates. The head was small, equipped with peg-like teeth. Nodosaurids differ from the contemporary ankylosaurids in the presence of side spines and absence of a tail club.

In contrast to the broad triangular-skulled ankylosaurids, the elongated snout and relatively narrow beak seems designed for more selective cropping or browsing. A solid shield of fused keeled plates protected the pelvic area, and are supplemented by flank spines. The limbs are slimmer than those of the ankylosaurids, and these animals probably could get about faster, even able to use their flank spines to charge and attack predators. Their appearance suggests that could also draw in their front legs and crouch down like a tortoise when attacked, with the body close to the ground an hard to overturn. MAK

Characters: Similar to Ankylosaurs except: skull elongate with rounded edges (this may be the primitive condition); skull pear-shaped in dorsal view; skull length greater than width; nares face laterally; narrow rostrum & beak (selective browser?); single armor plate at center of skull; cranial plates (not bones) large and symmetrically arranged; jugal and postorbital "horns" small, if present, and usually rounded; anteriorly concave and anteroposteriorly flattened quadrate; hemispherical occipital condyle is composed of the basioccipital only; occipital condyle set off from braincase by short neck angled downwards ~50º; prominent W-shaped basioccipital tubera; *basipterygoid processes* usually consist of pair of rounded, rugose stubs; transversely continuous and straight posterior margin of the pterygoid aligned with the quadrate shaft; coronoid process is very tall; teeth may have cingulum; tooth row hour-glass shaped, narrowest at mid-maxilla; cutting edge of premaxilla connected to maxillary tooth row by low ridge; tall neck spines; outwardly projecting spines on the neck and shoulders; no bony tail club; spines, spikes along sides of body and on shoulders; scapula with distinct ridge-like acromion process above the glenoid for *m. scapulohumeralis anterior*; coracoid large and elongate; plates over pelvis may co-ossify; ischium is ventrally bent near mid-length; armor generally thick and solid.

Links: DinoData: Nodosauridae; *Pawpawsaurus*; Nodosauridae; Nodosauridae after Carpenter, 2001; DINOSAURS: Family Nodosauridae; NODOSAURIDS; Gigantic ankylosauria from Utah (Dutch); Literature - Ankylosauria; The Journal of Vertebrate Paleontology. ATW020920.

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Ornithischia: Stegosauria

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Scutellosaurus
|  `--Eurypoda
|     |--Stegosauria
|     |  |--Huayangosauridae
|     |  |  |--Emausaurus
|     |  |  `--Huayangosaurus
|     |  `--Stegosauridae
|     `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
```

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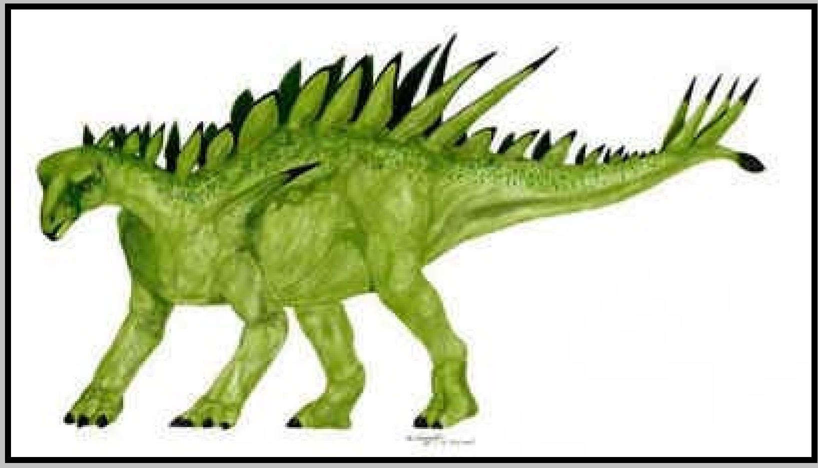
Suborder Stegosauria

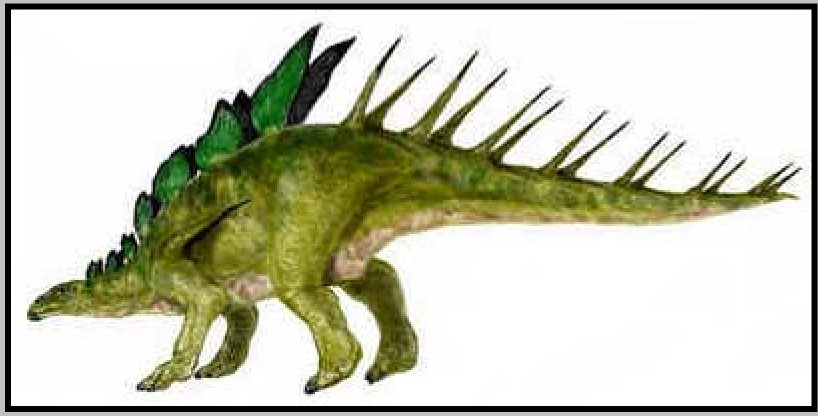
Plated dinosaurs - mostly Jurassic, spines along the back and tail for protection, plates served a thermoregulatory purpose. Quadrupedal, short forelimbs, slow-moving. Length 4 to 10 meters

The Stegosaurs are a distinctive component of the Jurassic megafauna. These striking dinosaurs are characterized by pairs of bony plates along the back (presumably for the purpose of thermoregulation) and varying numbers of pairs of spikes along the tail and, in some species the back, hips, and even shoulders. Despite their protective spikes, they were never a very diverse group. Reasonably common during the Middle and Late Jurassic, the stegosaurs were almost wiped out by the Tithonian extinction event. Stragglers continued on to the Early or middle Cretaceous, and perhaps even later on the island continent (as it was then) of India.

The stegosaurs are divided into a number of families, typically with only one well-known member each. These may or may not be monophyletic. Stegosaurs are not very diverse, and there is a reasonably good chance that we are looking at ancestor - descendant relationships, rather than separate clades.

The **Huayangosaurs** were earliest well-known forms, and lived during the Early to Middle Jurassic. They are generally much smaller than the later stegosaurids. The skull is short and high relative to later stegosaurs, and retains the archosaurian antorbital fenestra (opening in front of the eyes). Although *Huayangosaurus* is the only certain form, it is likely that other earlier types like *Tatisaurus* and *Emausaurus* also belong here. An early Cretaceous jaw of uncertain affinities called *Regnosaurus northamptoni* has been placed in this group, on the basis of its strong resemblance to the lower jaw of *Huayangosaurus*, but in view of the incomplete nature of the specimen and its much later date (contemporary with the latest advanced stegosaurines) one may remain skeptical.





UPPER: *Huayangosaurus tabii* Dong *et al.*. 1982 from the Middle Jurassic of China. About 4m. LOWER: *Kentrosaurus aethiopicus* Hennig 1915, from the Late Jurassic of Tanzania. About 5m and 450 kg. Both images © M. Shiraishi, reproduced with permission.

The **Dacentrurinae** were late persisting primitive types, that seem to have characteristics indicating a type ancestral to other stegosaurids (even if they themselves are too late in time to be an actual ancestor). The vertebrae are more primitive and the forelimbs longer in comparison to the hind-limbs. Although *Dacentrurus armatus* is the only certain species, an early femur has been referred to that species.

The **Kentrosaurinae** are primitive stegosaurids, small to large in size, with generally small spiky plates and numerous spikes along the tail, and sometimes the hips and shoulders as well. A *paraphyletic* group, they are transitional between the Dacentrurines and the stegosaurines.

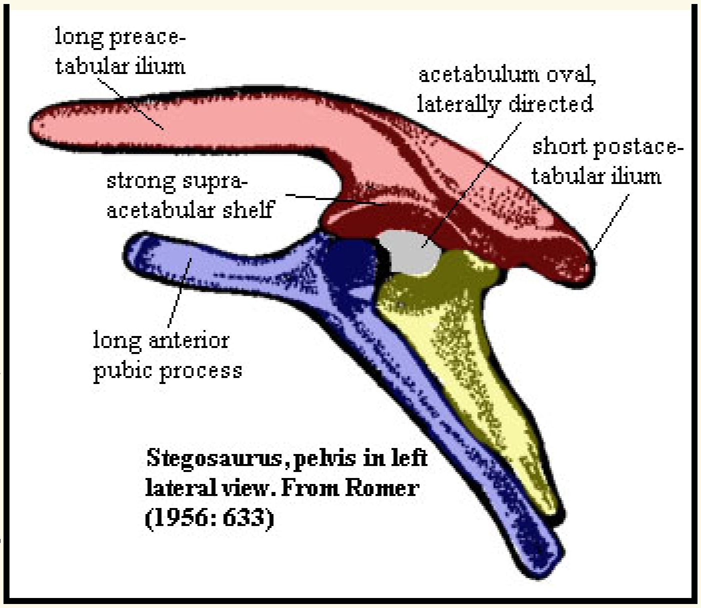
The **Stegosaurinae** are the most specialized stegosaurids, with generally larger plates and spikes that tend to be limited to the end of the tail, although primitive forms still retain additional spines. One could distinguish two tribes: the Tuojiangosaurini, which may be ancestral, and the Stegosaurini. The tuojiangosaurines generally retain the Kentrosaurine pattern of back and hip spines. The stegosaurines are distinguished by large size, no spines on hips or shoulders, only two (or rarely 4) pairs of tail spines, relatively short forelimbs, a small elongate head, and large plates in life covered with skin and blood vessels. This tribe includes only two genera, *Stegosaurus* and *Wuerhosaurus*. The controversial dinosaurologist Bob Bakker distinguishes between two types of *Stegosaurus* - those with long legs and relatively smaller plates (*Stegosaurus* proper) and a more primitive form with shorter legs and larger plates (*Diracodon*). Others are critical of proposing a new stegosaur genus on this basis. Also,different sources (both in print and on the Web) give different lists of species; e.g. some are synonymized with others. It may be that some of these species are only subspecies or local variants. MAK990724

Descriptions

Stegosauria: *Stegosaurus* > *Ankylosaurus*.

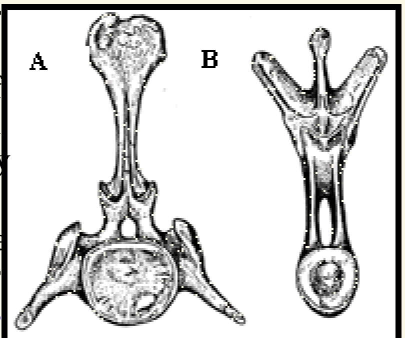
Range: mJ-upK, fl upJ.

Phylogeny: Eurypoda : Ankylosauromorpha + * : Huayangosauridae + Stegosauridae.



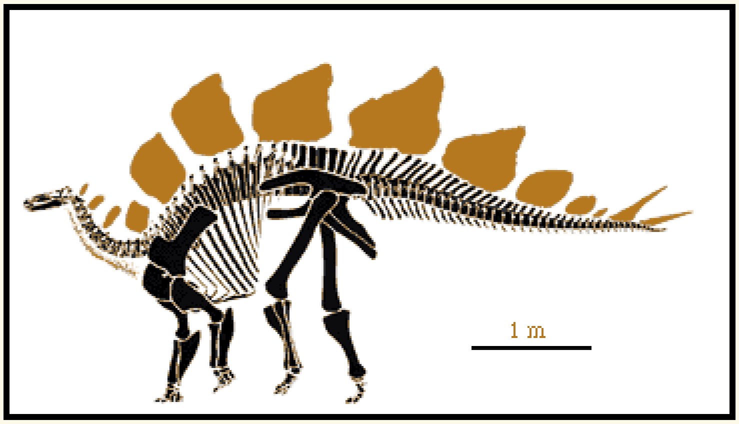
Stegosaurus, pelvis in left lateral view. From Romer (1956: 633)

Characters: Medium to large (to 9m) [G90]; ***skull:*** skull relatively small, low and wedge-shaped with long facial region [R56]; premaxilla & mandible covered with rhamphothecae[G97]; premaxilla dorsal process does not reach lacrimal [G90]; nares elongate ovals [R56]; nasals & maxillae elongate [R56]; nasals longest bone in skull [G90]; fleshy cheeks likely present with supporting ridges on maxilla & dentary for musculature [G90] [G97]; flat parietal plate separates small upper temporal fenestrae [R56]; orbit large for small skull, with 3 supraorbital (modified palpebrals) on dorsal rim [R56]; palpebrals exclude prefrontal & frontal from orbit [G90]; postorbital triradiate [G90]; jugal overlaps quadratojugal which overlaps quadrate [G90]; lateral temporal fenestra large [R56]; squamosal triangular & roofs posterolateral section of lateral temporal fenestra [G90]; quadrate probably immovable, with simple orthal chomping [G97]; quadrate nearly vertical ventrally [R56]; **$** quadrate pterygoid ramus with large oval fossa [SD92]; jaw articulation well below toothrow [R56]; **$** quadrate articular ramus ("head") large, rectangular & plate-like [SD92]; occipital condyle large & mostly from basioccipital [G90]; deep median keel on hard palate (may have supported soft secondary palate) from vomers, palatines & pterygoids [G90] [G97]; rounded, ventrally directed pterygoid flanges [G90] [R56]; pterygoid quadrate ramus slants sharply back (?) [R56]; pterygoid quadrate ramus forms large fossa or fenestra [G90]; pterygoid vacuities very small [G90]; pterygoid body overlaps basisphenoid [G90]; remarkably small brain; predentary present (single?) [G90] [G97]; predentary does not extend to as far as premaxilla [G90]; jaw, particularly dentary, elongate [R56]; coronoid eminence formed into long vertical ridge [G90]; coronoid emminence largely from surangular [G90]; ridge rises and hides posterior teeth in lateral view [G90]; articular broad & thick [G90]; teeth smaller than mot ornithischians [G90]; cheek teeth with simple crowns, bulbous cingulum & few wear facets; teeth with enamel on both surfaces [R56]; significant species differences in form & arrangement of teeth, although all generally foliate [G90]; ***axial:*** **$** no ossified tendons [G90] [SD92] [G97]; centra amphiplatyan anteriorly & strongly amphicoelous posteriorly [G90] [R56]; atlas arches fused to intercentrum [G90]; odontoid process present and ankylosed to axis centrum [G90]; short cervical ribs [R56]; anterior dorsal vertebrae with neural canal >50% diameter of centrum [SD92]; **$** dorsal vertebrae tall due to long neural arch pedicels > 150% centrum height [SD92]; upward-slanting articulations with ribs (increased size of body cavity) [G97]; neural canal enlarged in posterior cervicals (brachial plexus) and posterior dorsals (but cut here by septum) [G97]; diapophyses angled upward 50-60° in mid-dorsals (**$** per [SD92]), decreasing to 25-40° anteriorly & posteriorly [G97]; length of transverse processes increases posteriorly [G90]; plates supported by angled diapophyses and by ribs; mid-dorsal ribs with T-shaped crossection, flat dorsally [G97]; zygapophyses meet anteromedially to form V-shaped anterior slot [G90]; centra massive [G90]; sexual dimorphism(?) with additional 1st sacral rib (of 4-6) in some species; sacral enlargement of neural canal for sacral plexus, motor nerves for caudofemoralis and other leg muscles, and possibly glycogen body as in birds (unknown function) [G97]; caudo-sacral transition marked by assymetric vertebrae permitting lateral, but not vertical movement of tail [G97]; caudal vertebrae vary considerably with species [G90]; caudal neural canals small [G90]; anterior caudal centra laterally expanded expanded & posterior caudal centra almost square [G97]; **$** posterior caudal centra almost square [SD92 & G97]; ***appendicular:*** **$** parascapular spine with expanded base projecting posterolaterally from shoulder [G90] [SD92]; scapular blade becomes wider distally [G90]; **$** lower scapula (acromion process) broad & plate-like (except *Huayangosaurus*?) [G90] [SD92] [G97]; clavicles, interclavicles & (probably) sternum absent [G90]; forelimbs short & massive [G90]; humerus short, massive, with expanded ends [G97]; humerus with large deltopectoral crest & lateral epicondyle [G90]; **$** humerus with prominent triceps tubercle (see figure) and descending ridge [SD92]; manus elephantine & inflexible [G97]; **$** (1? or) 2 blocklike compound carpals in adults [G90] [SD92]; **$** intermedium & ulnare fused & no distal carpals [SD92][G97]; 5 short metacarpals with short digits, at least two with hoof-like unguals [G90] [G97]; long anterior process of ilium & short posterior process [R56]; short ischium with prominent emminence on dorsal midshaft [G90]; ischia in contact only



Stegosaurus: (A) anterior caudal and (B) dorsal vertebrae in anterior view from Galton (1997)

distally [G90]; **$** long anterior pubic process (>50% length of posterior pubic process) [SD92] [G97]; pubic anterior process distally expanded [G90]; **$** acetabulum oval & laterally directed [SD92] [G97]; strong supraacetabular shelf [R56]; femur columnar, (very) long, flattened anteroposteriorly & wide [G90] [G97]; femur lacks proximal constriction ("neck") [G90]; femur lesser trochanter small or absent [G90]; femur 4th trochanter as low ridge [G90]; tibia short, massive & may be fused with fibula distally [G90]; astragalus massive & articulates proximally only with tibia [G90]; calcaneum small and variable [G90]; metatarsals short, straight & divergent [G90]; pes with I absent & V reduced, II & IV symmetrical [G97]; pedal phalanges much larger than manual [G90]; pes II-IV with hoof-like unguals [G90] [G97]; ***integument:*** 2 parasagittal rows of anterior plates & posterior spikes; **$** "prominent osteoderms that angle slightly away from the sagittal plane and grade in form from ... plates to ... spikes ... ." [SD92]; plates are paired in all except *Stegosaurus* [G97]; plates supported richly vascularized tissue (thermoregulatory?); quadrupedal [G90], graviportal; low-level browsers.



Links: DinoData: Stegosauria; Literature - Stegosauria; Thyreophora: Stegosauria and Ankylosauria - EnchantedLearning.com; FPDM : Stegosauria; Stegosauria; ??????? Stegosauria (Japanese & English); Witmer's Lab Dinosaur Skull Collection: Thyreophora (!!!); DinoDatabase.com -- Discovery and Classification | Stegosauria; **恐竜**:剣**竜類** Stegosauria (models); STEGOSAURIA; Lecture 7 - Ornithischia - Stegosauria; STEGOSAURIA; Dinosaurier-Interesse - Dinosaurier- Gruppe der Stegosaurier (German); Natuurinformatie - Stegosauria (German); Thyreophora.

References: Galton (1990) [G90]; Galton (1997) [G97]; Romer (1956) [R56]; Sereno & Dong (1992) [SD92].

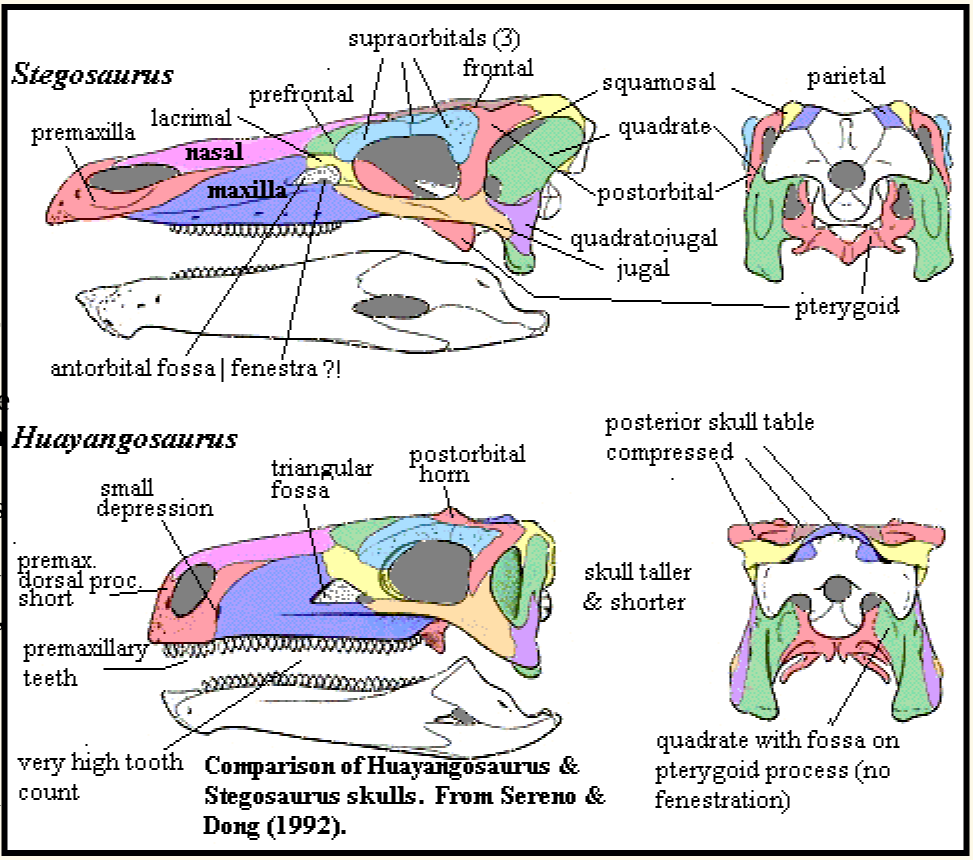
Note: [1] Romer's concept of the Stegosauria is a little different from current ideas. He did not have *Huayangosaurus*, and considered *Scelidosaurus* to be a stegosaurian. Therefore, his description (1956: 632-33) has been selectively incorporated and should be taken with some caution. **[2]** The fusion of the odontode process and axis centrum is strange. Something similar occurs in ceratopsians and is believed to be an adaptation for holding up the massive head. That makes good sense -- but why here? ATW040729

Huayangosauridae: *Regnosaurus* (probably), *Tatisaurus*?

Range: Early Jurassic to Early Cretaceous of Europe and China

Phylogeny: Stegosauria : Stegosauridae + * : *Emausaurus* + *Huayangosaurus*.

Comments: It is still controversial whether or not *Tatisaurus* is a proper stegosaurian, but it is the earliest known (but not the most primitive) member of the dinosaurian clade Thyreophora, a group that included various types of armoured dinosaurs. It is still not very far removed from its "fabrosaur" ancestors, but within a few million years *Tatisaurus*, or a form like it, evolved into large armoured quadrepeds. This poorly-known ornithischian has been related to *Scelidosaurus*, but seems to be more closely related to the Stegosauria. Possibly it represents a form transitional between or ancestral to the two groups.



Comparison of Huayangosaurus & Stegosaurus skulls. From Sereno & Dong (1992).

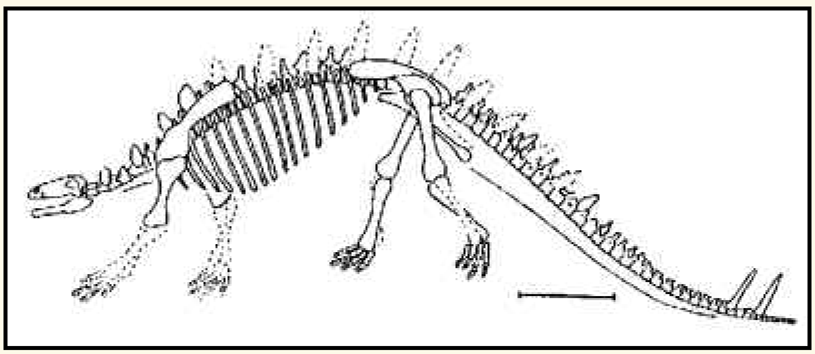
Characters: smaller than stegosaurids; ***skull:*** skull shorter, broader and taller than stegosaurids [SD92] [G97]; premaxillary attachment for beak present [SD92]; dorsal process of premaxilla short & broad [G90]; nares small [G90]; **$** small oval depression between maxilla & premaxilla on lateral snout [SD92]; retain antorbital fenestra [SD92]; antorbital fenestra set in deep, triangular antorbital fossa [SD92]; antorbital fossa rimmed by maxilla & lacrimal, with small contribution from jugal [SD92]; orbits located relatively far forward above posterior cheek teeth; prefrontal overlaps frontal and nasal [SD92]; **$** (possibly sexually dimorphic) little "horns" on postorbital [SD92]; posterior and median processes of postorbital overlap squamosal & jugal (respectively) [SD92]; parietal short (~50% frontal length) [SD92]; vomers short [G90]; braincase poorly known [G90]; stapes slender [G90]; external mandibular fenestra smaller than in stegosaurids [G90]; premaxilla with 7 teeth [G97]; **$** maxilla (and dentary [G90]) with 25-30 teeth [SD92]; no diastema on lower jaw [G97]; ***axial*:** vertebral count 8, 17-18, 4, 35-42 [G90]; **$** anterior dorsal ribs with intercostal flanges ("hamular processes" [G90]) and flared distal ends [SD92]; flared distal rib ends; postzygapohyses separated by notch [G90]; sacrum with 3 large foramina between transverse processes [G90]; ***appendicular:*** scapula without well-defined acromion process [G90]; coracoid wider than long & only slightly wider than scapular blade [G90]; forelimbs relatively long, with humerus 90% of femur length [SD92]; **$** intermedium, ulnare, pisiform and radiale fused to carpal block [SD92]; ilium anterior process broad, angles laterally ~35° [G90]; antitrochanter small [G90]; ischial peduncle pronounced [G90]; ***integument:*** spiked-shaped armor along the body midline; keeled armor scutes in a row down its sides [SD92].

Links: DinoData: Huayangosauridae; Dinosauria Translation and Pronunciation Guide H; Huayangosaurus; Stegosaurs, Ankylosaurs (October 8); New Page 5; Huayangosaurus; Um Corpo Cheio de Espetos (Portuguese); Stegosaurs; Huayangosauridae (German, very brief); DinoWight- Regnosaurus, an Isle of Wight stegosaur (one of the few pages with information on *Regnosaurus*).

References: Galton (1990) [G90]; Galton (1997) [G97]; Sereno & Dong (1992) [SD92] (characters from this ref refer to *Huayangosaurus* only).

Note: this group tends to be discussed in terms of its shared *primitive* characters -- a dangerous sign. ATW020208.

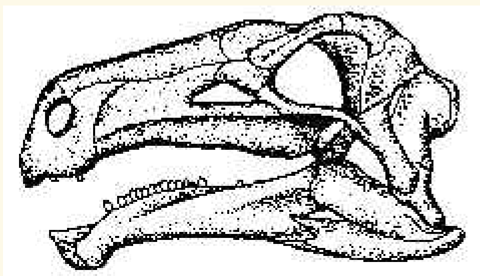
***Huayangosaurus*:**



Range: Middle Jurassic (Bathonian - Calovian) of China

Phylogeny: Huayangosauridae **:** *Emausaurus* + *.

Huayangosaurus taibii Dong, Tang, and Zhou, 1982
Age: Bathonian-Callovian
Place: north-east Pangea
Remains: complete skeleton, skull, fragmentary postcrania
Length: 4.3 meters
Weight: 400 kg



Comments: *Huayangosaurus* is one of the best-known stegosaurians, with remains belonging to over a half dozen individuals. The skull (*left*) is deep with a relatively short snout, and has what may be little "horns," which may be a gender-related character. It is also unique for having armor scutes, something like those of scelidosaurs and ankylosaurs, in a row down its sides. This is one of the characters which indicate that these three groups are descended from a common ancestor and may be combined in a single clade, the Thyreophora. *Huayangosaurus* is protected by two pairs of tail spikes and a pair of spines on the shoulders

Links: DinoData Dinosaurs H046 HUAYANGOSAURUS; Chinese Dinosaurs - Huayangosaurus taibaii; HUAYANGOSAURUS; Movie 5-Huayangosaurus; Huayangosaurus; Yahooligans! Science- Dinosaurs; UM CORPO CHEIO DE ESPETOS; New Page 5; STEGOSAURS, ANKYLOSAURS (October 8); Lecture 7 - Ornithischia - Stegosauria; Otago Museum hosts Dinosaur Exhibition.

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checked ATW060215

Ornithischia: Stegosauridae

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  |  |--Huayangasauridae
|  |  `--Stegosauridae
|  |     |--Dacentrurus
|  |     `--Kentrosaurinae
|  |        |--Kentrosaurus
|  |        `--+--Chialingosaurus
|  |           `--+--Chungkingosaurus
|  |              `--Stegosaurinae
|  |                 |--Lexovisaurus
|  |                 `--+--Stegosaurus
|  |                    `--Wuerhosaurus
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
```

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2. *Chungkingosaurus* X
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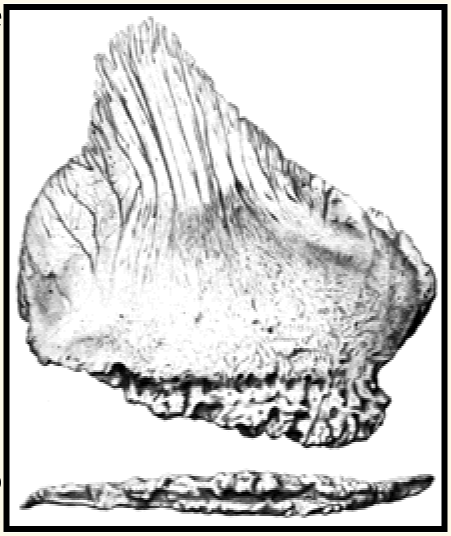
6. *Lexovisaurus* X
7. Stegosauridae X
8. Stegosaurinae X
9. *Stegosaurus* X
10. *Wuerhosaurus* X

Stegosaurus: Blushing Beauty or Jurassic Smart-Ass?

Stegosaurid thermoregulation



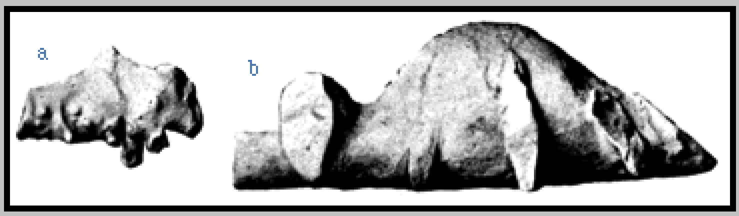
The photograph shows the side and top-bottom view of the large plates on the back of the *Stegosaurus*. Originally thought to have been a form of armour-plating, the plates of advanced stegosaurs were, as can be seen here, actually quite thin and full of holes for the accomodation of blood vessels. For all large animals heat disipation is a big problem (that is why African elephants have such large ears for example), and the stegosaur plates clearly served this purpose. The plates tend to be small and poorly developed (or even absent) in primitive stegosaurids, but more developed in more advanced forms, indicating that they conferred an adaptive advantage. The advantage may have been related to thermoregulation.

Alternatively, it may have related to sexual selection. That is, the plates may have primarily served a display function. Ankylosaurs, after all were equally big and hot and got along perfectly well without an on-board air conditioner of this kind. It may be more logical to assume that the function of the plates was simply to advertise one's sex, species and physical condition: more like an elephant's tusks than an elephant's ears.

One interesting speculation is that *Stegosaurus* blushed. That is, that these animals may have combined thermoregulation and display by forcing blood into the plates to change their color, depending on sex and season.

Stegosaurid brains

Stegosaurids had small brains by Dinosaurian standards, although not so small as to fall below the average range of reptilian brain to body weight ratio (the dim-witted dinosaur - all brawn and no brain is in fact a myth). *Stegosaurus* is famous for its "second brain" - actually an enlarged pelvic nerve plexus situated in the hip region. In fact all dinosaurs and birds and many other sauropsids have such organs (so do mammals, but not developed to such an extent). (MAK990724 & ATW020419)

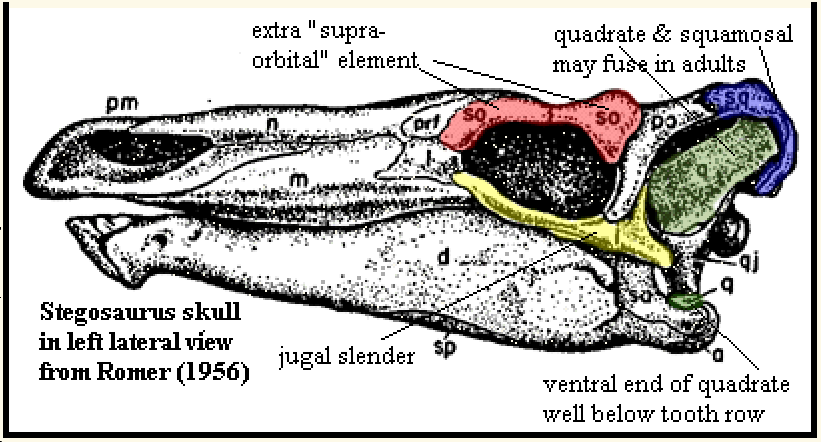


This figure shows the *Kentrosaurus* brain (a) next to the much larger pelvic nerve ganglion (b).

Descriptions

Stegosauridae:

Range: Middle Jurassic to Late? Cretaceous of Eur, NAm, Afr, & China.



Phylogeny: Stegosauria **:** Huayangosauridae + * **:** *Dacentrurus* + Kentrosaurinae.

Characters: ***skull:*** wedge-shaped skull [R56]; skull shallower & narrower than huayangosaurids [G97]; rostrum longer than in Huayangosaurids [G90] [SD92] [G97]; horn beak larger than huayangosaurids [G97]; premaxilla dorsal process long & thin [G90]; external nares relatively large [G90]; neomorphic "supraorbital" directly dorsal to orbits [R56]; jugal slender [R56]; quadrate dorsal head broadly contacts squamosal & paroccipital process [G90]; quadrate dorsal end may be fused to squamosal in adults [G97]; quadrate ventral end well below tooth row [R56]; quadrate mandibular condyle faces lateroventrally [G90]; occiput fairly narrow and solid [R56]; supraoccipital angled ~55° from vertical [G90]; paroccipital processes largely formed by opisthotic [G90]; vomers long, extending to end of tooth row [G90]; prootics extensively sutured with basisphenoid & contribute most of posterior floor of braincase [G90]; lagena moderately well developed [G90]; exoccipitals form much of posterior braincase walls [G90]; basisphenoid basioccipital process short & directed anteroventrally [G90]; sides of sella turcica ossified [G90]; orbitosphenoids present, thin, meet to floor olfactory tract [G90]; laterosphenoids present, short & thick [G90]; external mandibular fenestra larger than in huayangosaurids [G90]; premaxilla toothless [G97]; diastema present after predentary [G97]; maxilla with ~25 teeth or less, dentary with <23 [G90]; maxillary tooth row ends anterior to orbit [G90]; ***axial:*** vertebral count (*Stegosaurus*) 10, 16, 5, ~45 [G90]; rib heads remain distinct on all vertebrae [R56]; dorsal ribs fused to diapophyses to form almost solid dorsal plate up to sternum [G97]; caudal neural spines (see image at Stegosauria) tall, expanded & rugose distally [R56]; caudal neural spines "somewhat bifurcate at midlength" (presumably associated with armor articulation) [R56]; ***appendicular:*** scapula short, with thickened edge which "turns shrply forward well above the coracoid suture" [R56]; prominent acromial process [G90]; coracoid taller than wide [G90]; ilium anterior process angles laterally 40°-50° [G90]; ischial peduncle small & flat [G90]; antitrochanter large [G90]; length of prepubic process increased [G97]; femur lengthened to >145% (from 100% in huayangosaurids) length of humerus [G90] [G97]; femur with 4th trochanter reduced [R56]; poorly developed cnemial crest [R56]; tibia & fibula bow outward away from each other [R56]; astragalus (reduced) and calcaneum may fuse with with tibia and/or fibula [R56]; ***integument:*** flank osteoderms absent [G97].

Links: **DinoData: Stegosauridae**; Ornithischian Dinosaurs - Enchanted Learning Software; stegosauridae.htm (Spanish); Stegosaurids; ORNITHISCHIA.

References: Galton (1990) [G90]; Galton (1997) [G97], Romer (1956) [R56].

Note: [1] *Stegosaurus* and *Kentrosaurus* are sometimes referred to separate eponymous families within Stegosauria, differentiated by the absence and presence (respectively) of spines on the back. **[2]** Some of the descriptive material from Romer (1956: 633-34) has been incorporated on the assumption that his Stegosaurinae is equivalent to Stegosauridae. However, he was more concerned with distinguishing *Stegosaurus* and *Kentrosaurus* from *Scelidosaurus* than from *Huayangosaurus*, which was unknown at that time. 011201.

***Dacentrurus*:**

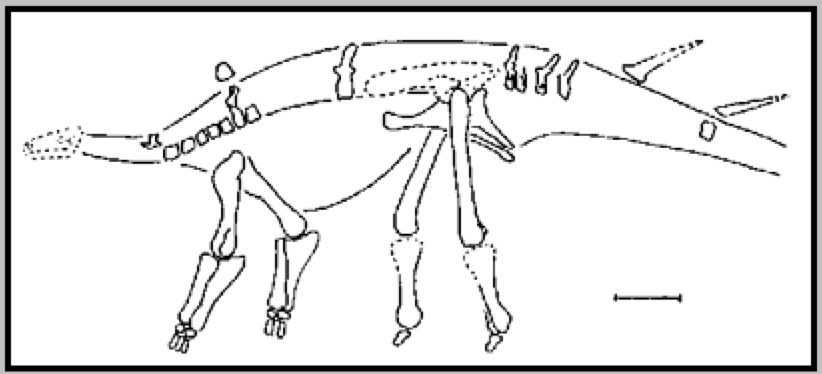
Range: Late Jurassic of Europe

Phylogeny: Stegosauridae **:** Kentrosaurinae + *.

Dacentrurus armatus (= *Omosaurus armatus* Owen, 1875)

Horizon: Lower Kimmeridge Clay of England, Argiles d'Octeville of France, unnamed unit of Portugal

Age: Oxfordian / early Kimmeridgian-late early Tithonian

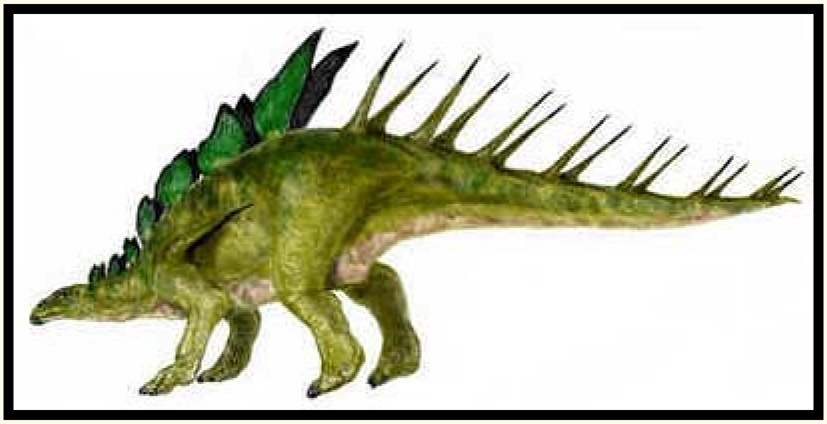


Dacentrurus armatus **Lucas, 1902b**

Place: European islands - middle Laurasia

Remains: two skeletons and assorted postcrania
Length: 7 to 10 meters
Weight: upto 6 tonnes

Comments: This is the first stegosaur described by science, although the original name, *Omosaurus*, had to be changed to *Dacentrurus*, (as it was already applied to another animal). It is the most primitive known stegosaurid, with primitive vertebrae and long forelimbs, and some researchers have suggested it deserves to be put in a separate family. It is also among the largest of the stegosaurs. There are also a number of specilised features in the vertebrae and hip that prevent from being an actual ancestor. As with many early-named European dinosaurs, the species seems to be something of a garbage taxon for fragmentary remains of a generally similiar type, as it is unlikely that one species would persist for a period of some 10 or 12 million years or so. Some remains suggest individuals of 10 meters in length, larger than the biggest *Stegosaurus*. MAK990724.

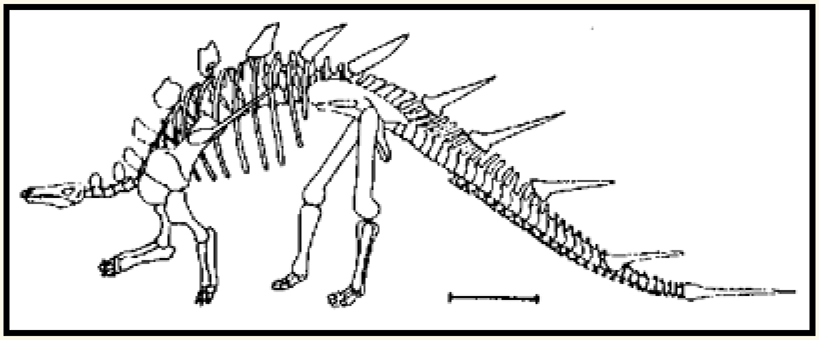


Kentrosaurinae: *Craterosaurus?*

Range: Middle Jurassic to Late? Cretaceous

Phylogeny: Stegosauridae **:** *Dacentrurus* + * **:** *Kentrosaurus* + (*Chialingosaurus* + (*Chungkingosaurus*) + Stegosaurinae))

Comments: These are relatively basal stegosaurids, small to large in size, with generally small spiked plates and numerous spikes along the tail, and sometimes the hips and shoulders as well. A paraphyletic group, they are transitional between the Dacentrurines and the Stegosaurines. MAK990724; ATW031018.



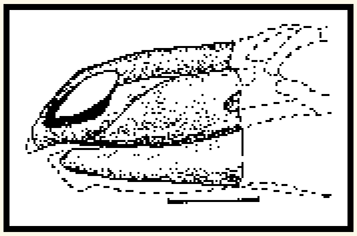
***Kentrosaurus*:**

Range: Late Jurassic (Kimmeridgian) of Africa

Phylogeny: Kentrosaurinae **:** (*Chialingosaurus* + (*Chungkingosaurus* + Stegosaurinae)) + *.

Kentrosaurus aethiopicus Hennig, 1915
Horizon: Tendaguru formation, Tanzania
Age: middle to late Kimmeridgian
Place: central Gondwana
Remains: remains of several individuals
Length: 2.5 to 5 meters
Weight: 450kg

Comments: *Kentrosaurus* is the best known of the primitive spiny stegosaurs. The six pairs of plates are small and located on the neck to the mid back, with the sixth pair transitional between plate and spine. Beyond this are five large pairs of spines along the back and tail, as well as a pair of prominent shoulder spines. Most specimens known are juveniles. The skull contains a number of primitive features. This animal lived at the same time as the larger and more advanced *Stegosaurus*. MAK990724.



***Chialingosaurus*:** *C. kuani* Young, 1959.

Range: Late Jurassic (Oxfordian) of China.

Phylogeny: Kentrosaurinae **::** (*Chungkingosaurus* + Stegosaurinae) + *.

Chialingosaurus

kuani Young, 1959
Horizon: Upper Shaximiao Formation, Sichuan, China
Age: Oxfordian
Place: north-east Pangea / east Laurasia
Remains: skull and skeletal fragments
Length: 4 metres
Weight: about 400 kg?

Characters: High narrow skull; slender limb-bones; front legs relatively long; femur, lesser trochanter triangular, with broad base; small, plate-like spines.

Image: model from **チアリンゴサウルス.**

Links: **DD: CHIALINGOSAURUS**; CHIALINGOSAURUS; Chialingosaurus. MAK990724, ATW031115.

***Chungkingosaurus*:**

Range: Late Jurassic (Oxfordian) of China.

Phylogeny: Kentrosaurinae **:::** Stegosaurinae + *.

Chungkingosaurus laminaplacodus Dong, Zhou, & Zhang,1983
Horizon: Upper Shaximiao Formation, Sichuan Province,China
Age: Oxfordian
Place: north-east Pangea / east Laurasia
Remains: partial skeleton
Length: 3 to 4 metres
Weight: about 400 kg

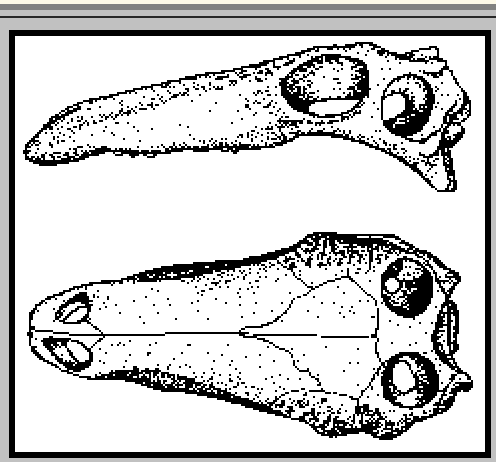
Comments: The skull is high and narrow skull, and the sacrum and humerus primitive, all indicating a less-specialised form than *Stegosaurus* or *Tuojungosaurus*. There are large thick spine-like bony plates (intermediate between spines and plates) and apparently four or five pairs of tail spines. May be transitional between Kentrosaurines and Stegosaurines. MAK990724.

Stegosaurinae: *Monkonosaurus, Paranthodon, Yingshanosaurus*

Range: Middle Jurassic to Late? Cretaceous

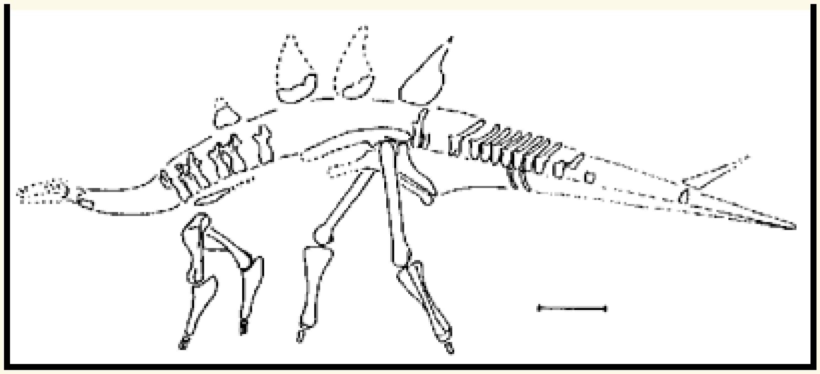
Phylogeny: Kentrosaurinae **:::** *Chungkingosaurus* + * **:** *Lexovisaurus* + (*Tuojiangosaurus* + (*Stegosaurus* **+** *Wuerhosaurus*)).

Comments: The stegosaurines are sometimes divided into two tribes. The "Tribe Tuojiangosaurini" is a paraphyletic taxon; intermediate between the basal kentrosaurs (which they resemble) and the "Tribe Stegosaurini," Generally, the Tuojiangosaurini retain the Kentrosaurine pattern of back and hip spines. The Stegosaurini are distinguished by large size, no spines on hips or shoulders, only two (or rarely 4) pairs of tail spines, relatively short forelimbs, small elongate head, large plates in life covered with skin and blood vessels. This tribe includes only two genera, *Stegosaurus* and *Wuerhosaurus*. MAK990724.



***Tuojiangosaurus* skull in left lateral and dorsal views.**

***Lexovisaurus*:**



Range: Middle Jurassic to Late Jurassic of Europe.

Phylogeny: Stegosaurinae **:** (*Tuojiangosaurus* + (*Stegosaurus* **+** *Wuerhosaurus*)) + *.

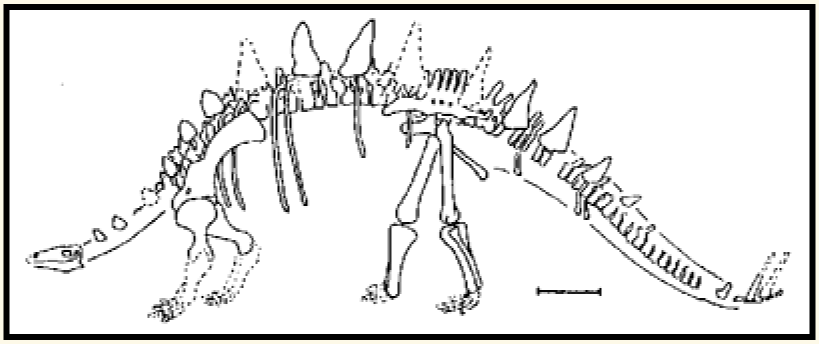
Lexovisaurus durobrivensis (Hulke, 1887)
Horizon: Lower Oxford Clay and Kimmeridge Clay of England, Marnes d'Arences of France
Age: Middle Callovian to early Kimmeridgian
Place: European islands - middle Laurasia
Remains: skeletal elements, 3 partial postcrania,
Length: 5 to 6 metres
Weight: upto 1.5 tonnes

Comments: Superficially quite similar to *Kentrosaurus*, this early stegosaurine is a more closely related to *Stegosaurus*. It has large thin plates, and spines on the hip. In view of the time difference i is unlikely that the fragmentary Kimmeridgian material belongs to the same species as the Callovian material.

Lexovisaurus? vetustus (Huene, 1910)
Horizon: England
Age: Late Bathonian
Place: European islands - middle Laurasia
Remains: juvenile femur

Comments: tentatively assigned to the genus *Lexovisaurus*, although the material is too incomplete to be sure. The oldest known stegosaurid. MAK990724.

***Tuojiangosaurus*:**



Range: Late Jurassic of China

Phylogeny: Stegosaurinae **::** (*Stegosaurus* **+** *Wuerhosaurus*) + *.

Tuojiangosaurus multispinus Dong, Li, Zhou, & Zhang,1973

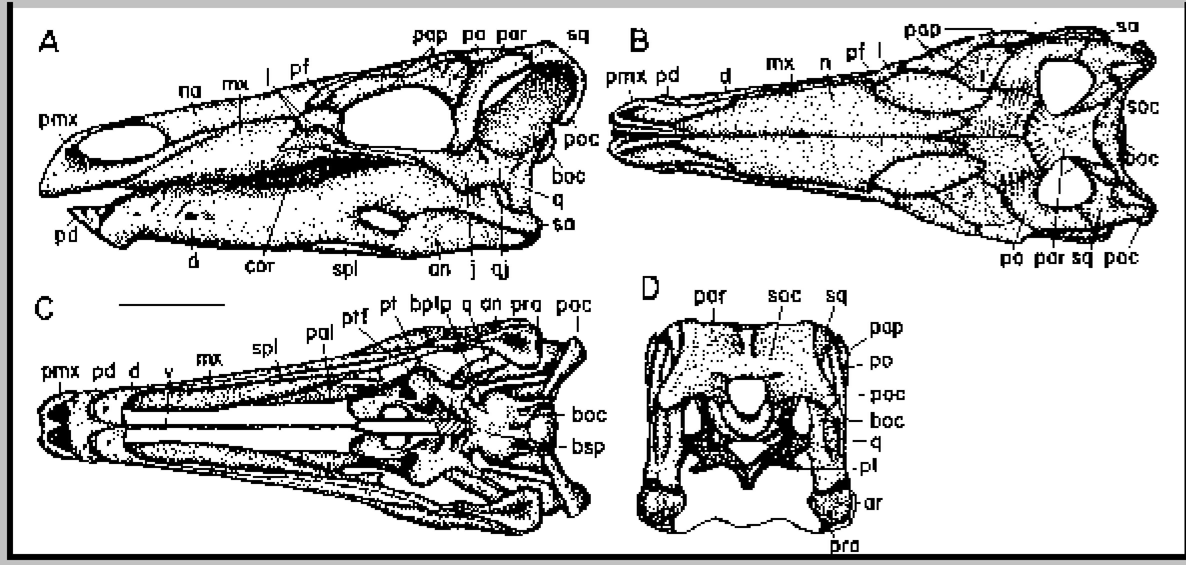
Horizon: Upper Shaximiao Formation, Sichuan, China
Age: Oxfordian
Place: north-east Pangea / east Laurasia
Remains: 2 partial skeletons
Length: 7 metres
Weight: 2 tonnes
Comments: The largest known Jurassic Asian stegosaur. The skull (*left*) is similiar to that of *Stegosaurus*. There 17 pairs of small spiny plates, as well as spines on the shoulders, hips, and tail. MAK990724.

***Stegosaurus*:**

Range: Late Jurassic to Late? Cretaceous

Phylogeny: Stegosaurinae **:::** *Wuerhosaurus* + *.

Note on *Stegosaurus*



***Stegosaurus* skull:** **an** angular, **ar** articular, **boc** basioccipital, **bptp** *basipterygoid process*, **bsp** basisphenoid, **cor** coronoid, **d** dentary, **j** jugal, **l** lacrimal, **mx** maxilla, **n** nasal, **pal** palatine, **pap** palpebrals, **par** parietal, **pd** predentary, **pf** prefrontal, **pmx** premaxilla, **po** postorbital, **poc** paroccipital process, **pra** prearticular, **pt** pterygoid, **ptf** pterygoid flange, **q** quadrate, **qj** quadratojugal, **sa** suarngular, **soc** supraoccipital, **spl** splenial, **sq** squamosal, **v** vomer.

species: The controversial dinosaurologist Bob Bakker distinguishes between two types of *Stegosaurus* -- those with long legs and relatively smaller plates (*Stegosaurus* proper) and a more primitive form with shorter legs and larger plates (*Diracodon*). Dinogeorge however is critical of proposing a new stegosaur genus on this basis. Also, different sources (both in print and on the Web) give different lists of species; e.g. some are synonymised with others. It may be that some of these species are only subspecies or local variants. However, for the sake of completeness (and with the risk of further muddling the issue....) we have listed all the types here.

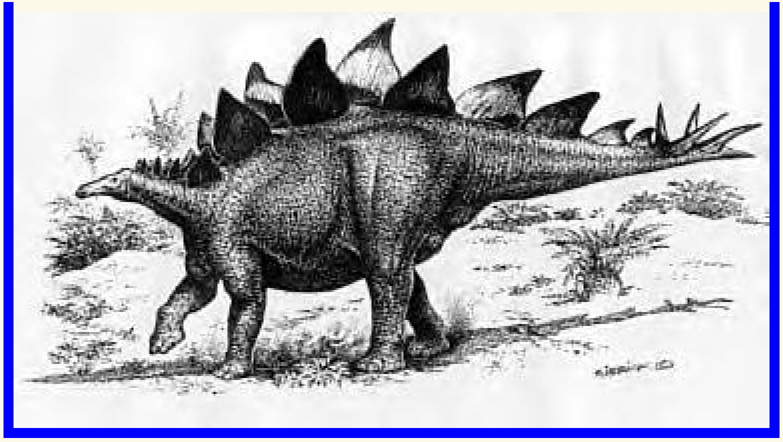
Stegosaurus armatus armatus Marsh,1887
Horizon: Upper Morrison formation, Colorado,Wyoming and Utah, USA
Age: early Tithonian
Place: west Laurasia
Remains: large number of skeletal elements
Length: 6 metres
Weight: 2 tonnes
Comments: The type species of the genus. Has longer legs and relatively smaller plates than *S. stenops*; 2 pairs of tail spines

Stegosaurus armatus ungulatus Marsh, 1879
Horizon: Upper Morrison formation, Wyoming and Utah, USA
Age: early Tithonian
Place: west Laurasia
Remains: large number of skeletal elements
Length: upto 9 metres
Weight: 5 tonnes
Comments: Along with *Dacentrurus armatus*, this is the largest known stegosaurid. The limbs are long and slender. It has four pairs of tail spines, and the middle part of the tail bears paired spine-plates. The sacral centra are broad and rounded and lack a ventral keel. This may be variant of *S. armatus*, rather than a distinct species.

Stegosaurus stenops stenops Marsh, 1877
Horizon: Morrison formation, Colorado,Wyoming and Utah, USA
Age: Kimmeridgian to early Tithonian
Place: west Laurasia
Remains: large amount of skeletal elements
Length: 6 to 7 metres
Weight: 2 tonnes
Comments: S. stenops has very large plates and relatively shorter legs. The sacral centra have a ventral keel. There are two pairs of tail spines. Bob Bakker sugests this species should be relocated under its original genus *Diracodon*

Stegosaurus stenops laticeps Marsh, 1881

Horizon: Morrison formation, Wyoming , USA
Age: late Kimmeridgian
Place: west Laurasia
Remains: large number of skeletal elements
Length: 6 metres
Weight: 2 tonnes
Comments: This form may be same as *S. stenops*



Stegosaurus longispinus Gilmore,1914
Horizon: Morrison formation of Utah, USA
Age: Early Tithonian
Place: west Laurasia
Remains: fragmentary skeleton
Length: 7 metres
Weight: 2 tonnes
Comments: This species is distinguished by two pairs of very elongate (a meter in length) tail spines. MAK990724.

Links: **DinoData Dinosaurs S113 STEGOSAURUS**; Stegosaurus - Dinosaur - Enchanted Learning Software; Stegosaurus (and you thought *we* were demented!); Home Page (Student site, but nicely done); BBC - Walking with Dinosaurs - Fact Files; Summing Up Stegosaurus, 1914; Stegosaurus (Danish). ATW030901.

***Wuerhosaurus*:**

Range: Early Cretaceous to Middle Cretaceous of China

Phylogeny: Stegosaurinae **:** *Stegosaurus* + *.

Characters: body relatively and short and wider at hip than other stegosaurids; proximal caudal neural spines very long;11 dorsal vertebrae; long, large, low, rounded back plates; back plates alternating, not paired; sacrum with almost solid dorsal plate; *thagomizer* with 4 spikes; forelimbs very short; ischium distal end dorsoventrally expanded.

Wuerhosaurus homheni Dong,1973
Horizon: Lianmuging Formation, Xinjiang Uygur Zizhiqu,China
Age: Valanginian/Hauterivian/Barremian/Aptian/Albian
Place: east Laurasia
Remains: partial skeletons
Length: 6 to 8 metres
Weight: 2 to 3 tonnes
Comments: Among the last of the stegosaurs, *Wuerhosaurus* is closely related to *Stegosaurus*, with a similiar arrangement of plates and spines. It differs in that *Wuerhosaurus* plates are long and low, unlike the tall lozenge-shaped plates of *Stegosaurus*.

Wuerhosaurus ordosensis Dong 1993
Horizon: Lianmuging Formation, Xinjiang Uygur Zizhiqu,China
Age: ?Barremian
Place: east Laurasia
Remains: partial skeletons
Length: 4 metres
Weight: about 500 kg
Comments: A small species of this genus

Links: Wuerhosaurus Fact Sheet - EnchantedLearning.com; WUERHOSAURUS; DinoData Dinosaurs W008 WUERHOSAURUS; Dinosaur museum (Chinese); ?????? ??? (Japanese).

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checked ATW060215

Ornithischia: Ornithopoda

Hypsilophodonts

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  `--+--Hypsilophodontidae
   |     |  |--Leaellynasaura
   |     |  |--Thescelosaurus
   |     |  `--+--Zephyrosaurinae
   |     |     `--+--Othnieliinae
   |     |        `--Hypsilophodontinae
   |     `--Hadrosauridae
   `--+--Heterodontosauridae
      `--Marginocephalia
         |--Pachycephalosauria
         `--Ceratopsia
```

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7. *Thescelosaurus* X
8. Zephyrosaurinae X

Editor's note: Parts of this page are in need of taxonomic and phylogenetic revision. For one thing, the Hypsilophodontidae are now considered a paraphyletic grade of early ornithopod-like cerapodans (Zheng et al. 2009, Butler et al. 2011, Dinosaur Supertree, Open Dinosaur Project); for another, the imformal subfamilies coined here are most likely polyphyletic, although some genera, such as *Othnielia* (= *Othnielosaurus*), would seme to contain several species. MAK120309

Ornithopoda

The Ornithopods are the second most succesful and complicated herbivorous group in Earth history (the first being the ungulates). In fact, the basal *Heterodontosaurus* shows some vaguely mammal-like dental adaptations. However, Mesozoic success must have lain in another direction -- perhaps several other directions. The branching structure of the group is still fairly unclear. The general sequence of evolutionary events is:

Heterodontosauridae
Hypsilophodontidae
Iguanodontidae
Hadrosauridae

However, it is not known whether the hypsilophodonts were a clad or a series of branches from a lineage leading from near *Heterodontosaurus* to the iguanodonts. There is now a general concensus that the iguanodonts are *not* a clade. That is, the traditional family of iguanodonts are indeed a series of intermediates between more basal ornithopods and the Hadrosauridae. The final flowering of the ornithopods, at the end of the Mesozoic were the specialized hadrosaurs of the Lambeosaurinae, with huge, elaborate nasal crests that may have acted as resonating chambers. We cannot see or hear them now, but it is impressive even to imagine a herd of *Parasaurolophus* on the move, hooves pounding the ground, blasting ear-splitting, braying calls -- an unstoppable brass and tympani crescendo like the *Dies Irae* from Verdi's *Requiem*. ATW020419.

The Hypsilophodonts

The hypsilophodonts are a paraphyletic assemblage of mostly small and lightly built, fairly primitive, ornithopods These small active bipedal animals were clearly the dinosaurian equivalent of small ungulate mammals like deer and gazelles.

In many current dinosaur cladograms, the term Hypsilophodontidae, referring to a sister taxon to the Iguanodontia, is now discarded as these animals are believed to be a paraphyletic succession (like "Pelycosauria"), rather than a clade in themselves. While I agree that hypsilophodonts are the most plausible ancestors of the Iguanodontia, I am not happy with the current phylogeny, as it ignores too much of the evidence of fossil record. In the evolutionary sequence *Hypsilophodon* - *Dryosaurus* - *Camptosaurus* - *Iguanodon*, the hypsilophodontids gave rise very early to the dryosaurs, perhaps only a few million years after evolving (both groups appeared in the middle or late Jurassic). Rather than the numerous ghost lineages implied in the currently popular cladogram of early ornithopod relationships, it is more likely there were a few groups, evolving alongside each other. However, details of hypsilophodont evolutionary relationships will have to await more and better fossils.

As well as typically small forms there were also unusual and specialized larger types. *Tenontosaurus* is sometimes considered a basal iguanodontian; *Muttaburrasaurus* is variously considered a basal iguanodontian, a specialized hypsilophodont, camptosaurid, or an iguanodontid. Both were large (around 6 meters)middle Cretaceous animals. Personally I think it is more reasonable to assume that a lot of the supposedly advanced iguanodontian features of these two genera are simply a result of adaptation to larger size, more efficient food-processing, etc. After all, the original iguanodontians appeared some fifty million years earlier at least, in the form of Late or even Middle Jurassic dryosaurs and camptosaurs. It is implausible that these larger hypsilophodonts should continue invisible for millions of years, suddenly appearing fully formed in the mid Cretaceous like Athena from the forehead of Zeus. What may be more likely is that they were side branches of one or more contemporary hypsilophodontid lineages already known from fossils. In any case, there is no doubt that a number of ornithopod types were evolving alongside each other and in parallel during the late Jurassic and throughout the Cretaceous. Thus *Thescelosaurus*, one of the last ornithopods, is also one of the most primitive, a living fossil continuing alongside more advanced forms. MAK011118.

Other Ornithopods

The single most important group of middle to late Mesozoic terrestrial herbivores, the Ornithopods include a diverse range of small to very large generalised mostly bipedal herbivores, almost all of anywhere from the Late Jurassic to Late Cretaceous periods, and ranging in size from less than a meter to over fourteen metres in length. At one time they were considered the ancestral types from which the other lines of Ornithischia developed. MAK010112.

Broadly speaking, there are three recognizable types. The **Hypsilophodontidae** were very small, as dinosaurs go, with almost parrot-like beaks and a distinctly bipedal stance. Some workers believe that the Marginocephalia are directly derived from this group. The **Iguanodontidae** are traditionally the transitional forms: much bigger than the hypsilophodonts, with elongated snouts and narrow tooth rows. "True" iguanodonts posess an unusual thumb-spike. In a cladistic sense, the Iguanodontia are rather hard to define. However, they certainly include the final group, the **Hadrosauridae**. Perhaps the hadrosaurids' most salient characteristic is the dental battery, with multiple generations of teeth all working simultaneously to form a remarkably effective food processing apparatus. ATW020420.

Descriptions

Cerapoda: (Sereno, 1986): Definition: Ornithopoda + Marginocephalia

Range: Early Jurassic to Late Cretaceous

Phylogeny: Genasauria: Thyreophora + * **:** Ornithopoda + Marginocephalia.

Characters: <6 premaxillary teeth; substantial diastema; asymmetrical enamel on teeth of both upper and lower jaws; absence of supra-acetabular buttress.

Links: **DinoData: Cerapoda**; ornithischia; Lectures 17 and 18 - Late Jurassic: Morisson, Tendaguru; Basal Ornithischia.

Note: This clade may be synonymous with Ornithopoda, or even Genasauria. The record of Triassic ornithischians is very sparse, and the major ornithischian groups clearly radiated from rather similar basal stock in that period. In particular, it is quite possible that the marginocephalians derived from an early hypsilophodont or perhaps a heterodontosaur. The idea that even Thyreophora derived from ornithopods is discussed by Conrad (2000). This position is less widely held, but cannot be entirely excluded. ATW010327.

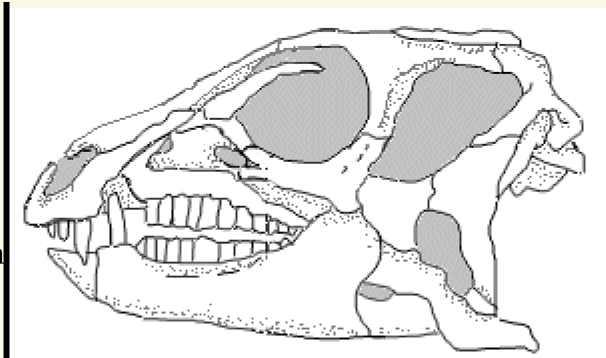
Ornithopoda: *Camptosaurus*.

Range: Early Jurassic to Late Cretaceous

Phylogeny: Cerapoda: Marginocephalia + * **:** Heterodontosauridae + (Hypsilophodontidae + Iguanodontia).

Characters: Premaxillary tooth row offset ventrally compared to maxillary; jaw joint well below level of tooth rows by ventral extension of quadrate. ATW991004.

Heterodontosauridae: *Abrictosaurus*, *Heterodontosaurus*, *Lanasaurus*.



Heterodontosaurus tucki: skull in left lateral view. After Smith (1997).

Range: Early Jurassic of South Africa and China

Phylogeny: Ornithopoda: (Hypsilophodontidae + Iguanodontia) + *.

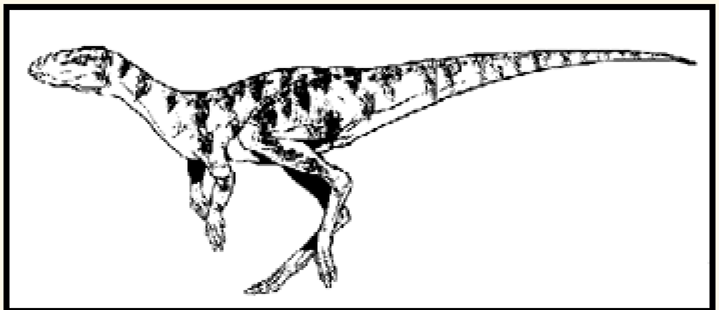
Characters: Small (1-2m, <20 kg); high-crowned cheek teeth with chisel-shaped crowns; denticles on distal 1/3rd of cheek teeth; large, caniniform teeth on premaxillae & dentary; small tusks perhaps restricted to males; teeth absent from tips of jaws (probable beak); enamel thickened on labial side of upper teeth & lingual side of lowers; neck short; ossified tendons on last dorsal, but not caudal vertebrae; tail long; powerful arms with possible digging ability; tibia & fibula fused; forelimbs markedly smaller than hindlimbs; astragalus & calcaneum likewise fused to crus; horizontal posture, but bipedal; may have dug for food.

Note: This group may also contain *Echinodon* (Late Jurassic of Europe).

Image: originally after In Hand Museum (former site), with osteology corrected and some details altered per Smith (1997).

Links: **DinoData: Heterodontosauridae**; Heterodontosaurus; Heterodontasaurus Tucki; Heterodontosaurus - Enchanted Learning Software; ornithischia; Untitled Document; Heterodontosauridae (Dutch); The Natural History Museum's Dino Directory; Heterodontosauridae; (Mikko's phylogeny); DINOSAURS- Family Heterodontosauridae (brief discussion); Dinosaurs-Exam 3 Notes AKA- Adrian's Uber-Notes; HETERODONTOSAURIDS; Heterodontasaurus Tucki; ORNITHISCHIA.

References: Galton (1986); Smith (1997); Weishampel (1984). ATW030426.

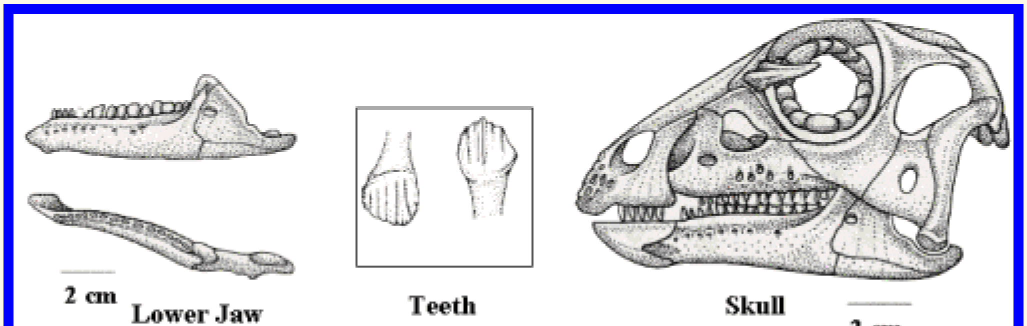


Hypsilophodontidae: *Hypsilophodon*. *Hypsilophodon* > *Iguanodon* ?

Range: Middle Jurassic to Late Cretaceous of Europe, North America, Australia, China, & Antarctica.

Phylogeny: Ornithopoda:: Iguanodontia + * **:** *Leaellynasaura* + *Thescelosaurus* + (Zephyrosaurinae + (Othnieliinae + Hypsilophodontinae)).

Characters: 1-4 m bipedal herbivores. **$** cingulum on dentary teeth; teeth present on premaxilla which may have also sheared against dentary teeth; broad, chisel-shaped teeth; continuous, if uneven occlusal surface; premaxillary tooth row (when present) below maxillary tooth row; also horn beak for cropping; subnarial ramus of premaxilla contacts prefrontal or lacrimal; maxilla rotates on peg & socket within premaxilla (pleurokinesis); highly mobile jaw allowed upper jaw to rotate out – shearing; fused parietals form medial crest; mandibular condyle below level of cheek teeth (long quadrates); **$** small quadratojugal; crescentic paroccipital processes; **$** sternal portion of ant ribs ossified; long tail with tendons partially ossified; tail with hypaxial (as well as epaxial) tendons; scapula shorter than humerus; long forelimbs, grasping (not running) hands; manus 2-3-4-?3-?1; **$** pre-pubic process extends upward toward tip of ilium & is rod-like, wider than deep; obturator process on ischium; tibia < femur (fast biped?); long, robust cursorial legs; pes 2-3-4-5-0. Embryos found with well-formed joint surfaces (mobile & less parental care?).



Hypsilophodon Dental Battery for Grinding Vegetation

Links: **DinoData: Hypsilophodontidae;** Lecture 14 - Late Jurassic: Morrison, Tendaguru; Willo: the Dinosaur with a Heart - Fast Facts; Zephrosaurus schaffi; Hypsilophodon - Dinosaur - Enchanted Learning Software; Dann's Dinosaur Info: LEAELLYNASAURA; Dinosaurier.org / Saurier-Web.de Forschungsnachrichten (German); CLADOGRAMS; DINOSAURIAN UNGULATES; Biology 356; DINOBASE, Sibbick's dinosaur pictures; Pretty Butte Paleontology- Catalog of Hypsiliphodontidae Fossils (nice images of bits and pieces); Saurier-Web.de Forschungsnachrichten (German: discovery of a comparatively huge hypsie, *Tenontosaurus*. We classify *Tenontosaurus* as a basal iguanodont. The difference is largely one of nomenclature -- see Note below); Paleontologia - GEOMODEL (There's a reason the Rennaissance began in Italy...); Dinosaurs-Exam 3 Notes AKA- Adrian's Uber-Notes.

Image: (reconstruction) ***Zephyrosaurus***; (skull and jaw elements) **Dinosaurs-Exam 3 Notes AKA- Adrian's Uber-Notes**.

Note: There is continuing doubt about the status of this taxon, some arguing that hypsilophodonts are a series of stem Iguanodonts. The difference really depends more on exactly how the Hypsilophodontidae are defined.

***Leaellynasaura*:**

Range: middle Cretaceous of Australia

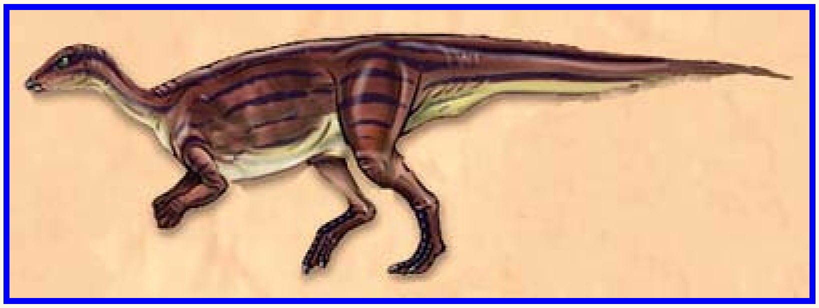
Phylogeny: Hypsilophodontidae: *Thescelosaurus* + (Zephyrosaurinae + (Othnieliinae + Hypsilophodontinae)) + *.

Leaellynasaura amicagraphica Rich and Rich, 1989
Horizon: Otway Group of Dinosaur Cove, Victoria, Australia
Age: early Albian
Place: South-East (Polar) Gondwana
Remains: partial skull (juvenile), isolated postcrania
Length: adult about 1 meters
Weight: about 7 kg

Comments: The best known of all the small Australian hypsilophodonts. Distinctive ridges on the unworn maxillary teeth different from those of the contemporary *Atlascopcosaurus*. The femur shows some primitive fabrosaur-like features. The eyes are very large, and the brain cavity shows an enlarged optic lobe, suggesting nocturnal vision. This animal lived in a polar environment, and hence needed to see during the long periods of darkness. If so, it was quite likely to have been endothermic (warm-blooded) as well. Even if the Antarctic climate was not as severe as it is today, the temperature still frequently dropped below freezing, and it is difficult to see how a small cold-blooded animal could remain active in such an environment. As with many of these animals, the incomplete nature of the material means that *Leaellynasaura*'s evolutionary relationships are unclear. It seems to have some similarities to the zephyrosaurines or possibly the Othnieliinae (*Thescelosaurus!*). Others place it with *Othnielia* and *Zephyrosaurus* in an unnamed new family. MAK011118.

Links: Dann's Dinosaur Info: LEAELLYNASAURA

***Thescelosaurus*:**



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

Phylogeny: Hypsilophodontidae: *Leaellynasaura* + (Zephyrosaurinae + (Othnieliinae + Hypsilophodontinae)) + *.

Thescelosaurus neglectus Gilmore, 1913
Horizon: Scollard Formation of Alberta, Frenchman Formation of Saskatchewan, Laramie Formation of Colorado, Judith River and Hell Creek Formations of Montana, Hell Creek Formation of South Dakota, and Lance Formation of Wyoming
Age: late Maastrichtian
Place: Eastern Asiamerica

Remains: 8 partial skeletons, along with cranial and postcranial elements
Length: 3 to 3.5 meters
Weight: 250 kg

Comments: one of the last of the dinosaurs, a contemporary of the great *Tyrannosaurus* and *Triceratops*, this animal was apparently very primitive by ornithopod standards. It was more heavily-built and stouter of limb then most hypsilophodonts, and probably, like its bigger cousins *Tenontosaurus* and *Muttaburrasaurus*, or even a small iguanodontid, and capable of getting about on all fours. Features distinguishing it from other hypsilophodonts are the presence of premaxillary (front upper jaw) teeth and five toes per foot. Its femur and tibia were of equal length, indicating a not very fast moving animal. There seem to have been bony studs or osteoderms along the back, perhaps to compensate for lack of fleetness of foot.

It is a strange fact that such a primitive and seemingly clumsy animal was able to flourish at the very end of the age of dinosaurs, at a time when many more specialized forms had already been driven into extinction. Perhaps its very primitiveness and generalized adaptations helped it in this regard. *Thescelosaurus* and its close cousin *Bugenasaura* must have had immediate ancestors living during the late Jurassic and the Cretaceous, but none have been found as yet. MAK011118.

Characters: 3-4 m; small head; beak; premaxillary teeth; orbits large; fairly massive, low slung body; long, pointed tail; short arms; 5 fingers; rod-like prepubic process; tibia shorter than femur; 4 toes.

Links: **DinoData THESCELOSAURUS**; Willo, the Dinosaur with a Heart; Thescelosaurus Printout - ZoomDinosaurs.com; ornithopoda (From the *Thescelosaurus!* site: **Best on the Web**); Thescelosaurus - Suite101.com; Dino Land Dinosaur Photos: Thescelosaurus; THESCELOSAURUS;

Image: from www.dinoheart.org, substantially modified. ATW010730.

Zephyrosaurinae: *Zephyrosaurus*, *Orodromeus*

Range: middle to Late Cretaceous of North America

Phylogeny: Hypsilophodontidae:: (Othnieliinae + Hypsilophodontinae) + *.

Although apparently less specialized than the Othnieliinae, these animals lived later (in the Cretaceous rather than the Jurassic period). One may wonder about the phylogenetic analysis, especially in view of the fairly scanty material available. They are distinguished by specialized skull characters, such as a bony boss or expansion on the jugal (cheek-bone), which means they are probably a monophyletic side-branch from the main line of ornithopod evolution. These were fast running animals.

Zephyrosaurus schaffi Sues, 1980a
Horizon: Cloverly Formation of Montana
Age: late Aptian-early Albian
Place: Western Laurasia
Remains: partial skull, postcrania
Length: 1.8 meters

Comments: Distinguished by an unusual skull. For more info, see the DinoData

Orodromeus makelai Horner and Weishampel,1988
Horizon: Two Medicine Formation of Montana, USA
Age: late Campanian
Place: Eastern Asiamerica
Remains: several individuals
Length: 2.5 meters
Weight: 10 to 70 kg

Comments: Features on the skull indicate a relationship with *Zephyrosaurus*. Teeth are primitive. In contrast to *Hypsilophodon*, the tibia (shin bone) is considerably longer than the femur (thigh bone). Nests once assigned to this species may actually belong to a small theropod. *Laosaurus minimus* Gilmore, 1924b from the late Campanian of

Alberta. MAK011118

Othnieliinae: *Othnielia, Yandusaurus*(?), *Drinker*.

Range: Middle to Late Jurassic.

Phylogeny: Hypsilophodontidae::: Hypsilophodontinae + *.


Othnielia

Introduction: A group of small Jurassic hypsilophodonts. As with others of the clan, the legs and tail are long, the body lightly built, and the forearms short. The teeth however are distinctive, being proportionally smaller, and completely covered in enamel (rather than only on the grinding surfaces). This may have indicated a tougher more abrasive food source.

Othnielia rex Galton, 1977b (= *Nanosaurus rex* Marsh, 1877b)
Horizon: ? Colorado, Utah, and Wyoming
Age: late Kimmeridgian and early Tithonian
Place: north-west Pangea / Western Laurasia
Remains: several partial skeletons
Length: 1.2 to 1.4 meters
Weight: 40 kg

Comments: Closely resembles *Hypsilophodon* in the structure of the skeleton, but some features mean it has been placed in a separate taxon

Othnielia nisti (Bakker, Galton, Siegwarth, and Filla, 1990) (= *Drinker nisti* Bakker, Galton, Siegwarth, and Filla, 1990)
Horizon: Upper Morrison Formation of Wyoming
Age: later early Tithonian
Place: north-west Pangea / Western Laurasia
Length: 30 cm (juvenile) - adults 1.4 meters
Weight: 37 kg

Comments: Presumably a relative or descendent of *Othnielia rex*, this little dinosaur is probably not different enough to deserve a new generic name. It had long spreading toes, indicating that it lived in swampy terrain. This small animal lived after the extinction of the Jurassic megafauna. MAK011118.

Image: by Michael Corriss, reproduced by permission.

Links: **DinoData Dinosaurs O059 OTHNIELIA;** Utahraptor and Othnielia Photos; Othnielia - Dinosaur - Enchanted Learning Software; OTHNIELIA; Othnielia; Othnielia; EXPO 2002; BBC - Walking with Dinosaurs - Fact Files; **無題 標準ページ**. ATW031008.

Hypsilophodontinae: *Hypsilophodon, Yandusaurus*

Range: Middle Jurassic to Late Cretaceous of China, Europe & North America

Phylogeny: Hypsilophodontidae::: Othnieliinae + *.

As used in the present limited context, refers to a fairly advanced small to medium-sized lightly-built fast-running bipedal herbivores. Although *Hypsilophodon* is the only genus known for certain in this assemblage, the very early (middle Jurassic) *Yandusaurus* may also belong here. The Late Cretaceous *Parksosaurus* may also be a hypsilophodontine, although it displays more advanced *Dryosaurus*-like features. These animals, or creatures very like them, evolved into dryosaurs. MAK

Yandusaurus hongheensis He, 1979

Horizon: Xiashaximiao Formation Sichuan, China
Age: Bathonian/Callovian
Place: north-east Pangea / Eastern Laurasia
Remains: Two nearly complete skeletons with skull.
Length: 1.5 to 2 meters
Weight: 10 to 43 kg

Comments: This early form may belong in the Hypsilophodontinae. MAK

Hypsilophodon foxii Huxley, 1869
Horizon: Wealden Formation of East Sussex, Maris, and Isle of Wight, England; and Las Zabacheras Beds, Provincia de Teruel, Spain
Age: Barremian
Place: European Islands (north-central Laurasia)
Remains: over a dozen partial or complete skeletons, and additional incomplete remains
Length: adults 2.3 meters
Weight: 70 kg

Comments: A number of partial and complete skeletons, mostly juveniles. It was at one time believed that this animal was arboreal, and there is a famous painting by Neave Parker showing it perched on a large branch. It was later realized that this was a purely ground living, active cursorial (running) animal. MAK.

Parksosaurus warrenae Sternberg, 1937
Horizon: Horseshoe Canyon Formation of Alberta
Age: early Maastrichtian
Place: Eastern Asiamerica
Remains: incomplete skeleton and skull.
Length: 2.4 meters
Weight: 70 kg

Comments: A late, advanced form, with a distinctive skull. More advanced than *Hypsilophodon* in some features, while more primitive in some features of the skull. The large eyes indicate well developed vision, possibly nocturnal or in dim light. Like other hypsilophodonts, this animal probably foraged among the forest undergrowth. MAK.

Links: DinoData Dinosaurs H064 HYPSILOPHODON; **DinoData Dinosaurs P040 PARKOSAURUS;** Paleontology and Geology Glossary- Y; YANDUSAURUS; Yandusaurus hongheensis; Hypsilophodon - Dinosaur - Enchanted Learning Software; DinoWight- Hypsilophodon, an Isle of Wight Hypsilophodontid; Eotyrannus attacking Hypsilophodon; FPDM - Hypsilophodon foxii; HYPSILOPHODON.

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checked ATW060211

Iguanodontia

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Iguanodontia
   |     |--Muttaburrasaurus
   |     `--+--Tenontosauridae
   |        |  |--Tenontosaurus
   |        |  `--Rhabdodon
   |        `--+--Dryosauridae
   |           `--+--Iguanodontidae
   |              `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
```

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6. "Tenontosauridae" X
7. *Tenontosaurus* X

Editor's note: Parts of this page are in need of taxonomic and phylogenetic revision. The unofficial families "Muttaburrasauridae" and "Tenontosauridae" should be discarded, the former being polyphyletic and the latter monotypal (though that wouldn't necessarily invalidate it) On the other hand, *Rhabdodontidae* is a proper taxan, and should be added for *Rhabdodon* and co (possibly also including *Muttaburrasaurus*) (McDonald et al. 2010) MAK120309

Descriptions

Iguanodontia: *Iguanodon* > *Hypsilophodon*.

Range: Middle? Jurassic to Late Cretaceous

Phylogeny: Ornithopoda:: Hypsilophodontidae + * **:** *Muttaburrasaurus* + (Tenontosauridae + (Dryosauridae + (Iguanodontidae + Hadrosauroidea)))

"Muttaburrasauridae"

Migrating *Muttaburrasaurus* herd. from Walking with Dinosaurs © 1999 ABC, BBC

Range: middle Cretaceous of Australia.

Phylogeny: Iguanodontia: (Tenontosauridae + (Dryosauridae + (Iguanodontidae + Hadrosauroidea))) + *.

Comment: It is possible that the large *Muttaburrasaurus* and the small *Atlascopcosaurus* and *Qantassaurus* are related, in which case they could be grouped in an unofficial family "Muttaburrasauridae". Whether this is true or not, there is no doubt that a number of unique hypsilophodontids or basal iguanodontians populated south-east Gondwanaland, at the time right on the south pole. This assemblage features a greater diversity of hypsilophodonts then anywhere else in the world. MAK011118.

Qantassaurus intrepidus Rich and Vickers-Rich, 1999
Horizon: Strzelecki Group of Victoria, Australia
Age: late Aptian
Place: South-East (Polar) Gondwana
Remains: partial lower jaws (two dentaries with teeth)
Length: about 1.8 meters
Comments: Differs from all known hypsilophodonts in having only 12 teeth in the lower jaw, indicating a shorter, deeper face.
Links: Dann's Dinosaur Info: QANTASSAURUS. MAK011118.

Atlascopcosaurus loadsi Rich and Rich, 1989
Horizon: Otway Group of Dinosaur Cove, Victoria, Australia
Age: early Albian
Place: South-East (Polar) Gondwana
Remains: partial upper jaw (Maxilla, teeth)
Length: 2.7 meters
Weight: 125 kg
Comments: Resembles *Zephyrosaurus* in the structure of its unworn maxillary teeth except for a more pronounced primary ridge Sues & Norman (1990). It is also suggested (ref *Thescelosaurus!*) that *Muttaburrasaurus* may be closely related to it, despite the latter's much larger size. Some isolated femora found at the same locality may or may not belong to this species. MAK011118.

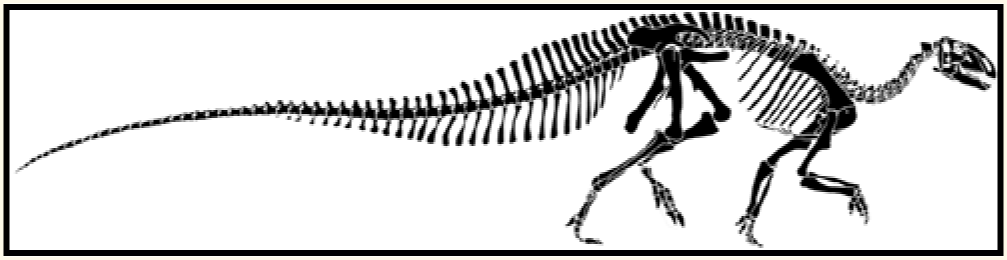
Muttaburrasaurus langdoni Bartholomai and Molnar, 1981
Horizon: Mackunda Formation of north-central Queensland; *Muttaburrasaurus sp.* from other localities
Age: middle Albian
Place: East Gondwana

Remains: Skull and partially complete skeleton, also a fragmentary skeleton
Length: 7 meters
Weight: 1100 kg
Comments: Perhaps Australia's best known dinosaur; certainly it represents one of the most complete skeletons of any dinosaur from this region. Originally included under the Iguanodontidae which it resembles in size and body proportions, and compared to *Camptosaurus* (similar cranial proportions), it is now thought to be more primitive than either. *Muttaburrasaurus* was most probably quadrupedal, with a broad low skull bearing a remarkable hollow chamber on the snout, reminiscent of *Altirhinus* (iguanodont) and *Kritosaurus* (hadrosaurid). This was probably a resonating chamber, although it may also have enhanced the sense of smell (both options are not exclusive, e.g. calls during the mating season, and smell to detect a mate). Unlike all other ornithopods, *Muttaburrasaurus* had a very powerful, ceratopsian-like shearing, rather than a grinding, dentition. Molnar (1991). This seems to represent an approach to increased chewing efficiency distinct from the iguanodontian one. Although it has been suggested that *Muttaburrasaurus* may have been partially carnivorous, this seems a misinterpretation of its unique and obviously efficient oral processing mechanism. The original identification of an *Iguanodon*-style thumb-spike also appears to be in error. A second skull is known, from a slightly earlier form, which appears to represent a more primitive (possibly ancestral?) species.

Links: Dann's Dinosaur Info: MUTTABURRASAURUS (**Best on the Web**). MAK011118.

References: Molnar (1991); Sues & Norman (1990)

Tenontosauridae: *Rhabdodon*, *Tenontosaurus*



Range: middle to Late Cretaceous of North America and Europe.

Phylogeny: Iguanodontia:: (Dryosauridae + (Iguanodontidae + Hadrosauroidea)) + * **:** *Tenontosaurus* + *Rhabdodon*.

Note: I have included here the Laurasian members of the family. If *Muttaburrasaurus* and related forms are tenontosaurs then the two lineages, geographically isolated, followed very different evolutionary paths, although both paralleled the contemporary camptosaurids and iguanodontids, and doubtless fulfilled a similar ecological role. Although the tenontosaurids are similar in overall size, and in skull proportions, to the iguanodontids, the structure and arrangement of the teeth could place them among the Hypsilophodontidae. MAK011118.

Links: DINOSAURS- Family Tenontosauridae (an increasingly useful and rapidly improving dino site). ATW030401.

Tenontosaurus: *T. tillettorum* Ostrom 1970; *T. dossi* Winkler *et al.*. 1997.

Range: middle Cretaceous of North America

Phylogeny: Tenontosauridae: *Rhabdodon* + *.

Characters: 1.5 to 7.5+ m; skull long & fairly deep; premaxilla toothless; orbits very large & somewhat rectangular; tail long; manus III with 3 phalanges; prepubic process narrower transversely then deep dorsoventrally

Tenontosaurus tillettorum Ostrom, 1970a
Horizon: Cloverly Formation of Montana, Cedar Mountain Formation of Utah, probably also Antlers Formation of Oklahoma, and Antlers and Paluxy Formations of Texas

Age: Aptian to Middle Albian
Place: Western Laurasia
Remains: over 25 skeletons, plus postcrania and teeth
Length: 6.5 meters
Weight: 500 kg
Comments: distinguished by its unusually long tail (which may or may not have been an aid in swimming), *Tenontosaurus* has the misfortune to be continually portrayed by dinosaur artists as being torn apart by a pack of hungry *Deinonychus*. It has been various identified as a hypsilophodont, an iguanodont, and in some separate taxon of its own. As the material spans some ten million years or more, it is not unlikely that several species are included here. MAK011118.

Tenontosaurus dossi Winkler, Murray, and Jacobs, 1997
Horizon: Twin Mountains Formation, Texas; possibly other locations as well
Age: late Albian
Place: Western Laurasia
Remains: at least two skulls and two incomplete skeletons
Length: 7 to 8 meters
Weight: up to 900 kg
Comments: Apparently more primitive than *T. tillettorum*, it is also larger. MAK011118.

Note: a very large, qudrupedal hypsilophodont?

Image: from Research Casting International

Links: DinoData Dinosaurs T035 TENONTOSAURUS; Tenontosaurus. The Natural History Museum's Dino Directory; Paleontology and Geology Glossary- Te; Dino Land Paleontology News- Nearly Complete Tenontosaurus ...; TENONTOSAURUS; Tenontosaurus (Spanish); Tenontosaurus pictures@ Prehistorics Illustrated; Academy of Natural Sciences, Philadelphia. Deinonychus ...; Tenontosaurus tillettorum; Neuigkeiten aus der Wissenschaft (German); The Sam Noble Oklahoma Museum of Natural History - NEWS. ATW030401.

Rhabdodon**:** *R. priscus* Matheron 1869; *R. septimanicus* Buffetaut & Le Loeuff 1991.

Range: Late Cretaceous of Europe

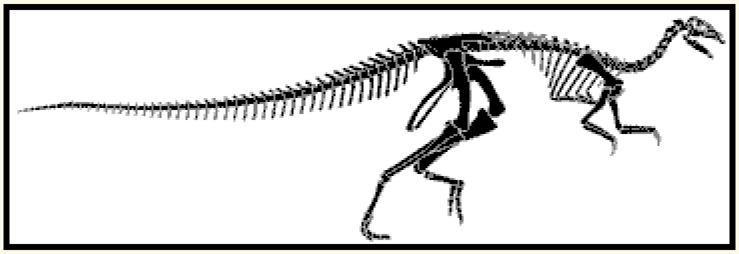
Phylogeny: Tenontosauridae: *Tenontosaurus* + *.

Characters: < 4.5 m; probable beak; coronoid process continuous with alveolar row; alveolar row strongly curved & without lateral shelf; lateral face of dentary smoothly rounded;

Rhabdodon priscus Matheron, 1869 (= *Mochlodon* Seeley, 1881, *Oligosaurus* Seeley, 1881, *Ornithomerus* Seeley, 1881; *see also* more synonyms at Dino Data entry).

Horizon: various deposits from Austria, France, Romania, and Spain
Age: Campanian and Maastrichtian
Place: Central Laurasia / Western Euramerica
Remains: teeth, isolated postcrania
Length: 4 to 4.5 meters
Weight: around 400 kg
Comments: A fairly common but poorly known late Cretaceous European ornithopod, for a long time considered an iguanodontid, it is now seen as an advanced early, or even proto-, iguanodontian. *R. septimanicus* Buffetaut and Le Loeuff, 1991 (France) and *R. robustus* (Nopcsa, 1900) (Maastrichtian of Romania) may or may not be separate species. In any case, given the wide stratigraphic and geographic range, it is likely that more than one species is included here. MAK011118.

Links: **DinoData Dinosaurs R013 RHABDODON**; RHABDODON; Pereda Suberbiola & Taquet; MUSEE. DINOSAURES - LES COLLECTIONS; dinosaurs. ATW030402.

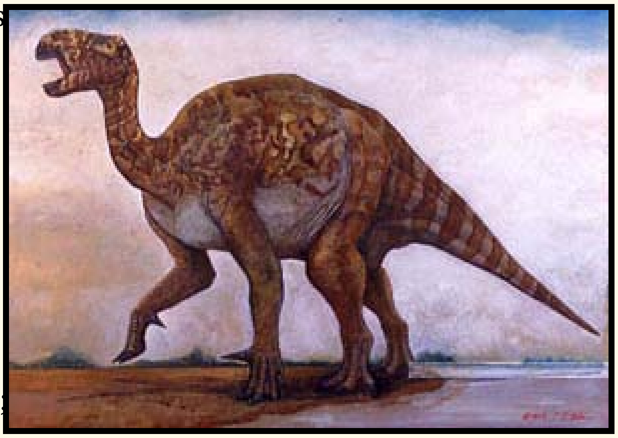


Dryosauridae: *Ankylopollexia?*, *Dryosaurus*, *Kangnasaurus*, *Valdosaurus?*

Range: Middle Jurassic to Middle Cretaceous of North America, Africa & Europe, possibly South America.

Phylogeny: Iguanodontia::: (Iguanodontidae + Hadrosauroidea) + *.

Links: Biologybase: Checklist of the Non-Avian Dinosaurs; Iguanodontia -- The Dinosauricon; Dryosaurus - Dinosaur - Enchanted Learning Software.



Iguanodontidae: *Iguanodon*. Sometimes used to include various transitional forms with varying development of: cris-cross ossified tendons in vertebral column; loss of premaxillary teeth; dental battery formation; fusion of wrist bones; sternal plate shape (kidney-shape to hatchet-shape).

Range: Late Jurassic to Late Cretaceous (depending on definition)

Phylogeny: Iguanodontia:::: Hadrosauroidea + *.

Characters: long, broad snouts with a horny beak; numerous very small grinding teeth; <3 dentary teeth per tooth position [H98]; maxillary tooth crowns with accessory mesial & distal ridges [H98]; longer neck; second and third fingers were blunt and hoof-like; **$**? spiked thumb fused to wrist; tibia < femur; opisthocoelous; larger; facultative quadruped; herbivorous.

Links: **DinoData: Iguanodontidae**; Biologybase: Checklist of the Non-Avian Dinosaurs; Iguanodon Bernissartensis; Iguanodon- Enchanted Learning Software; On the Classification of the Dinosauria (1870); Iguanodon - Suite101.com; see also *Camptosaurus* links under Ornithopoda.

References: Head (1998) [H98]. 010907.

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Ornithischia: Hadrosauroidea

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauroidea
   |     |--Ouranosaurus
   |     `--+--Nanyangosaurus
   |        `--+--Altirhinus
   |           `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
```

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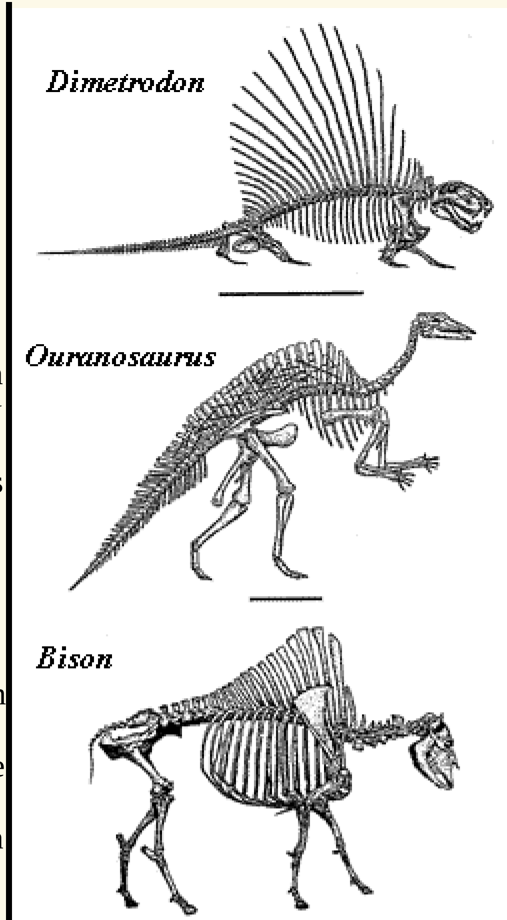
Mesozoic Cattle or Mesozoic Camels?

Iguanodon may be one of those rare cases in which we actually see the base of a significant radiation. Near - iguanodonts like *Ouranosaurus* and *Nanyangosaurus* may or may not turn out to be hadrosauroids, *i.e.* slightly more closely related to hadrosaurs than to *Iguanodon*. They are certainly very closely related to the iguanodontids; and the differences, if any, are tenuous. For example, when data from Head (2001) is run on PHYLIP, there are *no*



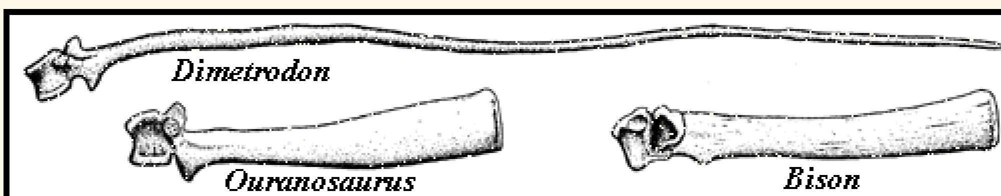
Three terrestrial tetrapods with elongated neural spines. From Bailey (1997).

synapomorphies which distinguish hadrosauroids from iguanodontids. *Ouranosaurus* comes out as the most basal hadrosauroid, but it is at least as different from the other basal hadrosauroids as it is from iguanodontids. **[1]** At a guess, *Ouranosaurus* will turn out to be a rather derived member of an early, African offshoot from the iguanodontid stem. However, despite much new data and a great deal of careful work over the last twelve years, notably by David Norman, these dinosaurs are all so similar to each other that we are not a great deal closer to understanding exactly where the branching occurs than when **The Dinosauria** was published in 1990. *See*, Weishampel & Horner (1990); Norman (1990). One significant problem may be the number of species referred to *Iguanodon*. The genus is overdue for revision. **[2]** But who has time and resources for so massive an undertaking?

(Perhaps some misguided reader is, even now, racing out his door in an attempt to become the answer to this entirely rhetorical question. The probability of such an occurrence is, admittedly, on the same order as the probability of spontaneous combustion. While intriguing to contemplate – everyone knows of at least one paleontologist who is worthy of immolation (spontaneous or otherwise) -- such an eventuality need not detain us long. The chance that your editors can contribute anything meaningful to the discussion of basal hadrosauroid phylogeny is thus remote. Like a hypothetical bull *Parasaurolophus* in rut, nature has equipped us to make impressive and sometimes attractive noises, but enjoined us to leave the field of actual combat to those better equipped for offensive action.)

Although its ultimate antecedents are somewhat vague, *Ouranosaurus* remains a fascinating subject. Phillipe Taquet, as he relates in an autobiography, spent much of his early career on the discovery and reconstruction of this dinosaur from the middle Cretaceous of Niger. Taquet (1998). **[3]** Not only does *Ouranosaurus* come from an unusual locale, but some of its anatomy is downright weird. Most notably, *Ouranosaurus* has very tall neural spines on its dorsal vertebrae. These elevated spines are tallest above the forelimbs, but extend all the way down to the first few caudals. Tall neural spines are not particularly unusual among dinosaurs, but the spines of *Ouranosaurus* are much longer than anything else in the phylogenetic neighborhood. For that reason, *Ouranosaurus* has customarily been illustrated as having a sailback, with the sail having some presumably thermoregulatory function, like *Dimetrodon*. See Ouranosaurus- Enchanted Learning Software; OURANOSAURUS.

This enduring image of the sailback hadrosauroid is difficult to explain. Bailey (1997) makes an airtight case that the spines have no resemblance to the relatively few terrestrial sailbacks known from tetrapod zoology and paleontology. texas dinosaurs; New Scientist | Dinosaurs. Rather, the spines are, in shape, size, distribution, mass and contour much closer to the hump-supporting spines of ungulates, most notably buffalo. **[4]** Like buffalo, the neural spines of many, perhaps all, iguanodontians were bound together by extensive tendons which stiffened the back and supported the head. We can be quite certain of this, since some of the tendons frequently ossified. *Ouranosaurus* is no exception. Consequently, the dorsal structure, whatever it was, could not have been fin-like. It had to be at least moderately thick transversely in order to enclose the tendons.



Anterior dorsal vertebrae of terrestrial tetrapods with elongated neural spines. From Bailey (1997)

In *bona fide* sailbacks, the spine's only substantial function is to support itself and a vascular network. If the function of the dorsal structure is thermoregulatory, its efficiency is much greater with a maximum surface to volume ratio. The greater the surface, the more efficient is the heat exchange. Transverse width decreases efficiency. Accordingly, where the function of the sail is thermoregulatory, the spines in are not only thin, but can and do become thinner distally. The distal parts simply have less weight to support. This is the pattern seen in the dorsal fins of fishes, in *Dimetrodon* and among iguanid lizards. By contrast, *Bison* and *Ouranosaurus* have massive spines that actually become thicker distally. In such humped animals, the dorsal structure is wide, heavy and rather far off the ground. Unless the hump is tightly constrained, it can generate lateral torque which will cause the animal to tip over. Like an overloaded bus going around a mountain curve, a sudden shift in weight can topple the whole structure with disastrous results. Accordingly, both natural selection and prudent bus drivers tightly lash top-loaded baggage. Hadrosauroids did not come equipped with baggage racks. Instead, like subway cars, they had a series of central poles onto which everything held tightly when rounding a corner or accelerating quickly. Without question, hadrosauroids were quieter and more sanitary than subway cars, but the principle is the same.

Bailey compares the environment and ecology of *Ouranosaurus* to the environment and ecology of ungulates, notably camels. He argues that in the Cretaceous, as today, Niger was at least seasonally arid, semi-desert, open country with a low browse line. In addition to fat storage for water reserves, Bailey speculates that the humps may have provided massive food reserves required for migration to isolated nesting or nursery areas, as well as providing tendon attachments for the forelimb muscles to allow more economical long-distance walking.

Although this sort of analogy to herd-living, open-country ungulates will always be somewhat conjectural, it is far from being completely speculative. Considerable evidence supports the idea (which may originally have been advanced by Peter Dodson) that hadrosauroids were the "ungulates of the Mesozoic." A recent study by Carrano *et al.*. (1999) attempted to test the hypothesis in a quantitative manner, using multivariate analysis of morphometric data. The results were not conclusive, but were encouraging. It is not beyond hope that this generalized hypothesis about hadrosauroid lifestyles can be tested. ATW020215

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[1] Under these conditions, the apomorphies of *Ouranosaurus* are (a) lateral expansion of the rostrum; (b) dorsoventral expansion of the anterior jugal; (c) large mandibular diastema (d) ventral ridge on sacral vertebrae; and (e) an anteroposteriorly narrow supratemporal fenestra. All of these characters are convergent on various hadrosaurids. Back.

[2] *See* the discussion in the notes following Hadrosauroidea. Back.

[3] Taquet's monograph was published as: Taquet, P (1976), *Geologie et paleontologie du gisement de Gadoufaoua (Aptien du Niger)*. **Cah. Paleontol. CNRS Paris**. 191 pp. However, I have not reviewed the original work. Back.

[4] Note that the *Bison* shown in the image is not the living *B. bison*, but its somewhat larger Pleistocene relatives, *B. antiquus* (skeletal reconstruction) and *B. latifrons* (isolated vertebra). Back.

Descriptions

Hadrosauroidea: *Probactrosaurus*, *Altirhinus*. Definition: *Hadrosaurus* > *Iguanodon*.

Range: Early to Late Cretaceous.

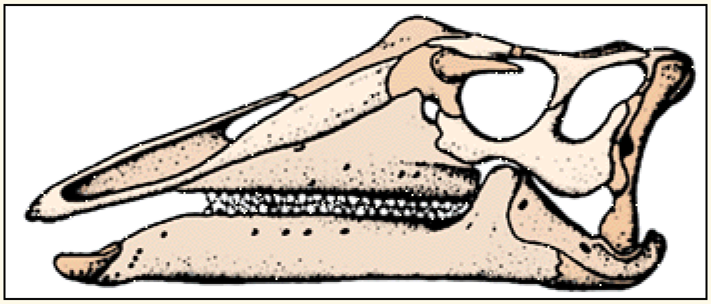
Phylogeny: Iguanodontia :::: Iguanodontidae + * : *Ouranosaurus* + (*Nanyangosaurus* + (*Altirhinus* + Hadrosauridae)).

Characters: **$?** laterally expanded distal rostrum ("duck bill") [H98] [N90* (synapomorphy of Iguanodontia)]; **$** narial fossa lengthened and defined laterally by raised rim [N90* (present in *Iguanodon* and absent in lambeosaurines)]; **$** postorbital skull narrow [N90* (also in iguanodontids)]; **$** squamosals approach midline of skull roof, separated only by narrow band of parietal [N90* (same in *Iguanodon*)]; **$** anterior end of jugal dorsoventrally expanded under orbit [N90*]; distal end of paroccipital process curves anteriorly [N90*]; **$** enlarged diastema [N90*]; tooth size reduced compared to iguanodontids [H98]; **$** 1+ maxillary and dentary tooth per tooth position [N90]; most have 3+ dentary teeth per tooth position [H98]; most have maxillary teeth symmetrical around a medial carina (but see **[1]**) [H98]; maxillary teeth without mesial & distal accessory ridges [H98]; **$** parallel, symmetrical accessory ridges on dentary teeth [N90]; **$** caudal neural spines longer then chevrons [N90*]; **$** scapular blade with convex dorsal margin [N90* (not true of *Ouranosaurus*)]; **$** ilium with small pubic peduncle [N90* (synapomorphy of higher-level clade within Iguanodontia)]; **$** ilium with antitrochanter [N90* (denies that *Ouranosaurus* antitrochanter is homologous)]; **$** ilium with long preacetabular process [N90* (same in one species of *Iguanodon*)]; **$** ischium straight [N90]; **$** dorsoventral expansion of prepubic process [N90* (synapomorphy of higher-level clade within Iguanodontia)]; **$?** loss of metatarsal I [N90] **$** distal tarsals 2&3 absent [N90* (may be fused or not)]; pes digit I absent [N90*].

References: Head (1998) [H98]; Norman (1990) [N90].

Notes: [1] *i.e.*, the tooth has a ridge running from base to crown and the teeth are symmetrical around that axis in lingual view. Head's (1998) description is confusing on this point. The text states that the maxillary teeth have a "single medial" carina. His Figure 13(a), however, purports to be in buccal view and shows a prominent ***median*** carina -- a carina which is in the middle, but on the lateral or buccal (not medial or lingual) face. Is the figure mislabeled or is *medial* a typographical error? See discussion at *median*. **[2]** Norman (1990) places *Probactrosaurus* as the sister of Hadrosauridae, and *Ouranosaurus* as an iguanodontid. Accordingly, the characters from [N90] actual characterize a different, unnamed group: *Probactrosaurus* + Hadrosauridae. **[3]** Characters marked [N90*] are from Norman's discussion of prior work by Sereno. See Sereno, PC (1986), *Phylogeny of the bird-hipped dinosaurs*. **Natl. Geog. Res.** 2: 234-256. Norman disagrees, and gives detailed, well thought-out reasons, some of which are noted above. The argument may turn on the proper interpretation of *I. atherfieldensis*, which Norman repeatedly uses as a counter-example to the synapomorphies he cites to Sereno. It is tempting to speculate that *atherfieldensis* might not be a species of *Iguanodon* after all. Norman himself has shown that *I. orientalis* (now *Altirhinus*) is actually a hadrosauroid, and perhaps the same is true of *I. atherfieldensis*. Alternatively, perhaps *Iguanodon* is paraphyletic. ATW020202.

***Ouranosaurus*:**

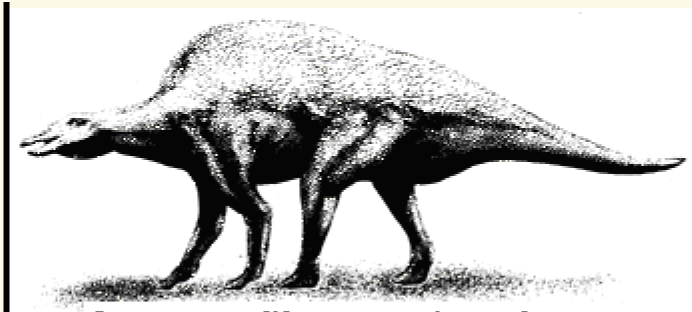


Range: Middle Cretaceous of Africa

Phylogeny: Hadrosauroidea **:** (*Nanyangosaurus* + (*Altirhinus* + Hadrosauridae)) + *. [H01] **[2]**

Characters: large bodied (7 m); low skull; broad, flat rostrum (duck bill) [H98] [N90]; lateral margins of nares widely flared [NW90]; long, sloping facial region [NW90]; premaxilla lateral processes reconfigured to support nasals [NW90]; anterior maxilla reconfigured as shelf to support premaxilla (as in lambeosaurines, but likely convergent) [H98] [NW90]; marked free palpebral; crest of "bumps" on nasals near frontal suture [NW90]; prefrontal more dorsal than in iguanodontids [NW90]; marked free palpebral; long axis of supratemporal fenestra oval & oriented anterolaterally [WX01]; anterior jugal somewhat dorsoventrally expanded (convergent with Hadrosauridae?) [H98]; quadrate shaft curved [WX01]; supraoccipital may be excluded from foramen magnum [NW90]; occipital condyle almost heart-shaped (seems inconsistent with figure) [NW90]; braincase low & broad as in hadrosaurids [NW90]; predentary very broad [NW90]; dentary with straight dorsal & ventral margins [WX01]; prominent diastema between predentary and 1st dentary teeth [H98]; <3 dentary teeth per tooth position [H98]; maxillary with 22 tooth positions, dentary with 23 [NW90]; maxillary tooth crowns with accessory mesial & distal ridges [H98]; tooth ultrastructure showing numerous odontoblasts and large canals parallel to odontoblast tracks (similar to certain living ungulates) [M88] **[1]**; vertebral formula 11/17?/6/40+ [NW90]; neck short; long (9x height of centra [NW90]) neural spines possibly supporting "sail" or, more likely, hump [B97]; spines robust, eliptical with long axis parallel to body axis [B97]; spines variably bowed, slanted and/or with expanded distal ends (all correlated with strong, distally applied, anteroposterior strains as in *Bison*) [B97]; neural spines interconnected by (partially?) ossified tendons [B97]; hoof-bearing digits 2&3 on forelimbs; manus 1 with spike [NW90]; ischium shaft relatively straight [N90]; pes with phalangeal formula 03450 [NW90]; low browser in open, arid or seasonally arid environments [B97] .

Links: DinoData: Ouranosaurus; Ouranosaurus-Enchanted Learning Software; Ouranosaurus; Ouranosaurus (also in French); Ouranosaurus The Natural History Museum's Dino Directory; Ouranosaurus Finished; FPDM : Ouranosaurus nigeriensis; Ouranosaurus; Dinosaur Impressions by Taquet; dinos.htm;


Ouranosaurus: life reconstruction as a hump-backed dinosaur from Bailey (1997)

References: Bailey (1997) [B97]; Head (1998) [H98]; Head (2001) [H01]; Michard (1988) [M88]; Norman (1990) [N90]; Norman & Weishampel (1990) [NW90]; Wang & Xu (2001) [WX01].

Notes: **[1]** Michard (1988) describes these tubules as having an inner covering including odd, circular structures. For a variety of reasons, I suspect these are artifacts. However, it is interesting that the "tubules géants" were not filled with matrix as were the odontoblast tubules -- or were filled with something which was destroyed by the (acid) preparation for scanning electron microscopy, leaving only the circular structures. Michard does not believe these are vascular canals (blood vessels) because of their irregular distribution and because they are surrounded by concentric layers of dentine. However, they may be the *remains* of a temporary vessel network, most of which was resorbed during tooth development. This would be consistent with the very long odontoblast tracks. How else could the odontoblasts be fed and their wastes removed during their long migration? Michard observes that the density of these tubules (where present) was much greater near the pulp cavity -- again consistent with a vascular role. Michard states that comparative work was under way by various other workers, but I have not seen it. **[2]** Head's (2001) cladogram is ambiguous. When I run his data set, *Ouranosaurus* comes out as a hadrosauroid, but, as Head notes, the synapomorphies in this part of phylospace are weak and rather unconvincing. **[3]** See also discussion at Mesozoic Cattle? ATW020208.

***Nanyangosaurus*:**

Range: Lower? or Middle Cretaceous of China.

Phylogeny: Hadrosauroidea **::** (*Altirhinus* + Hadrosauridae) + *.

Characters: length about 4.5 m; 6 sacral vertebrae; caudal neural spines larger than chevrons; front and hind limbs similar to hadrosaurids; at least one anterior dorsal vertebra slightly opisthocoelous; all posterior dorsals platycoelous; dorsal centra with heart-shaped ends; some dorsals fused, lacking ventral keel (pathological?); 6 "true" sacrals, with one additional vertebra at each end associated with sacrum; sacral centra flattened & wide; caudal vertebrae platycoelous; ventral groove on posterior sacrals; caudal vertebrae progressively lose diameter faster than length, so most distal caudals are elongate; forelimb slender; distal humerus dorsoventrally expanded; metacarpal I absent; metacarpals II, III & IV partially fused; metacarpals III & IV robust with expanded distal end on IV; phalanges robust; manual phalanx IV(1) wider than long; unguals hoof-like; distal ischium moderately curved with well-developed foot; femur straight in lateral view; femur with medial distal condyle more than twice as wide as lateral; anterior intercondylar groove is tunnel-like; distal femoral condyles not fused; proximal tibia transversely wide; fibula semilunate in proximal view; astragalus & calcaneum fused and rectangular anteriorly with a weak ascending process; metatarsal I absent, metatarsal II deeper proximally than metatarsal III; pedal unguals hoof-shaped.

Links: **DinoData: Nanyangosaurus**; Nanyangosaurus -- The Dinosauricon; Dinosauria Translation and Pronunciation Guide N; nanyangosaurus.

References: Norman (1990).

Notes: **[1]** the skull is not known. **[2]** According to Norman (1990), variable concavity of the centra and centra with heart-shaped ends are characters of immature specimens of *Iguanodon*. They both result from incomplete ossification -- of the centra and neural arch pedicles, respectively. Immature *Iguanodon* likewise exhibit sacrodorsals which become true sacrals in mature specimens. It seems unclear what, if anything, really distinguishes *Nanyangosaurus* from *Iguanodon*. ATW020201.

***Altirhinus*:** = *Iguanodon orientalis*.

Range: Middle Cretaceous of Mongolia

Phylogeny: Hadrosauroidea **::** Hadrosauridae + *.

Characters: length up to ~8m [NS00]; dorsally expanded rostrum; beak wide and anteroventrally oriented [NS00]; nasal strongly flexed dorsally [NS00]; nasals with elongate rostral process [NS00]; internasal groove present [NS00] (could be cartilaginous extension of premaxilla?); antorbital fenestra "occluded" (covered by frontal in lateral view?) **[1]** [NS00]; dentary deflected ventrally [NS00]; posterior dentary and maxilla with 3 teeth in each vertical tooth row [NS00]; carpals not fused [NS00]; manus I with laterally compressed ungual spike [NS00](as *Iguanodon*?); manus IV with short, broad ungual [NS00]; ilium with thick, downturned anterior process [NS00]; brevis shelf absent [NS00]; ilium with strong trochanteric ridge above body of ischium [NS00] shaft of ischium straight, but with axial twist [NS00].

Links: **DinoData: Altirhinus**; Altirhinus; Altirhinus Fact Sheet - EnchantedLearning.com; Witmer's Lab Dinosaur Skull Collection: Other Ornithischia; Altirhinus (Portuguese); Dinosauria Translation and Pronunciation Guide A.

Image: *Altirhinus*

References: Norman (1990), Norman & Sues (2000) [NS00]

Notes: **[1]** this section of the frontal is broken off in the image. **[2]** The description of the ilium differs only a little from the description of *Iguanodon* in Norman (1990). However, *Iguanodon* has a narrow brevis shelf, and the shaft is twisted outward. *Id*. 020201.

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checked ATW060215

Ornithischia: Hadrosauroidea: Hadrosauridae

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   |     |--Hadrosaurinae
   |     `--Lambeosaurinae
   `--Marginocephalia
      |--Pachycephalosauria
      `--Ceratopsia
```

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3. Lambeosaurinae X

Hadrosaurid Relations and Anatomy

What is a hadrosaurid?

As briefly mentioned in the main entry, it's a little hard to say what a hadrosaurid is. The Hadrosauroidea have a standard cladistic definition: all iguanodontians closer to *Hadrosaurus* than to *Iguanodon*. This is a smidgen unclear since we don't know exactly where in the Iguanodontia the hadrosaurs branched off. There is even some support for the idea that the lambeosaurines and hadrosaurines may be separately derived from the Iguanodontia. However, the fact that we don't know what goes *into* the hadrosauroid box doesn't mean we aren't defining the box properly.

Matters are otherwise with the hadrosaurids. There are two current definitions of Hadrosauridae: (1) the last common ancestor of lambeosaurines, hadrosaurines, *Telmatosaurus*, *Secernosaurus*, and (one supposes) now *Protohadros*, and all of its descendants; and (2) only lambeosaurines plus hadrosaurines (sometimes called "Euhadrosauria"). Brett-Surman (1997). The first definition seems hopelessly *ad hoc*. The second leaves a large, ugly mess of stem species between Hadrosauroidea and Hadrosauridae. Most writers, with the notable exception of Sereno, surrender to temptation and put a name to what is a essentially a grade or phenetic level between Hadrosauroidea and the Late Cretaceous lambeosaurines and hadrosaurines. That unprincipled practice will be followed for purposes of this essay. For those purposes, we may disguise our immoral behavior by defining Hadrosauridae as the LCA of *Protohadros* and *Hadrosaurus*. However, by means of winking, smirking, and secret paleo hand signals, we will know that it *really* means "something that seems to be more than half-way to *Hadrosaurus* from *Iguanodon*."

The discovery of *Protohadros*

Head (1998) believes that *Protohadros* is the most primitive hadrosaurid known, and this specimen does seem like a good place to start. It is from suitably early in the Cretaceous and really does look like an illegitimate cross between a *Muttaburrasaurus* and a wanton hadrosaurine. As we will see, it may not be quite that simple. However, like the site of the Dallas-Ft. Worth airport near which *Protohadros* was found, they had to put the thing somewhere, and half-way in between was as good a spot as any. Having picked that spot, let us look around.

Some 95 My before the city fathers of Dallas and Fort Worth floated their bond issue for the airport at Flower Mound, the bloated corpse of a recently deceased hadrosauroid floated out into the quiet waters of a little bay near the western edge of the Interior Sea. As with many a bond issue, the warm gasses generated by corruption soon ceased to be enough to support the dead weight. It sank and was duly covered with sediment. Many years later, an enthusiastic engineer from the Texas Highway Department apparently blew most of the fossil into dust with high explosives. However, a reasonably complete, if disarticulated, cranium remained. This was discovered by Gary Byrd of Dallas in 1994 and was eventually described by Jason Head as *Protohadros byrdi*.

Bring me the head of *Protohadros byrdi*

One of the annoying things about paleontology is the barrage of bone names and descriptions. Even after one gets used to the names, it is hard to see how and why the thing fits together. Fortunately, it is relatively easy to describe the cranium of hadrosaurs as a series of structural units which fit together in a sensible way. This is not to say that the biomechanics are easy. The way parts move relative to each other is often a factor of many variables other than bone shape. But at least the cranium, considered as a static structure, makes pretty good sense. Perhaps the best way to look at this description is as a series of architectural analogies which may help in getting a feel for the stresses and interdependencies of the skull.

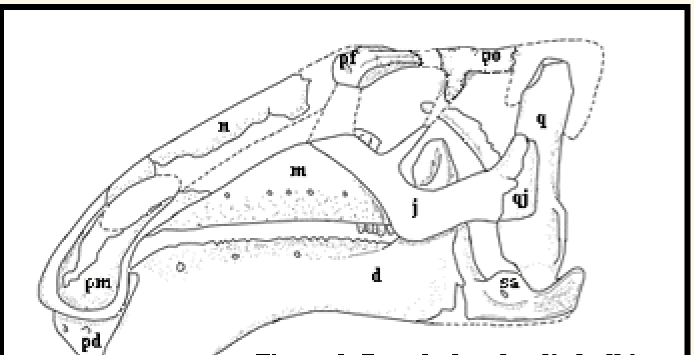


Figure 1. Protohadros byrdi skull in left lateral view. After Head (1998).

The skull of *Protohadros* is not complete. The palate, jaw suspension and braincase are present only in parts, the rostrum was shattered, and a good deal of the nasal and premaxilla are missing. Some bones are missing entirely from the dorsal skull (the "skull table"). The structure of the dermal bones is fairly standard, and we may fill in the gaps from the surprisingly similar hadrosaurine, *Gryposaurus*, or other relatives as illustrated in Weishampel & Horner (1990). The braincase will, frankly, be glossed over for now. The reconstruction at right (Fig. 1) is adapted from Head (1998). For some reason, I was unable to obtain complete correspondence between Head's reconstruction and the recovered elements as figured in his paper. Accordingly, I have taken the liberty of slightly modifying the prefrontal and postorbital region. Since the problem is almost certainly at my end, I have retained the outline deduced by Head.

The abbreviations used are as follows: **d** dentary; **j** jugal, **m** maxilla, **n** nasal, **pd** predentary, **pf** prefrontal, **pm** premaxilla, **po** postorbital, **q** quadrate, **qj** quadratojugal, **sa** surangular.

The Pillars: quadrates and maxillae

The foundation of the skull of *Protohadros* are the two tall columns formed by the quadrates at the rear of the skull and two massive, anteriorly elongated, pyramidal maxillae at the center of the skull. Because both the maxillae and the quadrates have a number of articulations, their precise shapes are very complex. However, as a first approximation, they are a set of vertical columns (the quadrates) and a set of horizontal columns (the maxillae) which stabilize the skull in those two dimensions. These two paired elements anchor the skull.

The upper arch: the skull table

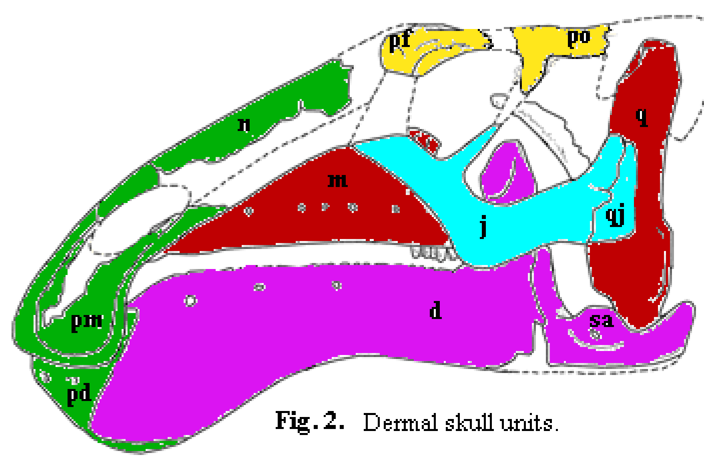


Fig. 2. Dermal skull units.

Except for the rostrum (the "muzzle"), which supported only on the maxillae, and the occiput, which is supported only on the quadrates, all of the other skull units can be understood as bridges between these two pillars. The dermal skull can then be conceptualized as shown in Figure 2.

The elements shown in yellow make up an upper arch (or double arch) often referred to as the skull table. In addition to the prefrontal and postorbital in the figure, the arch in life would include additional dermal bones. The lacrimal is the missing trapezoidal bone at the front of the orbit. The missing "tooth-shaped" block at upper rear of the skull is made up of the squamosal and parietal. In many archosaurs, the parietal is a large element which "caps" the skull. In advanced hadrosaurs, the parietal tends to be a fairly small, thin element separating the upper temporal fenestrae -- yet another pair of holes which are located on top of the head just in front of the quadrates. The squamosal dominates the posterior of the upper arch and significantly overhangs the quadrate at the posterior margin.

The (missing) lacrimal is primarily supported by the jugal. It apparently contacted the jugal just forward of the jugal-maxillary articulation, then overlapped onto the apex of the maxilla. The lacrimals themselves are missing, but one of the maxillae preserves the articular surface. The maxilla includes a slot for the bottom of the lacrimal which prevents it from sliding forward. At the other end of the upper arch, the (also missing!) squamosal is, in other hadrosaurids, believed to have formed a synovial joint with the top of the quadrate: that is, a membrane-lined joint that may have permitted a noticeable range of motion around the axis of the quadrate. The motion would have been limited. A flange extends out from the side of the quadrate towards the midline (i.e. into your screen fro the left quadrate in the figure) which would have prevented extensive rotation. Finally, this region was also the origin of the major jaw adductors, the critical muscles responsible for closing the jaw.

The upper arch is shaped as a double arch and, in other archosaurs, there is a significant vertical bar between the orbit and the lower temporal fenestra behind it. In hadrosaurs, the contact between the jugal and postorbital is always slight. Presumably this contact was also at least somewhat flexible, since it is otherwise hard to see how the postorbital-jugal articulation could have taken any significant stress without shattering.

The central bar: the jugal arch

The central bar is formed by the jugal and quadratojugal. These elements were preserved in *Protohadros*, although they are somewhat distorted. The jugal had, as is typical of the group, a broad medial contact with the maxilla which was probably fairly inflexible, as were the articulations at the posterior end involving the quadratojugal and the quadrate. On the other hand, as is also the case in most hadrosaurs, the jugal is thin and does not seem to be fixed at all towards the center. Therefore, it seems likely that the jugal could bow outward by a measurable amount.

The lower arch: the mandible

Even for a hadrosaur, the lower jaw of *Protohadros* is impressive. The dentary accounts for most of the mass. "Behind" (i.e. medial to) the dentary, the inner surface of the lower jaw was covered in part by an angular (not recovered) which reinforced the dentary - surangular articulation. A large coronoid process rises vertically from the dentary for the attachment of mandibular adductors.

The size of the jaw may relate to the size of the maxillae, which were also outsize for the group. For a hadrosaur, *Protohadros* had a longish tooth row, possibly because the maxilla was so large. As a result, the dentary is equally stout to support the corresponding (36) tooth rows in the lower jaw. Note that a heavy anterior jaw would actually help stabilize the jaw in action. The jaw swings open on the relatively gracile surangular - quadrate articulation. However, the adductor muscles act on the coronoid and on the main shaft of the dentary less than halfway along its length. If the body of the dentary anterior to the adductor attachment were light or short, there might be a tendency to dislocate the jaw when the adductor muscles were working hard and the mouth was open. A long, heavy dentary anterior to the muscle attachments tends to generate an upward force on the surangular when the jaw is open and thus stabilize the surangular on the joint with the quadrate.

The rostrum

The rostrum in hadrosaurids is certainly their most peculiar feature. It is made up of the nasals and the recurved premaxillae. For convenience, the predentary is included as well, although it is mechanically part of the mandible.

The anterior ends of the premaxillae are roughened and vascularized. As a result, there is a solid consensus that it was covered by a horn beak of some kind. The predentary is a neomorphic bone unique to the genesaurs which bears the same type of surface. Therefore, it is generally felt that the hadrosaurs had upper and lower beaks which probably were sharpened and served to slice off vegetation which was then fed through the dental battery by muscular cheeks.

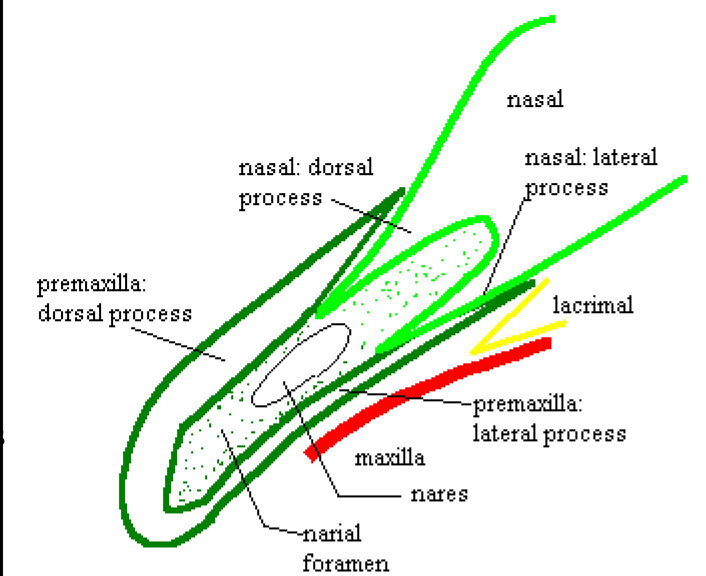


Fig. 3. Schematic of hadrosaurine rostrum in left lateral view

Much of the nasal of *Protohadros* is missing, but the rostrum itself seems to have been constructed along the same lines as in most hadrosaurids: a pair of facing, interlocked tripods. The principle mass of each premaxilla is found in two processes which ascend the line of the maxilla: (a) a lateral process which contacts the maxilla (more so in *Protohadros* than in most because of the size of the maxillae) but is offset from the midline and (b) a dorsal process which follows the midline of the skull, but is raised above the maxillae. Since the dorsal processes of the two premaxillae meet at the midline, the result is a 3-pronged structure. Each of the three prongs joins a corresponding element of the nasal at a scarf joint, as shown in Figure 3. In addition, the maxillae bear dorsal processes which insert in the bottom of the rostrum and provide further support (again, more so in *Protohadros* than in most).

The result is a remarkably strong, flexible structure which may have absorbed the considerable stresses generated by the beak in any number of ways, since it was capable of bending, torsion, and sliding depending on the anatomical details of the species. Ultimately, the forces could be directed against the mass of the maxillae themselves or back, through the upper or lower arches to the quadrate. For this remarkable piece of engineering alone, it is no wonder that the hadrosaurs were such a successful group.

Discussion

It is important to remember that this description has omitted two important skull units: (a) the palatal bones and braincase and (b) the occiput. Conceptually, these form a central, internal bar through the center of the skull and a cross-bar between the two quadrates, respectively. However, even without these elements, we can make some slightly educated guesses about *Protohadros* and hadrosaurids in general.

One of the critical issues about hadrosaurids is the extent to which they were capable of lateral and longitudinal jaw movements: side-to-side and antero-posterior movements. This is important because such movements allow the animal to grind food, not simply to slice or crush it. As Head concludes (albeit for slightly different reasons), *Protohadros* seems capable of both to a limited extent. Or, rather, our examination of the dermal skull suggests that its design was capable of tolerating such movements. The central bar seems fairly stiff, but capable of bulging outward in response to compression. The upper arch is similarly designed to flex upward, although the critical squamosal is missing. Again, the dermal skull will not tell us if or how compression was achieved, but it does suggest that the skull was adapted to accommodate such a force and that it might well have resulted in a longitudinal grinding action with the teeth.

A second, and far more tentative, suggestion from this osteological tour is that *Protohadros* may not be quite as basal as Head asserts. Head's conclusion is based on the usual parsimony analysis. The difficulty is that, as we have seen, there is really less here than meets the eye. That is, much of the cranium is preserved, but the missing pieces tend to be unusually important. Unfortunately, this is true of a number of early hadrosaurids. However, Head was able to perform the analysis with 20 characters and 9 species, although two specimens (*Probactrosaurus* and *Gilmoreosaurus*) have considerable missing data.

Even here, at least one of the characters is debatable. For example, *Protohadros* is scored as not having "dorsoventral expansion of the rostral end of jugal." In fact, the rostral ends of both jugals are fairly broken up. The left jugal is obviously missing most of the rostral end. The right has been sagitally sheared, and the rostral end is uneven, so that its dimensions are unclear. Further, as Head notes, this bone has clearly been deformed, so that it may be unsafe to draw firm morphological conclusions.

Head recovers only one apomorphy for *Protohadros*, a relatively large "maxillary diastema", i.e. a portion of the anterior maxilla which is toothless. It is unclear how meaningful this is. First, *Protohadros* has a very large pair of maxillae. It is unclear from the text and figures whether the size of the diastema is being determined as an absolute size, or relative to the size of the maxillae and, in either case, whether this potentially ambiguous criterion was consistently applied across the various taxa in the study. Second, it is unclear how significant this character is, since the advanced hadrosaurines, which *Protohadros* otherwise generally resembles, have the same characteristic.

These are probably quibbles. *Protohadros* clearly lacks a substantial suite of synapomorphies present in all other hadrosaurids, and these observations should not be taken too seriously. The bottom line is not that Head's conclusion is wrong, but only that we are as yet some distance from understanding the shape and origin of the hadrosaurid family tree. ATW 000704.

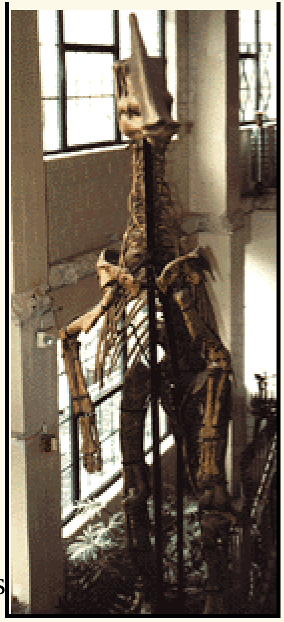
Descriptions

Hadrosauridae: (= Euhadrosauridae) *Hadrosaurus* + *Parasaurolophus*

Range: Early to Late Cretaceous of North America, South America, Europe & Asia.

Phylogeny: Hadrosauroidea **::** *Altirhinus* + * **:** Hadrosaurinae + Lambeosaurinae.

Characters: Long, narrow skull; **$?** laterally expanded distal rostrum ("duck bill") [H98]; broad, flat bill overhung by horn rhamphotheca from premaxilla, extending out & down over lower jaw; **$** expanded dorsal process of maxilla, with migration of antorbital fenestra to posterodorsal surface of maxilla [H98]; cranial crest from nasal and recurved premaxilla; cheeks very likely; **$** modified pleurokinesis, with jugal-lacrimal joint rather than lacrimal-prefrontal [N90]; free palpebrals (*i.e.* palpebra with free distal end); fused, generally small parietal; squamosal overhangs quadrates; **$** medial jugal loses articulation with ectopterygoid [H98];



expanded anterior jugal [H98] **[2]**; jugal with elongated postorbital contact [H98]; posterior process of jugal forms long scarf joint with quadratojugal (indicative of lateral flexing of cheek in chewing) [H98]; quadrates gracile, with narrow mandibular condyle [H98]; (possible **$**) paraquadratic foramen absent [H98]; predentary present; dentary large, with tall, sometimes recurved coronary process; angular positioned medially [H98]; surangular foramen absent [H98]; prominent diastema between predentary and 1st dentary teeth [H98]; complex dental battery with 3-5 teeth per position & up to 5 replacement teeth; 40+ tooth positions [H98] **[2]**; **$** teeth crowns firmly cemented together to form dental battery [N90]; dentary teeth symmetrical around a medial carina [H98]; dentary teeth small compared with iguanodonts [H98]; teeth bear enamel only on non-articulating face; softer dentine wears against opposite teeth with self-sharpening; massive, triangular maxillae; unique jaw motion with lateral & longitudinal motion; entire front half of mouth (premaxillae and part of maxillae) toothless; about12 cervical & 8-12 sacral vertebrae (not all fused to pelvis); tail and much of dorsal vertebral column strongly stiffened with frequently ossified tendons; scapula with long, dorsally expanded blade; coracoid small; long forelimbs; **$** humerus with S-curve [N90]; **$** humerus with strong, extended deltopectoral crest [N90]; **$** reduction of wrist bones, with carpals reduced to 2 small, rounded bones [N90]; loss of fused carpus [H98] **[2]**; **$** loss of metacarpal I [N90] and entire manus I [N90] [H98] **[2]**; digital pads on manus; **$** ilium with large antitrochanteric process [N90]; femur with "fully enclosed" (?) anterior intercondylar groove [N90]; hoof-like unguals; skin impressions show interlocking polygonal tubercles in various patterns; midline frill along back & tail. *Maiasaura* eggs, nests & embryos: altricial young.

Image: *Saurolophus angustirostris*, courtesy of (& much thanks to) mathematical.com.

Notes: **[1]** As discussed in the essay, an alternate definition of Hadrosauridae takes in a number of more basal hadrosauroids which are neither hadrosaurines nor lambeosaurines. These Notes initially used the latter definition, as does Head (1998). However, this usage now (2/02) seems unworkabley vague. Some editing has been done to conform the Notes to the stricter definition, but there are undoubtedly remaining references to "hadrosaurids" *sensu lato*. **[2]** Head disagrees. He ascribes these views to Forster, CM (1997), *Phylogeny of the Iguanodontia and Hadrosauridae*. **J. Vert. Paleontol.** 17: 47A.

Links: **DinoData: Hadrosauridae**; Hadrosaurus foulkii: 1858; Literature - Hadrosauria (literature); Hadrosaurian Dinosaurs; Lecture 20: Late Cretaceous II; Cladistic Classification and its Applications in Dinosaur Paleontology; HADROSAURIDS; Untitled Document. Hadrosaurs - Paleontology and Geology Glossary (brief, good discussion); HADROSAURIDS (brief, oversimplified discussion); Pretty Butte Paleontology- Catalog of Hadrosauridae Fossils (some good details of individual bones); DINOSAURS- Family Hadrosauridae (very good discussion); hadrosauridae.htm (Thescelosaurus! site with quality discussion); 13-2 (art); Hervíboro Ornitísquio Cretácico tardío (65-97 millones años ... (Spanish: with basic anatomy); Hadrosauridae (German).

References: Head (1998) [H98]; Norman (1990) [N90]; Weishampel & Horner (1990) [WH90]. ATW030721.

Hadrosaurinae: *Anatotitan, Edmontosaurus, Gryposaurus, Hadrosaurus, Lophorhothon, Maiasaura, Prosaurolophus, Saurolophus, Shantungosaurus*.

Range: Late Cretaceous

Phylogeny: Hadrosauridae **:** Lambeosaurinae + *.

Characters: Generally larger than lambeosaurines [C+99]; reflected premaxillary lip; snout wide; nares very large; depression around nares extrending onto nasal; cranial crest absent or low & solid; basioccipital excluded from foramen magnum; teeth broad and low; no marginal denticles; neural spines low; slender limbs; narrow prepubic & ischium; ischium reduced distally; possibly prevalent in more open environments than lambeosaurines [C+99].

Image: *Maiasaura* from the Wittmer Lab..

Links: **DinoData Classification Hadrosaurinae**; Witmer's Lab Dinosaur Skull Collection: Other Ornithischia; Hadrosaurinae; Biologybase- Family index to Dinosaur checklist; Hadrosauridae- Hadrosaurinae (Mikko's Phylogeny); 13-2 (Shiraishi's reconstructions); Stars of the Show (A to I) (several good images, see the skin impression); Hadrosaurian Dinosaurs (UCMP -- the usual solid, but elementary stuff); DINOSAURIAN UNGULATES (ORNITHOPODS) (November 12) (excellent lecture notes); .-Dinosauria-. (Spanish: brief, but well done & well illustrated, with emphasis on anatomy); .-Dinosauria-. (same site in English).

References: Carrano *et al.*. (1999) [C+99]; Head (1998) [H98]. ATW021122.

Lambeosaurinae: *Parasaurolophus*.

Range: Late Cretaceous

Phylogeny: Hadrosauridae **:** Hadrosaurinae + *.

Characters: generally smaller than hadrosaurines [C+99]; **$** premaxillary foramina absent [H98]; premaxilla completely surrounds nares; **$** anterior maxilla reconfigured as broad medial shelf to support premaxilla [H98]; maxilla contact with jugal truncated, rounded; completely separate nasal passages; nasal passages in supraorbital position; expansive hollow crests in adults; exclusion of frontal from orbit; short parietals; anteriorly bowed quadrates; basioccipital participates in foramen magnum; tall neural spines; caudal spines very tall; humerus robust; deltopectoral crest projects laterally & distally; ventral sacral ridge (?); ischial foot present; crest developed post-natally; sexual dimorphism [C+99]; possibly prevalent in more closed (forested) environments than hadrosaurines [C+99].

Image: *Lambeosaurus* skull from **Research Casting**. It reminds one a great deal of Baron Samedi, a Voudou lwa.

Links: **DinoData Classification Lambeosaurinae;** Hadrosauridae- Lambeosaurinae (Mikko's version of the same); 13-2 (M. Shiraishi's reconstructions); Re- Javelina Hadrosaurs [was- Re- Hadrosaurs etc] (nomenclature); Hadrosaurs - Paleontology and Geology Glossary (simple definition and examples); DINOSAURIAN UNGULATES (ORNITHOPODS) (November 12) (superb lecture notes: **Best on the Web**); Freeman-Lynde GEOL3350 Chapter 10 Notes (functional speculations on nearial crest).

References: Carrano *et al.*. (1999) [C+99]; Head (1998) [H98]. ATW030802.

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checked ATW060211

Ornithischia: Heterodontosauridae

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Fabrosauridae
`--+--Thyreophora
   |  |--Stegosauria
   |  `--Ankylosauria
   `--Cerapoda
       |--Ornithopoda
       |  |==Hypsilophodontidae
       |  `--Hadrosauridae
       `--+--Heterodontosauridae
Echinodon
Fruitadens
Heterodontosaurus
Tianyulong
          `--Marginocephalia
             |--Pachycephalosauria
             `--Ceratopsia
```

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2. *Fruitadens* X
3. Heterodontosauridae X
4. *Heterodontosaurus* X
5. *Tianyulong* X

Life reconstruction of *Tianyulong confuciusi*, showing protofeather-like structures, based on traces found preserved with the fossil skeleton. Quills, proto-feathers, and similar structures may have been a standard feature of small ornithodira (including dinosaurs and pterosaurs) in general, although they were lost with larger dinosaurs (by analogy with modern elephants, hippos etc). Late Jurassic of China
Artwork by Nobu Tamura, via Wikipedia, GNU Free Documentation/Creative Commons Attribution

Heterodontosauridae

The heterodontosaurs were small bipedal Early Jurassic forms. They averaged about a metre in length. They are among the earliest and most primitive members of the dinosaurian suborder Ornithopoda, which was to attain great importance during the Cretaceous, especially the Late Cretaceous period. (In some modern cladistic classifications, they are considered a "sister group" of, but not directly ancestral to, the Ornithopoda). All Ornithopods, including Heterodontosaurs, had very well-developed teeth, which means that they chewed their food in their mouths, rather than swallowed it and let it ferment and be ground up by gastroliths (stomach stones) as did*Anchisaurus* and plateosaurid prosauropods. Once thought to be of late Triassic age, it is now known that the rocks in which their fossil remains are found date from the Early Jurassic. They were a short-lived group that never really ousted the predominant Prosauropods as top herbivore. Heterodontosaurs probably evolved from "fabrosaurs" or from early Scutellosaurs, such as *Tatisaurus*, possibly some time in the early Hettangian:

> The Heterodontosauridae were bipedal forms that foraged 1 meter above the ground. The skull was sturdily built and had a well-developed dentition with robust, closely spaced cheek with distinct wear facets along the length of the tooth row. These dinosaurs would have been capable of processing relatively tough plant material (Weishampel 1984; Galton 1986).
> *Terrestrial Ecosystems Through Time*, pp.356

As with the Carnian rhynchosaurs and the Norian and Rhaetian melanorosaurids, the heterodontosaurs seem to have experienced a brief period of diversity, before becoming extinct, possibly as a result of changing vegetation patterns. Before they died out though, the Heterodontosaurs gave rise to one of the most successful and long-lived of the dinosaurian lines, the hypsilophodontid and dyrosaurid dinosaurian "gazelles", which attained world-wide distribution during the Jurassic and Cretaceous.

Heterodontosaurids are known mostly from skull material, with distinctive tusks found in most individuals. They may be closer to the marginocephalians than to the ornithopods, due to their jugal (cheek-area) bosses and tusks, which are also known in pachycephalosaurians. MAK991008.

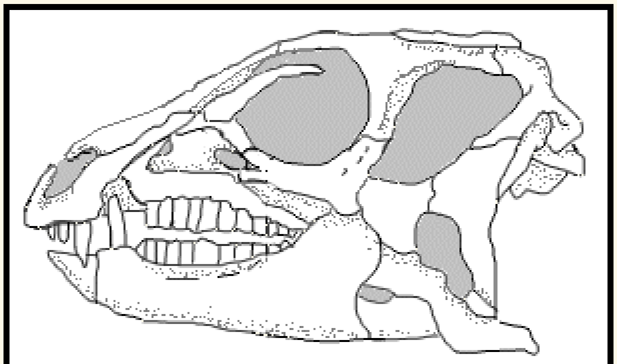
Phylogeny.

In relation to other groups: Originally understood as basal Ornithopoda (e.g. Paul Olsen lectures, Weishampel et al.. 2003), heterodontosaurs are now considered either basal ornithischian (Butler et al. 2007, Zheng et al. 2009, Butler et al. 2011, Open Dinosaur Project) or stem marginocephalia (Xu et al. 2006, Dinosaur Supertree). The first option assumes the same Cerapodan and basal Ornithopod characteristics evolving independently (by convergence) in heterodontosaurs and ornithopods, the second implies mosaic evolution (the retention of primitive, "fabrosaur" like traits in more derived ornithischians). It also has the advantage of bridging the stratigraphic gap between early ornithischia (late Triassic / early Jurassic) and early marginocephalia (late Jurassic). We have assumed the latter hypothesis for the purpose of the phylogeny in this unit.

Within Heterodontosauridae: There is little commonality between the various heterodontosaur cladograms (Butler et al. 2011, Butler et al. 2011, Pol et al., 2011) other than tending to place *Echinodon* in a basal position and *Heterodontosaurus* as derived, in reverse of the stratigraphic sequence. This may however be an artifact of the cladistic analysis, as *Heterodontosaurus* is known from very complete remains, and *Echinodon* from very incomplete. For this reason we have not attempted o present a phylogeny for this group. MAK120309

Descriptions

Heterodontosauridae: *Heterodontosaurus, Fruitadens, Tianyulong*



Heterodontosaurus tucki: skull in left lateral view. After Smith (1997).

Range: Early Jurassic to Early Cretaceous of Afr, EAs, Eur, NAm, & SAm

Phylogeny: originally Ornithopoda: (Hypsilophodontidae + Iguanodontia) + *. (e.g. Paul Olsen lectures, Weishampel et al.. 2003) Now considered either basal ornithischian (Butler et al. 2007, Zheng et al. 2009, Butler et al. 2011, Open Dinosaur Project) or stem marginocephalia (Xu et al. 2006, Dinosaur Supertree). The first assumes identical Cerapodan and basal Ornithopod characteristics developed by convergence in heterodontosaurs and ornithopods, the second mosaic evolution (the retention of primitive, "fabrosaur" like traits in more derived ornithischians). We have assumed the latter hypothesis for the purpose of the phylogeny in this unit MAK120309

Characters: Small (1-2m, <20 kg); high-crowned cheek teeth with chisel-shaped crowns; denticles on distal 1/3rd of cheek teeth; large, caniniform teeth on premaxillae & dentary; small tusks perhaps restricted to males; teeth absent from tips of jaws (probable beak); enamel thickened on labial side of upper teeth & lingual side of lowers; neck short; ossified tendons on last dorsal, but not caudal vertebrae; tail long; powerful arms with possible digging ability; tibia & fibula fused; forelimbs markedly smaller than hindlimbs; astragalus & calcaneum likewise fused to crus; horizontal posture, but bipedal; may have dug for food. ATW

Image: originally after In Hand Museum (former site), with osteology corrected and some details altered per Smith (1997).

Links: DinoData: Heterodontosauridae; Heterodontosaurus; Heterodontasaurus Tucki; Heterodontosaurus - Enchanted Learning Software; ornithischia; Untitled Document; Heterodontosauridae (Dutch); The Natural History Museum's Dino Directory; Heterodontosauridae; (Mikko's phylogeny); DINOSAURS- Family Heterodontosauridae (brief discussion); Dinosaurs-Exam 3 Notes AKA- Adrian's Uber-Notes; HETERODONTOSAURIDS; Heterodontasaurus Tucki; ORNITHISCHIA.

References: Galton (1986); Smith (1997); Weishampel (1984). ATW030426.

Heterodontosaurus tucki *Heterodontosaurus tucki* Crompton & Charig 1962

Horizon: Upper Elliot Formation, Cape Province, South Africa (Hettangian / Sinemurian).

Remains: 2 complete skulls, 1 associated with a complete skeleton, fragmentary jaw

Comments: The best-known heterodontosaurid. A largely complete skeleton is known, showing relatively large, powerful hands and arms, including a strong thumb claw. *Lycorhinus angustidens* Haughton 1924, known from an isolated dentary, may be a synonym. *Abrictosaurus consors* Hopson 1975 (= *Lycorhinus consors* Thulborn 1974), a smaller form with smaller tusks, may be a juvenile or a female of the same or a different but related species. *Lanosaurus scalpridens* Gow 1975 known only from an Isolated maxilla from the Upper Elliot Formation, Orange Free State, South Africa (Late Hettangian / Sinemurian) has since been identified with *Lycorhinus*. In short, and following the orientation of Paul 2010, the original diversity of South African heterodontosaurs can be reduced to one or at most two species. However authors of several recent cladistic studies (Butler et al. 2011, Pol et al.., 2011) regard *Heterodontosaurus*, *Abrictosaurus*, and *Lycorhinus* as three distinct species. *Dianchungosaurus lufengensis* Yang 1982, once considered a contemporary heterodontosaurid from China (Dark Red Beds, Lower Lufeng Series Yunnan, Hettangian/Sinemurian) turned out to be a chimera of prosauropod and mesoeucrocodylian remains. MAK120309

Tianyulong confuciusi X.-T. Zheng, H.-L. You, X. Xu, and Z.-M. Dong, 2009

Horizon: Western Liaoning Province, China. Originally reported as being from the Early Cretaceous Jehol group, but actually from the Tiaojishan Formation, dating from the late Jurassic (Wikipedia)

Comments: Notable for the row of long, filamentous integumentary structures apparent on the back, tail and neck of the specimen. The similarity of these structures with those found on some theropods suggests their homology with feathers and raises the possibility that the earliest dinosaurs and their ancestors were covered with homologous dermal filamentous structures that can be considered primitive feathers ("proto-feathers"). (Wikipedia)

Image: Life reconstruction of *Tianyulong confuciusi*. Artwork by Xing Lida, from Zimmer, 2011), via Fantasy Game Book, Feathered Dinosaurs and the Dinosaur Lag Effect

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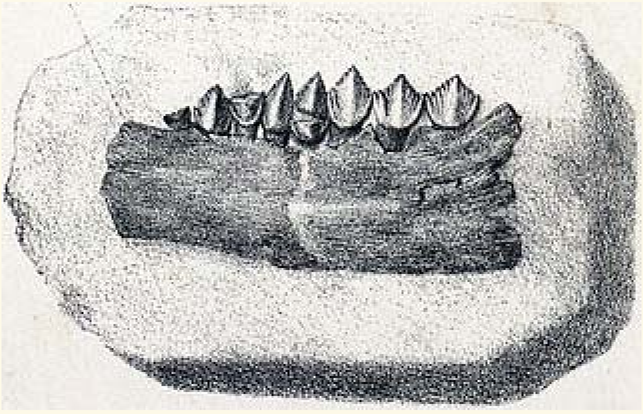
Fruitadens haagarorum Butler, Galton, Porro, Chiappe, Henderson, and Erickson, 2009

Horizon: Middle Morrison Formation (Early-Mid Tithonian) of Colorado.

Comments: lower "canine" but appears to lack the upper counterpart; has replacement teeth. A diminutive form, 65-75 cm long, known from partial remains from at least four individuals of varying stages of growth. (Thescelosaurus). MAK120309

Echinodon: Owen 1861. *E. beckelsi* Owen 1861.



Range: Late Jurassic or Earliest Cretaceous of England.

Phylogeny: originally Thyreophora: (*Scutellosaurus* + Eurypoda) + *.; now considered a basal heterodontosaur

Links: **DinoData: *Echinodon***; ECHINODON; Paleontology and Geology Glossary: E; DinoDictionary.com | E - Dinosaurs; Dinazors o´Dorzet, Gyde fer Grockles; ?????? ??? (Japanese).

Note: *Echinodon becklessi* Owen 1861 is a small (60 cm) heterodontosaur (previously considered a basal thyreophoran) from the Tithonian (Late Jurassic) or Earliest Cretaceous of England. Some North American materials may also be referred to this taxon. This has since been named *Fruitadens haagarorum*. The remains and characteristics of *Echinodon* are discussed in detail in the discussion on Ornithischia. ATW020807 MAK020420. revised MAK120309

Image: Lithograph showing teeth and jaw fragments of *Echinodon*, found in Dorset by Samuel Beckles. From A History of British Fossil Reptiles, by *Richard Owen*, Lacertians Pl. 11 ; via Wikipedia; public domain

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Ornithischia: Ceratopsia

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--+--Heterodontosauridae
      `--Marginocephalia
         |--Pachycephalosauria
         `--Ceratopsia
```

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This page is being revised

Marginocephalia

The Marginocephalia or "fringed heads" were a specialised group of Ornithischians defined by a small shelf or frill at the back of their skull. There are two main types, the dome heads and the horned dinosaurs, which evolved from a common ancestor during the early Cretaceous. With the exception of one or two questionable Gondwana forms, the group appears to be limited to Laurasia.

Descriptions

Marginocephalia: *Stenopelix*.

Range: Early Cretaceous (perhaps much earlier) to Late Cretaceous of China & North America.

Phylogeny: Cerapoda: Ornithopoda + * **:** Pachycephalosauria + Ceratopsia.

Characters: Narrow parietal shelf; post squamosal shelf; short post maxillary plate; vomers contact maxilla (maxillae meet on midline) rather than premaxilla; premaxillae excluded from internal nares; no obturator process on ischium; pubis short, with loss of pubic symphysis.

Links: **DinoData: Marginocephalia**; Introduction to the Marginocephalia; Marginocephalia - EnchantedLearning.com; New Page 6; The Natural History Museum's Dino Directory; Pachycephalosaurs and Ceratopsians (November 5). ATW011227.

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checked ATW060107

Ornithischia: Pachycephalosauria

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--Marginocephalia
      |--Pachycephalosauria
      |  |--Homalocephalidae
      |  `--Pachycephalosauridae
      `--Ceratopsia
```

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1. Pachycephalosauria X
2. Pachycephalosauridae X

This page is being revised

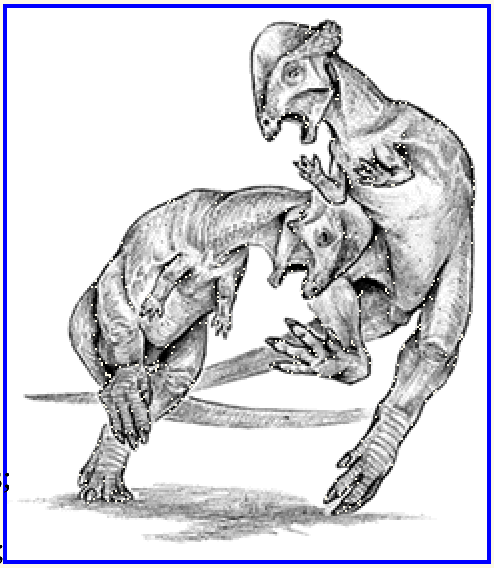
Pachycephalosauria

Dome headed dinosaurs, superficially resemble the ornithopods; bipedal, small to medium-sized, with a bony "battering ram" head. It has frequently been supposed that this peculiar skull feature was used in fights over territory or mates. However, the assumption has been strongly questioned based on the relative weakness of the neck.

These creatures walked on their hind legs and looked much like Ornithopd dinosaurs (with which they were originally clasisfied). It is now known that they are much more closely related to horned dinosaurs (Ceratopsians). Pachyephalosaurs (literally "thick headed lizards") evolved skulls ornamented with knobs and spikes, the purpose of which is still not completely clear. There were two main groups: thehomalocephalids, which had heads that were flat, and the pachycephalosaurids, in which the top of the head was rounded, like a bony bowling ball. It used to be thought that the pachycephalosaurs rammed each other at high speed, but the rounded skulls would have made this impractical. Perhaps the ornamentation served some sort of intraspecific, probably sexual display and rivalry purpose.

Descriptions

Pachycephalosauria: *Yaverlandia*. *Pachycephalosaurus* > *Triceratops*.



Range: Early to Late Cretaceous of China & North America.

Phylogeny: Marginocephalia: Ceratopsia + * : Pachycephalosauridae + Homalocephalidae.

Characters: Dentition heterodont & small; maxillary & posterior (distal) dentary teeth mediolaterally compressed, with leaf-shaped crowns bearing denticles; premaxilla retains teeth (primitive); frontal and parietal thickened dorsoventrally; external surfaces of skull strongly ornamented, usually tubercles on postorbital & squamosal; basicranium foreshortened; dorsal vertebrae strongly consolidated with double ridge-groove between zygapophyses of adjacent vertebrae; sacral and anterior caudal vertebrae have long ribs; intertwined ossified tendons on distal (?) caudals; scapula slender and much longer than shortened humerus; pubes small & excluded from acetabulum; pelvic girdle broad; no obturator process on ilium. Head-butting? Unsettled issue – certainly butted something.

Image: *Stegoceras* by Matt Celeskey, **Hairy Museum of Natural History**.

Links: **DD: Pachycephalosauria**; Pachycephalosaurus and Pterodactylus; WMNH - Pachycephalosaur dorsal vertebra; FPDM : Pachycephalosauria; Pachycephalosauria after Sereno, 2000; Literature - Pachycephalosauria; Lecture 19: Late Cretaceous I. ATW011130.

Homalocephalidae: flat-heads.

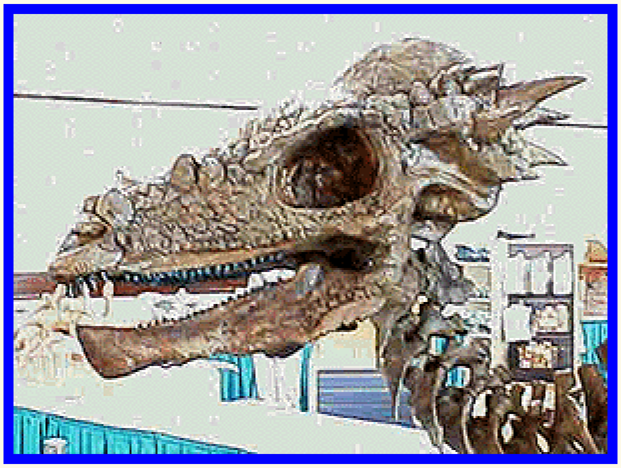
Range: Early Cretaceous of China.

Phylogeny: Pachycephalosauria: Pachycephalosauridae + *.

Characters: Skull evenly thickened & flat dorsally with numerous pits; supratemporal fenestrae present & relatively large.

Links: link; link (with rotatable skull).

Pachycephalosauridae: More specialized Pachycephalosaurs? *Pachycephalosaurus, Prenocephale, Stegoceras, Stygimoloch*.



Range: Early to Late Cretaceous of China & North America.

Phylogeny: Pachycephalosauria: Homalocephalidae + *.

Characters: Frontals & parietals greatly thickened & fused into single dome-like structure; no upper temporal fenestra; base of skull shortened in some; ridge-and-groove articulation between dorsal vertebrae possibly provided greater rigidity to backbone; long tail; very broad pelvis; long, low ilium; widely positioned femora; tail with the basketwork of ossified tendons.

Image: of *Pachycephalosaurus* (Graves Museum) courtesy of Michael Corriss.

Links: **DinoData: Pachycephalosauridae**; Biologybase: Checklist of the Non-Avian Dinosaurs; Pachycephalosaurus- Enchanted Learning Software; Pachycephalosauridae; Homalocephale; pachycephalosauria; Prenocephalae; pachycephalosauria cladogram; The Natural History Museum's Dino Directory; New Page 6; DINOBASE, Sibbick's dinosaur pictures; Pachycephalosauridae (photo of vertebra, but otherwise unremarkable); Pretty Butte Paleontology- Catalog of Pachycephalosauridae ... (images of isolated dome!); 7 (M. Shiraishi's gallery). ATW030718.

checked ATW060107

Ornithischia: Ceratopsia

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Thyreophora
|  |--Stegosauria
|  `--Ankylosauria
`--Cerapoda
   |--Ornithopoda
   |  |==Hypsilophodontidae
   |  `--Hadrosauridae
   `--+--Heterodontosauridae
      `--Marginocephalia
         |--Pachycephalosauria
         `--Ceratopsia
            |--Psittacosauridae
            `--+--Protoceratopsidae
               `--+--Centrosaurinae
                  `--Ceratopsinae
```

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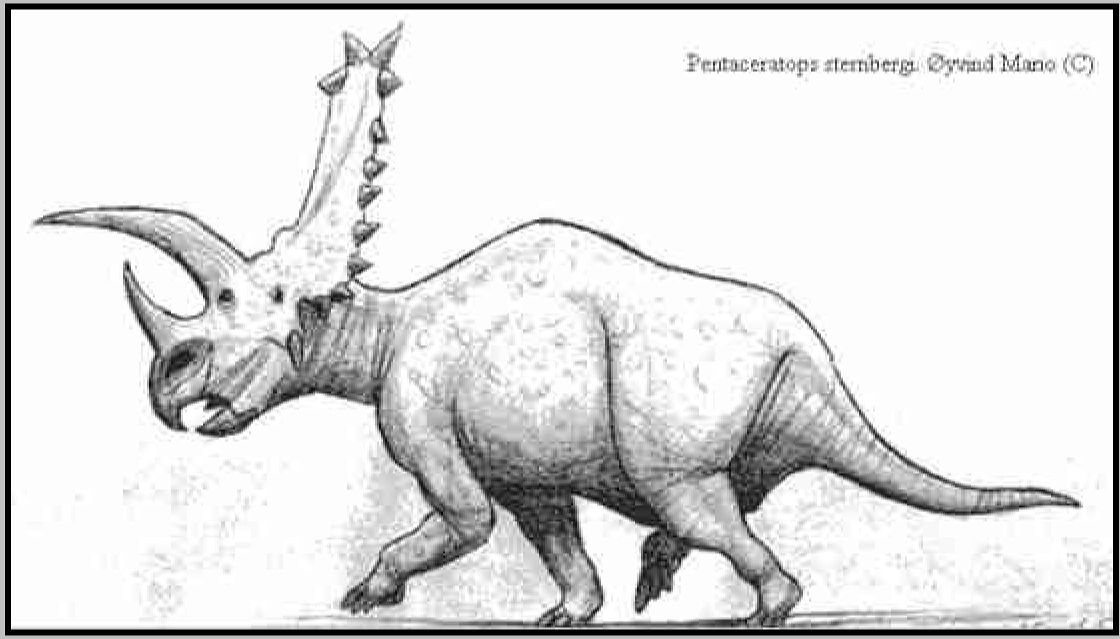
Ceratopsia

Ceratopsia - horned dinosaurs, small to large parrot-beaked dinosaurs, divided into the primitive early Psittacosauridae - parrot-beaked dinosaurs, stocky animals about about 1.5 meters long, and the Neoceratopsia or horned dinosaurs, including both horned and hornless types, all equipped with a bony frill, and the medium-sized to larger ones quadrapedal. Included here area number of famous late Cretaceous types like *Styracosaurus*, *Triceratops*, etc.



Pentaceratops sternbergi **- (drawing copyright Øyvind M. Padron)**

The Ceratopsians were the last of the major dinosaurian groups to evolve; first appearing during the Aptian or Albian. They are also among the most geographically limited, none being known outside the Asiamerican (eastern Asia + western North America) landmass. Reputed "Neoceratopsia" from Mid-Cretaceous southern Australia are probably not of this group. They may pertain to an unknown lineage of herbivorous quadrapedal Gondwanaland Predentata. Only the very most specialised Ceratopsia (the family Ceratopsidae, known only from the Senonian of western North America) developed horns and grew to a large size. (*Triceratops horridus* was about the size of a modern elephant).

Descriptions

Ceratopsia: ~Ceratopia Marsh

Range: Early to Late Cretaceous of Asia & North America.

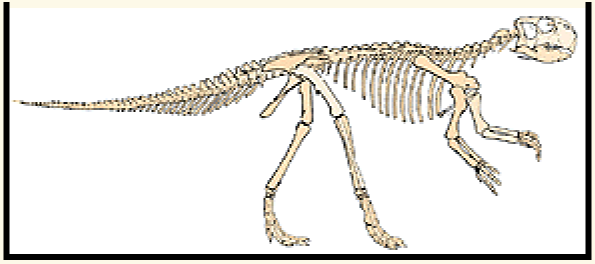
Phylogeny: Marginocephalia: Pachycephalosauria + * **:** Psittacosauridae + (Protoceratopsidae + (Centrosaurinae + Ceratopsinae).

Characters: Unique single rostral bone, usually with rugose surface indicated horn beak; maxilla at least 2/3 as tall as length; broad, inflexible mandibular symphysis (i.e. where mandibles grow together); jaw typically narrow, with flaring jugal (so skull triangular in dorsal view); tall snout w relatively broad premaxilla. Commonly parietal shelf (not necessarily a frill) overhanging occipital skull; often nasal & supraorbital horns. Teeth replaced very rapidly; achieved scissor-like vertical shear & high coronoid process gave additional leverage on lower jaw. Shelf may have started as giving increased length to mandibular adductor muscles. Presumably served in more derived species for display and possibly defense.

Links: dinodata.

Psittacosauridae: *Psittacosaurus* (= *Protiguanodon*).

Range: Early Cretaceous of Asia.



Phylogeny: Ceratopsia: (Protoceratopsidae + Centrosaurinae + Ceratopsinae)) + *.

Characters: 1-2m early ceratopsian. Enamel primarily on one side of teeth, for upper teeth, thickened side is on the outside, reverse on lower teeth, cerating self-sharpening effect; crowns of even hatchlings show shear wear; tall, parrot-like snout with neomorphic unpaired rostral bone inserted between premaxillae (opposes predentary); nares high; anteriorly vaulted palate; distance from orbit to front of skull <40% of skull length, shortest of all dinosaurs (even oviraptors??); nasal extends as processes *ventral* to nares; premaxilla forms lateral surface of snout, broadly separating maxilla from nares; antorbital fenestrae and fossae absent; elongated jugal; slight parietal frill; post-cranial skeleton similar to basic Ornithischian pattern, especially Hypsilophodonts; moderately long, outstretched tail stiffened by (sometimes ossified) tendons along spine; arms ~58% length of legs; likely facultative biped; **$** 2 outer digits of manus reduced; manual unguals expanded & slightly hoof-like; tibia » femur (cursorial); 4 functional digits on pes; gastroliths common (unlike derived Ceratopsians); skin impressions broadly similar to other Ornithischia.

Links: **DinoData: Psittacosauridae**; Psittacosaurus- ZoomDinosaurs.com; Lectures 12: Early Cretaceous; Psittacosaurus mongoliensis; New Page 6; DINOBASE, Sibbick's dinosaur pictures; ?????? Vertebrates (Chinese); ORNITHISCHIA; Biologybase: Checklist of the Non-Avian Dinosaurs; Psittacosaurus The Natural History Museum's Dino Directory. ATW020118.

Protoceratopsidae: *Leptoceratops*, *Protoceratops*.

Range: Late Cretaceous of Asia & North Amweica.

Phylogeny: Ceratopsia:: (Centrosaurinae + Ceratopsinae) + *.

Characters: Unclear whether clade or grade. No orbital or developed nasal horns; Rare in NAm, common in Asia.

Links: Paleo Mont Park; Fighting Dinosaurs.

Centrosaurinae: *Styracosaurus*.

Range: Late Cretaceous of North America.

Phylogeny: Ceratopsia::: Ceratopsinae + *.

Characters: Long nasal horns, hooks & processes on parietals; short, square squamosals; bone "finger" projecting into back of nares; in some, orbital & nasal horns appear as irregular, thickened bone pads (for horn spikes?); divergent ornamentation developed as approaching adulthood -- young of all species appear the same. Bone-beds common -- perhaps herds.

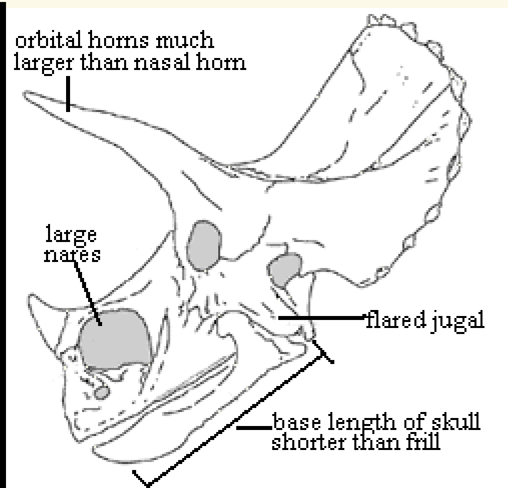
Links: **DinoData: Centrosaurinae**; Centrosaurus nasicornis.

Ceratopsinae (= Chasmosaurinae): *Chasmosaurus, Torosaurus, Triceratops*.

Range: Late Cretaceous of North Amweica.

Phylogeny: Ceratopsia::: Centrosaurinae + *.

Characters: Up to 8m (generally larger than centrosaurs), with skull up to 2.5 m. Complex, large narial opening with many fenestrae and bone processes; short nasal and long orbital horns; snout relatively short; neotenous epinasal



Triceratops skull: left lateral view, showing various ceratopine characters

bone on ant of nasal horn; some (e.g. *Triceratops*) had frontal sinus between horns and braincase, possibly used as shock absorber in combats (as in bovids) or as part of extensive system of vascularized cavities in thermoregulation; large conical epijugal horn on flared cheek; spikes absent from parietal (? *Triceratops* had epoccipitals as shown); frill longer than basal length of skull, with bend in middle (secondary reduction in *Triceratops*); squamosal concave and extends full length of frill; no known bone beds found (solitary?).

Links: **DinoData: Chasmosaurinae**; Biologybase: Checklist of the Non-Avian Dinosaurs; Abstract: Marcot; Chasmosaurinae; Literature - Ceratopsia; Ceratopsinae -- The Dinosauricon; The Evolution of Dinosaurs; GEOL 104 Dinosaurs- A Natural History; Torosaurus Fact Sheet - EnchantedLearning.com; GEOL 104 Lecture 20- Marginocephalia- That's using your head!; Adrian's Dinosaur Notes Page (For Dr. Masons g180 Class); Figure 5; Triceratops. ATW030125.

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Ornithischia Classification

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Fabrosauridae
`--+--Thyreophora
   |  |--Stegosauria
   |  `--Ankylosauria
   `--Cerapoda
       |--Ornithopoda
       |  |==Hypsilophodontidae
       |  `--Hadrosauridae
       `--+--Heterodontosauridae
          `--Marginocephalia
             |--Pachycephalosauria
             `--Ceratopsia
```

Contents

Order Ornithischia

Traditional classification

The following is based mainly on Carroll (1988), as the most recent comprehensive linnaean classification of the Vertebrates, with more recent groups added. Each taxon is listed by rank, name, and original author, and followed by a short description. Some additions have also been made from Paul 2010 and Holtz 2011. Linnaean names may not match their cladistic equivalents. New taxa are indicated by inverted commas. MAK120308 120312

Infraclass Archosauromorpha Huene, 1946 (*cont.*)
Holoorder Ornithischia Seeley, 1888 "bird-hipped" dinosaurs
Suborder Ornithopoda Marsh, 1881 generalised bipedal, herbivorous dinosaurs, mostly a "wastebasket taxon" for anything taht doesn't fit in the other groups. L Trias to L Cret, Cosm.
Family Pisanosauridae Casamiquela, 1967 the most primitive group of ornithischians, monospecies only, L Tr of S Am
Family Fabrosauridae Galton, 1972 small bipedal generalised ancestral ornithischians, E Jur to M Jur of S Afr, EAs.[1]
Family Heterodontosauridae Romer, 1966 small bipedal early specialised forms, E Jur to E Cret of S Afr, Eur, EAs.

Family Hypsilophodontidae Dollo, 1882 small bipedal, cursorial, generalised ornithopods, ancestral to later groups, M Jur to L Cret. Cosm.[2]

Families not specified - a number of iconic types such as *Muttaburrasaurus* (M Cret of Aus) and *Tenontosaurus* (M Cret of N Am) that don't fit easily into the established groups, perhaps require monospecific families or subfamilies

Family Rhabdodontidae medium-sized ornithopods that represnet a distinct evolutionary line - L Cret of Eur

Family Dryosauridae small to medium sized, bipedal, cursorial, ornithopods, intermediate between hypsilophodonts and iguanodonts, Monogeneric. L Jur of E Afr, N Am.

Family Iguanodontidae Cope, 1869 large to very large, bipedal and faculatively quadrapedal, ornithopods, intermediate between dryosaurs and hadrosaurs. L Jur to L Cret, Eur, N Am, As.

Family Hadrosauridae "duck-billed" dinosaurs, large to very large, bipedal and faculatively quadrapedal, ornithopods, highly specialsed dental batteries, frequently with head crests. E to L Cret, N Am, As, Eur, SAm.

Subfamilies not specified - a large assortment of various primitive and unspecialised Hadrosaurus, E to L Cret, N Am, As, Eur, SAm.

Subfamily Saurolophinae - flat-headed, broad-Snouted hadrosaurs - L Cret of N Am & E As

Tribe Maiasaurini—unspecialised, primitive, broad-snouted duckbilled dinosaurs - L Cret of N Am

Tribe Saurolophini—spike-crested duckbilled dinosaurs - L Cret of N Am & E As

Tribe Edmontosaurini— very broad-snouted (classic "duck bill" dinosaurs - L Cret of N Am & E As

nbsp; Subfamily Lambeosaurinae - crested hadrosaurs - L Cret of N Am

Tribe Saurolophini - tube crested lambeosaurines

Tribe Corythosaurini (=Lambeosaurini) - helmet crested lambeosaurines

Suborder unspecified[3]

Family Scelidosauridae Cope, 1869 - Ancestral armoured types - mostly Early Jurassic. Quadrupedal, ancestral armoured dinosaurs. Includes light running forms and large heavily armed types. Length 1 to 4.5 meters E Jur of Eur, NAm, As

Suborder Stegosauria Marsh, 1877 - Plated dinosaurs - spines along the back and tail for protection, plates served a thermoregulatory purpose. Quadrupedal, short forelimbs, slow-moving. Length 3 to 10 meters M Jur to E Cret of N Am, Eur, As, Afr

Family Huayangosauridae - Primitive plated dinosaurs; M Jur of E As

Family Stegosauridae Marsh, 1877 advanced plated dinosaurs; M Jur to E Cret of N Am, Eur, As, Afr

Subfamily Kentrosaurinae - small plates, shoulder spines, spikes along back and tail - usually given family rank (Kentrosauridae); may be monotypic - L Jur of Afr, ?Eur

Subfamily Dacentrurinae - tail spikes like *Stegosaurus*, otherwise resembles *Kentrosaurus* L Jura of Eur

Subfamily Stegosaurines - advanced stegosaurs, alternatinbg paired plates, no shoulder spines; L Jur to E Cret of NAm & EAs

Suborder Ankylosauria Osborn, 1923 heavily armoured dinosaurs, 2 to 10 meters long, quadrupedal, slow moving, and fed on soft vegetation.

Family Polocanthidae - ancestral ankylosaurs - L Jur to L Cret of Eur, N Am, EAs & Ant.

Family Nodosauridae Marsh, 1890 - with spikes on the shoulders - E to L Cret of Eur & N Am

Family Ankylosauridae Brown, 1908 - with a war club at the end of the tail - E to L Cret of E As & N Am

Suborder Pachycephalosauria Sternberg, 1945 (Only one family; Homalocephalidae Dong, 1974 is comprised of juvenile pachycephalosaurids only)

Family Pachycephalosauridae Sternberg, 1945 dome headed dinosaurs, superficially resemble the ornithopods; bipedal, small to medium-sized, with a bony "battering ram" head. L Cret of NAm & E As

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Family Protoceratopsidae Granger & Gregory, 1923 small to medium sized ancestral hornless forms, bipedal or quadrapedal L Cret of EAs & NAm

Subfamily Leptoceratopsinae - short frilled protoceratopsids - L Cret of E AS & N Am

Subfamily Bagaceratopinae - Small-horned, lump-nosed Frilled Dinosaurs - L Cret of Eur & E As

Subfamily Protoceratopsinae - advanced, deep-tailed protoceraptopsids - L Cret of E As

Family Ceratopsidae Marsh, 1890 large to gigantic horned dinosaurs, quadrapedal, rhino-like L Cret of NAm

Subfamily Centrosaurinae - short-frilled horned dinosaurs

Subfamily Chasmosaurinae - long-frilled horned dinosaurs

Hybrid classification

This section is part of a discontinued and impractical attempt to integrate the rank-based Linnaean and the phylogeny-based Cladistic systems . We have distinguished between monophyletic and paraphyletic taxa (or clades and grades), as indicated by the following key regarding prefixes:

- **para-** for a paraphyletic (an ancestral or evolutionary grade defined only by shared primitive features and lack of specialised features) according to consensus opinion
- **holo-** for holophyletic (=monophyletic)
- **ambi-** for when different cladistic analyses dissagree as to whether a taxon is paraphyletic or monophyletic
- **mono-** for a monotypal taxon
- **evo-** for when a taxon is considered monophyletic according to current consensus cladistic studies, but morphologically and/or stratigraphically intermediate and so considered to have given rise to other taxa according to evolutionary systematics or a general gradistic perspective (which implies reversals (loss of original synapomorphies) and a non-parsimony-based phylogeny)

For the phylogenetic arrangement, see the dendrogram page MAK120308 120312

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Holoorder Ornithischia Seeley, 1888 "bird-hipped" dinosaurs
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Holosubfamily Centrosaurinae - short-frilled horned dinosaurs

Holosubfamily Chasmosaurinae - long-frilled horned dinosaurs

Notes

[1] either a wastebasket taxon for any really primitive ornithischians (apart from *Pisanosaurus*) or limited to one or two Early Jurassic species from southern Africa. if the former, the boundaries between the the Fabrosauridae and other stem groups such as the Scelidosauridae and the Hypsilophodontidae are very poorly defined

[2] another ancestral/generalised/wastebasket taxon; generally, all ornithopods beneath the level of dryosaurs. Like other paraphyletic (ancestral) taxa, hypsilophodonts are defined in terms of shared primitive features (plesiomorphies)

[3] Essentially, basal Thyreophora. Although monophyletic Thyreophora and Cerapoda are sometimes given subordinal rank, we have followed Carroll (1988) in retaining the five classic ornithischian suborders

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Links: The major dinosaur families at Enchanted Learning; Taxon tree; Linnean Ornithischia, dinosaur mailing list

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Ornithischia: Dendrogram

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Fabrosauridae
`--+--Thyreophora
   |  |--Stegosauria
   |  `--Ankylosauria
   `--Cerapoda
       |--Ornithopoda
       |  |==Hypsilophodontidae
       |  `--Hadrosauridae
       `--+--Heterodontosauridae
          `--Marginocephalia
             |--Pachycephalosauria
             `--Ceratopsia
```

Contents

Dendrogram

Note: the following dendrogram is still to be revised - MAK120308

```
Ornithischia X MH, Th, ToL
|--Fabrosauridae •X
`--Genasauria X
   |--Thyreophora X
   |  |--Echinodon •X
   |  `--+--Scutellosaurus •X
   |     `--Eurypoda X
   |        |--Stegosauria X Th, MH
   |        |  |--Huayangosauridae X
   |        |  |  |--Emausaurus •X
   |        |  |  `--Huayangosaurus •X
   |        |  `--Stegosauridae •X
   |        |     |--Dacentrurus •X
   |        |     `--Kentrosaurinae X
   |        |        |--Kentrosaurus •X
   |        |        `--+--Chialingosaurus •X
```

```
  |        |           `--+--Chungkingosaurus •X
  |        |              `--Stegosaurinae X
  |        |                 |--Lexovisaurus •X
  |        |                 `--+--Tuojiangosaurus •X
  |        |                    `--+--Stegosaurus •X
  |        |                       `--Wuerhosaurus •X
  |        `--Ankylosauromorpha X ToL
  |           |--Scelidosauridae •X
  |           `--+--Minmi •X
  |              `--Ankylosauria X ToL, MH, Th
  |                 |--Ankylosauridae •X Th, MH, ToL
  |                 `--Nodosauridae •X MH, ToL
  `--Cerapoda X
     |--Ornithopoda X Th, MH
     |  |--Heterodontosauridae •X MH
     |  `--+--Hypsilophodontidae X
     |     |  |--Leaellynasaura •X
     |     |  |--Thescelosaurus •X
     |     |  `--+--Zephyrosaurinae •X
     |     |     `--+--Othnieliinae •X
     |     |        `--Hypsilophodontiniae •X
     |     `--Iguanodontia X MH
     |        |--Muttaburrasaurus •X
     |        `--+--Tenontosauridae X
     |           |  |--Tenontosaurus •X
     |           |  `--Rhabdodon •X
     |           `--+--Dryosauridae •X
     |              `--+--Iguanodontidae X Th
     |                 `--Hadrosauroidea X MH
     |                    |--Ouranosaurus •X
     |                    `--+--Nanyangosaurus •X
     |                       `--+--Altirhinus •X
     |                          `--Hadrosauridae X Th
     |                             |--Hadrosaurinae •X MH
     |                             `--Lambeosaurinae •X Th, MH
     `--Marginocephalia X
        |--Pachycephalosauria X Th, MH
        |  |--Homalocephalidae •X
        |  `--Pachycephalosauridae •X
        `--Ceratopsia X , Th, MH
           |--Psittacosauridae •X MH
           `--+--Protoceratopsidae •X
              `--+--Centrosaurinae •X Th
                 `--Ceratopsinae •X
```

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Ornithischia: References

Abbreviated Dendrogram

```
DINOSAUROMORPHA
|--+--THEROPODA
|  `--SAUROPODOMORPHA
|
ORNITHISCHIA
|--Fabrosauridae
`--+--Thyreophora
   |  |--Stegosauria
   |  `--Ankylosauria
   `--Cerapoda
      |--Ornithopoda
      |  |==Hypsilophodontidae
      |  `--Hadrosauridae
      `--+--Heterodontosauridae
         `--Marginocephalia
            |--Pachycephalosauria
            `--Ceratopsia
```

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Tianyulong

Sauropodomorpha: Overview

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      `--Sauropoda
         |--Cetiosauridae
         `--Neosauropoda
            |--Diplodocomorpha
            |  |--Rebbachisauridae
            |  `--Diplodocidae
            `--Macronaria
               |--Brachiosauridae
               `--Somphospondylii
                  |--Euhelopodidae
                  `--Titanosauria
                     |--Nemegtosauridae
                     `--Titanosauridae
```

Contents

Camarasaurus; Image from Dinopedia

The Majestic Sauropods

The most impressive and characteristic of all the dinosaurs are the sauropods, not only the largest animals to live on land, but alos the most successful and long-lived of any megafauna. In this unit we presnet a brief overview of these awesome creatures, along with their ancestors, the prosauropoda [1]. Sauropods and prosauropods together make up the Sauropodomorpha, or "sauropod forms", although most sauropodomorphs are actually sauropods proper, the prosauropods being only a group of late Triasisc and Early Jurassic short-lived primitive forms. Although all shared the same large bodied, long necked, small headed form, these spectacular animals nevertheless evolved along a number of distinct evolutionary lineages, reaching their greatest diversity during the late Jurassic. By the late Cretaceous, only the titanosaurs remained, but, rather than being remnant holdovers, these populated every continent and included dwarf forms as well as giants, and even specialised armoured forms MAK120303

Notes

[1] Being paraphyletic, Prosauropoda is an invalid taxon in the cladistic paradigm (but not in evolutionary systematics), being replaced by rather vague and clumsy alternatives such as basal sauropodomorpha. We have however retained the term in both the colloquial and the linnaean sense.

Sauropodomorpha: Overview

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
|--Prosauropoda
`--Sauropoda
   |--Cetiosauridae
   `--Neosauropoda
      |--Diplodocomorpha
      |  |--Rebbachisauridae
      |  `--Diplodocidae
      `--Macronaria
         |--Brachiosauridae
         `--Somphospondylii
            |--Euhelopodidae
            `--Titanosauria
               |--Nemegtosauridae
               `--Titanosauridae
```

Contents

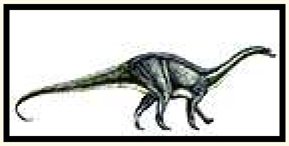
Introduction

The Sauropodomorpha constitute one of the two main groups of herbivorous dinosaurs, the other being the Ornithischia. There are two main subgroups, the small to large Triassic Prosauropoda and their giant cousins or descendents the Sauropoda. It is possible to trace a progressive morphic sequence from the small lightly built early thecodontosaurian prosauropods through the large plateosaurs, melanorosaurs and vulcanodonts to the giant Sauropoda of the Jurassic and Cretaceous.

But even the most primitive ancestral prosauropods had the same long neck, tiny head, and weak peg-like teeth which characterized the greatest of the later giants. The sauropodomorphs in fact were "pin-headed" herbivores. Their bodies grew extremely large, but the heads remained tiny. And like modern ostriches and emus, and extinct moas and elephant birds (*Aepyornis*), these ancient long-necked pinheads swallowed stones (*gastroliths*) which remained in the stomach to aid in digestion. This bird-like stomach processing of food differs greatly from the ornithischian and mammalian oral processing which relied on grinding teeth.

The first known prosauropod dinosaurs were small, lightly built bipedal forms of the family Thecodontosauridae. Slightly later, larger anchisaurids are found which were probably capable of walking on all fours as well as on their back legs. Early in their history, some of these small and primitive prosauropods developed into increasingly larger forms. These lines continued to evolve parallel to each other after the initial radiation; each independently evolving a gravimorphic form (like the reverse of a Weight Watchers contest), just as the various theropod lines independently took up the gravimorphic tendency. This is indicated by the steady increase in size and bulk of these creatures. The small ancestral types, like thecodontosaurs and anchisaurs, were only 1.5 to 2.5 meters in length, and a svelte 25 kg in weight. From these there evolved the larger types: the lightly-built massospondylids (4 to 5 metres long), the large yunnanosaurs (up to 7.5 metres), and the diverse plateosaurs, the most common of the early prosauropods.

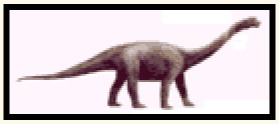
The big plateosaurs, in particular, were much larger and heavier than their close anchisaur cousins, with lengths of 4 to 10 (or even 12) metres, and weights of up to 1500 kg. Their increasing size drove them closer to the earth, making them more comfortable with quadrupedal than with bipedal locomotion, although they may still have been able to walk on their hind legs if the situation required.



The increase in size continues with another line, the melanorosaurs. Melanorosaurs, which may have evolved from something like the early plateosaur *Sellosaurus* (length 3-6 metres), were large herbivorous animals, 7 to 12 metres long, and one or two tonnes in weight, which may have been closely related to the huge sauropod dinosaurs of the Jurassic and Cretaceous, and were strictly limited to a quadrupedal pose.

A related line, the blikanosaurs, represent an independent and parallel evolution of stocky types that are so far known only from a single medium- sized (length 5 metres) Late Triassic form.

The various prosauropod lines survived well into the Jurassic, and so were contemporary with the earliest giant sauropods. They were probably ousted by the increasing diversity of more efficient herbivorous ornithopod and sauropod dinosaurs in the early Jurassic. They represented, for the most part, early and short-lived evolutionary branches; parallel experiments in gravimorphism.

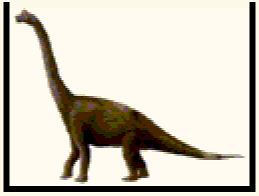


With the early Jurassic appeared the first true sauropods (the Vulcanodontidae or "volcano tooth", rather inappropriately so called because what were at first thought to be teeth of this type were found between layers of volcanic ash). Unfortunately, the fossil record of Early Jurassic sauropods is still very incomplete, although by the Pliensbachian or Toarcian age at least one large and specialized form, *Barapasaurus tagore* (length 15 to 18 metres, weight 15 tonnes), is known. Some 10-20 million years later, by the Middle Jurassic period (Bathonian Age) we find several different families (Brachiosauridae, Shunosauridae, and Cetiosauridae) existing side by side. These early sauropods were 8 to 21 metres long, with weights from 1 to 30 tonnes, depending on the species. The giant, *Apatosaurus*-sized, 21 metre form was possibly the species *Cetiosaurus oxoniensis*. *Cetiosaurus* or "whale saurian" is so called because the bones unearthed in England during the Nineteenth Century were originally thought to be from a prehistoric whale. The unknown ancestors of these different types must have diverged from *Vulcanodon*-like stock during the middle of the Early Jurassic.

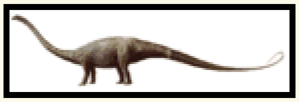
Basically then, early sauropod evolution meant a rapid increase of body size. Beginning with the two-metre long thecodontosaurs and anchisaurs of the Triassic Carnian age, within a few millions of years (Norian and Rhaetian ages) the plateosaurs and melanorosaurs had reached lengths of 8 to 12 metres, and weights of one to two tonnes. By the Early and Middle Jurassic (Pliensbachian to Bathonian ages), the Sauropoda proper appeared and diversified, with several parallel lines of evolution, some species being 15 to 20 metres in length and 12 to 30 tonnes in weight.

By the middle Jurassic at latest, the sauropods were world-wide in distribution, their fossil remains being known from Europe (England), Africa (Morocco and Madagascar), South America (Argentina), China, and Australia (Queensland). As in the Triassic, all the continental land masses were joined together and, although there was now the beginning of a separation into north (Laurasia) and south (Gondwanaland), there were no serious geographical barriers to migration. Hence animals could become global in distribution.

At least as early as the middle Jurassic, the Sauropods had branched into two main clades, which can be called the Macronaria and Diplodocomorpha. Both had long necks for



reaching far and/or high up into vegetation, but they differed in body shape, and hence feeding behavior. The macronarians included, as their most advanced representatives, the Brachiosaurs ("arm saurians"), which had long fore-arms (hence the name) a larger, more globular head, stronger teeth, shorter tail, and a sloping giraffe-like back, enabling them to walk and browse from trees. They were huge beasts, yet still quite slightly built relative to their size. They flourished from the Middle Jurassic to the Mid-Cretaceous.

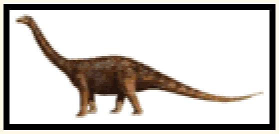


The diplodocomorphs had longer hind limbs, a long tail, more slender bodies, and a smaller, longer head with fewer teeth. Using their tail as a prop, some researchers believe that they could rear up on their large hind legs and feed from the tops of trees, reaching leaves that were beyond the reach of the Brachiosaurs. It was as if they were, in an elephantine way, trying to regain the bipedal posture of their distant ancestors. Meanwhile, the much smaller ornithischian dinosaurs - the ornithopods and stegosaurs - browsed on the undergrowth. Some diplodocomorphs, especially types like *Diplodocus*, were very lightly built. Others, like the closely related *Apatosaurus* (or "*Brontosaurus*"), were much more heftier.

There is still uncertainty regarding the relationships between the different groups of sauropods. But all of the advanced (Late Jurassic to Cretaceous) sauropods had specially hollowed-out vertebrae, which not only lightened the animal but also suggest the presence of avian-style air-sacs (identical hollows being found in the vertebrae of birds) and an advanced metabolism. In contrast, the earlier (Middle Jurassic) and more primitive sauropods had solid vertebrae.

The Late Jurassic was the golden age of sauropods; the age of giants. The great *Apatosaurus*, the almost unbelievably long-necked *Mamenchisaurus*, and *Brachiosaurus*, and the imaginatively named *Supersaurus*, *Ultrasaurus*, and *Seismosaurus*, attained lengths of 20 to 40 metres and weights of 30 to 50 tonnes or more.

While most sauropods disappeared at the end of the Jurassic (possibly the victims of one of the many mass-extinctions that characterize the history of life), some, such as the brachiosaurs, survived and flourished into the Cretaceous period. But by the mid-Cretaceous they, too, declined, perhaps through changing vegetation and (during the late Cretaceous) climatic patterns, or competition from the fast evolving ornithischian dinosaurs.



But the sauropods were far from finished. During the Late Cretaceous, a new family of sauropods, the Titanosauridae ("titanic saurians"), attained world-wide distribution, being known from every continent except most of Asiamerica (where ornithischians were the dominant herbivores) and Australia (where late surviving primitive types, the Austrosaurs, held sway). For the most part, these newcomers had nothing of the of their predecessors, and despite their name they were often small (by sauropod standards only!), around 12 meters long, and rather uniform in appearance. It was the spectacular array of ornithischians that made the Cretaceous such an interesting time -- strangely named beasts like "duckbills" and "boneheads", and various types of armoured and horned dinosaurs.

But there were also a few giants among them as well. Several species of titanosaurids were the size of the Jurassic *Apatosaurus* ("*Brontosaurus*"), and the great *Antarctosaurus giganteus*, known from the latest Cretaceous of South America, is estimated to have been as large as or even larger than the biggest *Brachiosaurus* - 30 metres long, 50 tonnes or more in weight. All these Late Cretaceous types survived right until the very end of the Mesozoic, when they were exterminated by the same catastrophe that wiped out the rest of the dinosaurs. (MAK 000117)

Sauropodomorpha: "Prosauropods"

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--o SAUROPODOMORPHA
      `--+-- Thecodontosaurus
         `--+-- Efraasia
            |--o Prosauropoda
            |  `--+--+--Plateosauridae
            |     |  `--+--Massospondylidae
            |     |     `--Yunnanosaurus
            |     `--Riojasaurus
            `--o "Anchisauria"
               |--Anchisaurus
               `--+--Melanorosauridae
                  `--o Sauropoda
                     |--Cetiosauridae
                     `--Neosauropoda
                        |--o Diplodocomorpha
                        |  |--Rebbachisauridae
                        |  `--Diplodocidae
                        `--o Macronaria
                           |--Brachiosauridae
                           `--o Somphospondylii
                              |--Euhelopodidae
                              `--o Titanosauria
                                 |--Nemegtosauridae
                                 `--Titanosauridae
```

Contents

Taxa on This Page

1. *Anchisaurus* **X**
2. *Efraasia* **X**
3. Massospondylidae **X**
4. Melanorosauridae **X**
5. Plateosauridae **X**
6. Prosauropoda **X**
7. Riojasaurus **X**
8. Sauropodomorpha **X**
9. *Thecodontosaurus* **X**
10. *Yunnanosaurus* **X**

Sauropodomorpha

At the time of this writing (7/00), the unofficial Chief Panjandrum of the Basal Sauropodomorpha is Professor Michael Benton of the University of Bristol. Prof. Benton's particular domain in phylostratigraphic space-time extends out into the sere and barren wilderness of mid-Triassic Dinosauriformes, through the high pass between the Theropoda and Sauropoda, and into the slim, but fertile valley of Upper Triassic and Lower Jurassic Prosauropoda. Recently, forces from Chicago's Field Museum attempted an incursion with prosauropods from the earliest Late Triassic of Madagascar. Flynn et al. (1999). But Flynn's specimens were not securely dated, and Benton immediately countered with *Saturnalia*, a basal sauropodomorph from the Upper Triassic of Brazil (Langer et al. (1999)) and a redescription of *Thecodontosaurus* from Triassic Bristol itself. Benton et al. (2000). The latter move was especially dramatic, as the holotype of *Thecodontosaurus* was destroyed by pin-point Nazi bombing in World War II (undoubtedly the loss of this primitive prosauropod was intended as a stunning blow to British combat paleontology). At the last, Benton was forced to call up his ultimate reserves: casts, paratypes, privately held bits and pieces, and even previously unidentified shards salvaged from the smoking ruins of the Bristol City Museum in 1944.

So, just what does this territory consist of? That's a harder question. In researching this essay, I had set myself the task of trying to determine what Prof. Benton was up to: was there a master hypothesis in back of this recent activity? I am happy to report total failure on that front. I can only state the obvious. Benton and his students have repeatedly made the point that the ancestral sauropodomorph was a remarkably small, gracile creature with a small head and short fore-limbs. Recently, they have suggested that the root of Dinosauria may lie closer to the pterosaurs than previously thought. But the bigger questions remain unresolved.

What is the relationship between the sauropods and prosauropods? Many sauropod workers feel that sauropods are, as originally believed, descended from the prosauropods. That is, traditional Prosauropoda is paraphyletic or, more correctly, that Prosauropoda and Sauropodomorpha are the same. This is consistent with the stratigraphic absence of any sauropod remains until the early Jurassic. However, Benton et al. conclude that this is incorrect and that the prosauropods and sauropods diverged early from a common ancestor. However, they point out that the support for this hypothesis is weak. Furthermore, the analysis in Benton et al. (2000) was performed without the inclusion of the *Saturnalia* material, which has been named but not yet described in any detail.

Saturnalia might have some strange effects on the results. On the one hand, almost all of the informative characters of *Saturnalia* are prosauropod. So, for example, the teeth are lanceolate, with coarse serrations oriented at 45 degrees to the vertical, there are three sacral vertebrae, the anterior iliac blade is short and pointed, and the tibia is much shorter than the femur. There is almost nothing distinctive to identify it as related to the Sauropoda. This is not terribly surprising, since by definition, all sauropodomorphs must be referable to one or the other daughter clade.

On the other hand, *Saturnalia* has some characters so primitive as to raise a few eyebrows. Most notably, the acetabulum (where the hind limb attaches to the pelvis) is not completely open. The open acetabulum is a well-established, in fact possibly the *most* well-established characteristic of Dinosauria. So this is a little like finding a crocodile with fur. The tibia is strongly S-curved and may be distinctly bent off the mid-line (its hard to tell from the photograph). The ankle joint is said to be "similar to that of *Herrerasaurus* ... with a broad ascending process of the astragalus." Langer et al. (1999) at 513-14.

The bottom line is that *Saturnalia* seems to have just about everything it needs to be a prosauropod, but lacks various features apparently shared by all other dinosaurs, or at least by all sauropodomorphs as traditionally understood. If this is all true, one is forced to the tentative conclusion that Sauropodomorpha is *poly*phyletic. Sauropods and prosauropods may have developed independently from each other. That is, Sauropodomorpha (considered as, say, the last common ancestor of *Plateosaurus* and *Alamosaurus* and all of its descendants) may be synonymous with Saurischia or Dinosauria. ATW 000716.

Descriptions

Sauropodomorpha: *Saturnalia*.

Range: Late Triassic to Late Cretaceous.

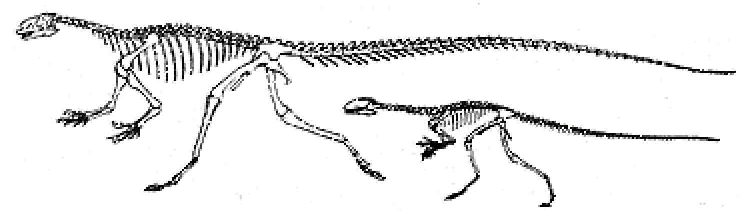
Phylogeny: Saurischia: Theropoda + * **:** *Thecodontosaurus* + (*Efraasia* (Prosauropoda + Anchisauria)) + Sauropoda.

Characters: **$** Small skull (< 1/2 length of femur); peg-like teeth with (**$**) spatulate or lanceolate crowns; **$** anterior end of premaxilla and dentary deflected down; **$** external nares enlarged; **$** 10+ cervical vertebrae; mid and posterior cervical vertebrae longer than dorsals; trunk long relative to hind limb; 3+ sacral vertebrae (with addition of caudals); humerus with deltopectoral crest extending 50+% of bone length; ungual of manus1 much longer than other manual phalanges; acetabulum open (partially closed in *Saturnalia*); **$** anterior process of ileum short and pointed; **$** proximal portion of pubes deep; tibia > femur; ascending process of astragalus fits into slot formed by descending process of tibia; **$** ascending process of astragalus broad; distal tarsals absent; short feet with large claw on pes 1 (at least as long as other phalanges). Gastroliths frequently present; all or almost all herbivorous. Not a strongly supported clade, as most characters may be secondary to high browsing; may be synonymous with Prosauropoda, or conceivably polyphyletic within Saurischia.

Links: **DD: Sauropodomorpha**; Lecture 11 - Triassic; Sauropodomorpha; Saurischian Dinosaurs - Enchanted Learning Software; Sauropodomorpha -- The Dinosauricon; Basal Sauropodomorpha; Sauropodomorpha (characters, lecture notes); FPDM - Sauropodomorpha (Fukui Museum -- still a good site, but not quite what it was); GEOL 104 Lecture 21- Sauropodomorpha- Size matters (Tom Holtz' very clear and useful lecture notes); Ficha Sauropodomorpha; · · ·Sauropodomorpha); Chapter 12 - Clade Sauropodomorpha; Lec 10 - SAUROPODOMORPHA.

References: Benton *et al.* (2000); Flynn *et al.* (1999); Langer *et al.* (1999). ATW030828.

Thecodontosaurus: *Thecodontosaurus antiquus* Morris, 1843, *Thecodontosaurus caducus* Yates, 2003a

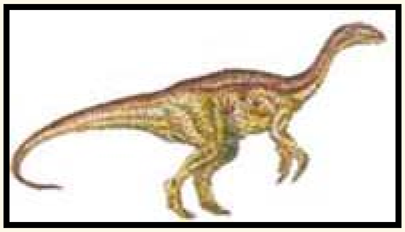


Thecodontosaurus antiquus: reconstructed adult and juvenile skeletons. From Benton et al. (2000).

Range: upT of Eur.

Phylogeny: Sauropodomorpha **:** * + (Efraasia (Prosauropoda + Anchisauria))

Characters: Small (~2 m), probably bipedal, lightly built; spoon-shaped, saw-edged cheek teeth (or "leaf-shaped with larger serrations on the front and back edges"); teeth slightly recurved [B+]; **$** dentary less than half length of mandible [B+]; anterior tip of lower jaw slightly down-curved [B+]; orbits proportionately large; **$** long *basipterygoid process* (as in sauropoda) [B+]; cervical vertebrae with long, low neural arch and anteroposteriorly long neural spine; dorsal vertebrae with pronounced, strongly reinforced, transverse processes [B+]; sacral vertebrae (probably 3) with wide, tightly fused ribs [B+]; long tail with "notably" platycoelous centra [B+]; slim limbs; scapula broad, curved, somewhat platelike [B+]; humerus with prominent deltopectoral crest [B+]; humerus with ends "twisted" by about 60° as in other prosauropods [B+]; ulnae triangular in cross-section [B+]; radius very much reduced [B+]; **$** posterior iliac blade squared off [B+]; digits 5/5; metacarpals, esp. I, not very robust; large, clawed thumbs.



Links: **DinoData: Thecodontosauridae**; Thecodontosaurus -- The Dinosauricon; Dinosaurs and Evolution 8; Thecodontosaurus (German); Thecodontosaurus (Italian).

References: Benton et al. (2000) [B+]

Note: Given its historic and phylogenetic importance -- not to mention the trouble Benton *et al.* had to go to in order to reconstruct this animal -- *Thecodontosaurus* deserves much more attention than it is given here. 010914.

Efraasia: *Efraasia minor* (Huene, 1908)

Range: upT of Germany

Phylogeny: Sauropodomorpha **:::** * + (Prosauropoda + *Anchisauria*)

Comments: This unfortunate dinosaur seems to have suffered from something of a personality crisis, having has gone through a number of taxonomic alterations since its discovery. Because the postcrania were associated with Rausiuchian jaws, it was considered to be a very primitive theropod dinosaur, and named *Teratosaurus*, Much later it was discovered that *Teratosaurus* was a chimera; a confusion of two different animals whose jumbled remains have been found together, in this case a basal Sauropoda and a Rausiuchian. The name *Teratosaurus* was retained for the (non dinosaurian) jaws. Having been finally acknowledged as a prosauropod, *Efraasia* was then identified with the plateosaur *Sellosaurus* for the next eighteen years or so. Finally, more recent, study has revealed it to be a more primitive sauropodomorph, one that predates the Plateosaur-Sauropod split. But although near the base of the sauropodomorph family tree, it was still a large animal, attaining upto 6 meters in length. *Efraasia* can be considered a larger and slightly more advanced cousin of *Thecodontosaurus*, with which it was more or less contemporary.

Links: Taxonomic history of the genus *Efraasia* Galton, 1973

References: Yates 2003

MAK050117

Prosauropoda:

Range: Late Triassic to Early Jurassic

Phylogeny: Sauropodomorpha **:::** "Anchisauria" + * **:** ((Plateosauridae + (Massospondylidae + *Yunnanosaurus*)) + *Riojasaurus*). (note: despite considerable recent interest, the subdivision of * may amount to no more than "small, medium and large" The taxonomy here is based in part on a simplification of Galton (1990).]

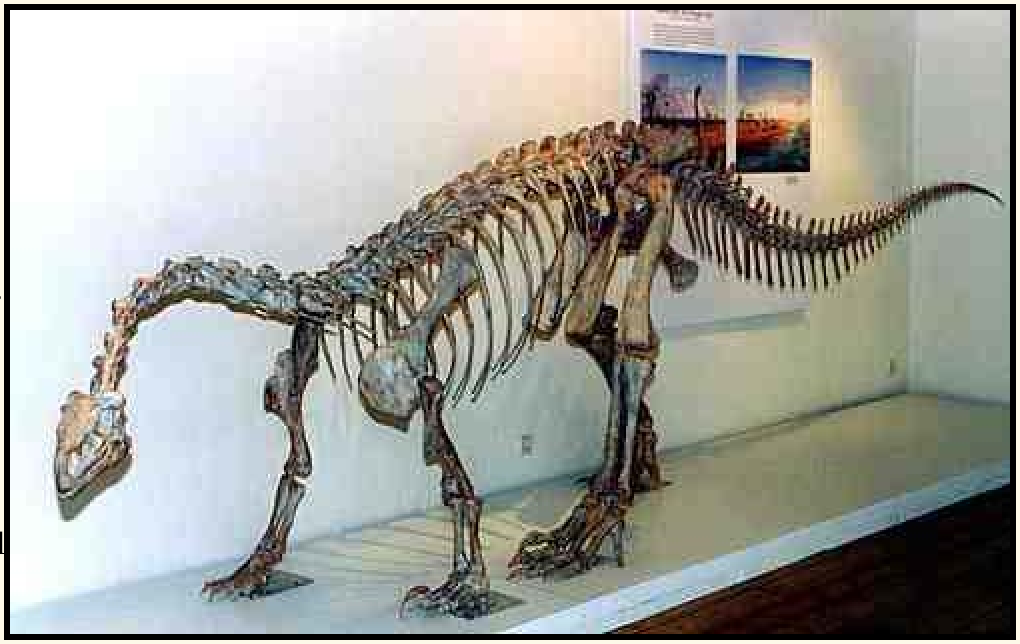
Discussion: Originally considered the most primitive suborder of Sauropodomorpha, the Prosauropoda are now either considered a paraphyletic assemblage of early sauropodamorpha, or, more usually a sister clade to the sauropoda proper. While there is considerable evidence on both sides of the question, but many workers favor the idea that sauropods branched off from basal saurischian stock, rather than being descended from prosauropods. Research by Adam Yates now indicates that both Prosauropods and Sauropods diverged from an early "thecodontiosaurid" ancestor, with *Anchisaurus* (previously considered a primitive "prosauropod" or basal sauropodamorph) representing the most primitive (but not the earliest) known Sauropod. To avoid confusion with the conventional concept of Sauropods as massive quadrapedal herbivores, I have used the term "Anchisauria" to designate Sauropoda *sensu* Yates. In view of this rearrangement, some of the following synapomorphies should now be considered plesiomorphic.

The Prosauropoda (now minus the "Thecodontosauridae" and *Anchisaurus*) are first known from the latest Carnian or early Norian Caturrita Formation of Brazil, if the 2.5 meter long *Unaysaurus tolentinoi* does indeed turn out to belong here [Leal *et al.* (2004). They quickly dominated the large plant-eater ecological niche previously filled by dicynodonts and rhynchosaurs up until the Carnian (however Dicynodonts still continued in some areas). Withina few short million years they had grown into very large forms like *Plateosaurus*, *Euskelosaurus*, and *Riojasaurus*, which attained lengths of 6 to 10 metres and weights of up to 2 tonnes, and had become an obligatory quadraped due to large size. Despite the superficial similarity, these animals were only distantly related to the Vulcanodont sauropods (MAK 991008, revised MAK050117)

Characters: **$** Articular with a narrow, prong-shaped retroarticular process and a marked medial embayment behind the glenoid in dorsal view; **$**Distal ends of anterior dorsal neural spines with centrally placed lateral processes; **$** Skull about 1/2 length of femur; supposed keratinous beak and fleshy cheek; $ jaw articulation slightly below maxillary teeth (brings teeth to bear serially in slicing, scissor-like motion); **$** marked ascending process of maxilla; uniform foliate teeth w coarse marginal serrations; **$** distal ischial process triangular; **$** distal part of pubes "apron-shaped" (see Lecture 11); manus I w large, pointed ungual; manus IV & V reduced; pes V vestigial. No display structures known. Herbivorous. Tended to increase size and become more quadrupedal. Extremely successful in upT.

Links: Image map; DinoData: Prosauropoda; Lecture 11 - Triassic; Sauropodomorpha -- The Dinosauricon; Literature - Prosauropoda; Project Prosauropod: Discover a Dinosaur with us.; Thecodontosaurus.

Plateosauridae: *Plateosaurus*



Range: upT-lwJ.

Phylogeny: Prosauropoda :::: (Massospondylidae + *Yunnanosaurus*) + *.

Characters: Medium to large size. As the boundaries of the clade are vague, the following is a description of *Plateosaurus*. Skull narrow; postorbital portion curved ventrally; nostrils large; jaw articulation well below teeth; teeth regularly replaced; no wear facets on teeth; teeth do not articulate; cervical ribs delicate and oriented post.; 10 caudal, 15 trunk vertebrae; thin gastralia present; 3 sacrals; clavicle present; radius about 50% length of humerus, ulna 75%(?); proximal carpals unknown, perhaps cartilaginous (thus manus not weight-bearing?!); manus I at 45 deg to axis of hand; ant process of ilium pointed; acetabulum perforate, w crest; 4th trochanter very prominent & located in distal half of femur (indicates quadrupedality); tibia length 75% of femur (slow); distal tarsals III & IV disk-like and triangular; all metatarsals of similar thickness; common in Norian Europe.

Notes on *Plateosaurus*: Galton 2001 2002 has shown that the type specimen of *Plateosaurus engelhardti* is distinct from the well-known specimens usually placed under that name, and has reinstated *Plateosaurus longiceps* as the next available name for these animals. *Plateosaurus longiceps* (= *P. trossingensis*) is thus a valid species, but *P. erlenbergiensis* is generically indeterminate. Most specimens (from Halberstadt, Trossingen, Stuttgart-Degerloch, France, Switzerland and Greenland belong to *P. longiceps*, but the Bavarian ones are *P. engelhardti*. [synopsis Mortimer 2001]. The less well known *P. engelhardti* is more heavily built and quadrupedal; *P. longiceps* is more lightly built and represents most specimens of *Plateosaurus*, including the famous Trossingen remains [ref. Justin Tweet - Sauropodomorpha]. Adam Yates considers that Galton has not gone far enough in the paper, as the two species share no synapomorphies, and suggests that a generic name needs to be applied to *P. longiceps*. For the present, we have retained the name *Plateosaurus*

A third species - *Plateosaurus gracilis* Huene 1907-08, more usually placed in a separate genus *Sellosaurus*, is less derived and occurs slightly earlier (Middle Stubensandstein). It was a large animal for its time, 4 to 6 meters long. Galton 2001 suggested Sellosaurus is more than one species- Efraasia diagnostica and Sellosaurus gracilis. [synopsis Mortimer 2001]. According to Yates 2003 *Sellosaurus gracilis* contains a substantial amount of variation, and it has been found that there are two discrete taxa . The more common one is a generalised (plesiomorphic) species called *Efraasia minor*; the less common one shares a number of synapomorphies with *Plateosaurus engelhardti* and is placed in this genus as *Plateosaurus gracilis* . It represents the beginning of the Plateosaur lineage, a group that evolved parallel to the main sauropod ancestry, and quickly evolved to large size.

Links: Dinosaur Database; Plateosauridae; Plateosaurus; Walking with Dinosaurs - Plateosaurus; The Dinosaur Museum; Plateosaurus engelhardti Meyer, 1837

MAK050117

Massospondylidae: *Ammosaurus*, *Gyponyx*, *Massospondylus*.

Range: Late Triassic and Early Jurassic of South Africa and North America

Phylogeny: Prosauropoda ::::: *Yunnanosaurus* + *.

Introduction: Length: 4 to 5 metres. This lightly built plateosaur was an abundant member of the south Gondwanaland fauna. As with the east Laurasian Lufeng fauna, large predators seem to be rare or non-existent (or perhaps conditions were not suitable for their preservation). There appears to be only one species *Massospondylus*, which existed unchanged for a considerable period of time. Remains of what may be a second species from the Sinemurian of Arizona indicate that this genus had a very wide distribution, although it is absent from the Lufeng in China, where its place is taken by *Lufengosaurus*.

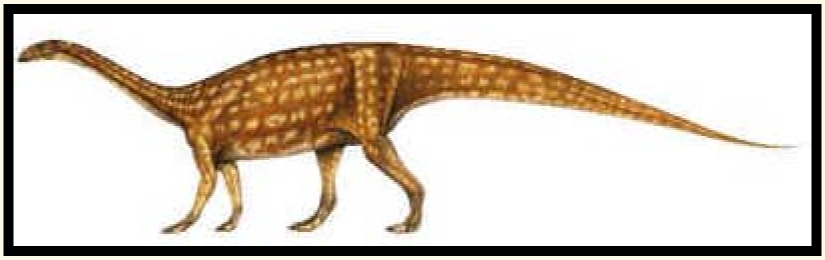
Massospondylus is very similiar to *Plateosaurus*, but is distinguished by its smaller build and somewhat more primitive jaw structure. Peter Galton (1990) places *Massospondylus* in its own family, the Massospondylidae, while Gregory Paul (1988) takes the contrary position and considers it a species of *Plateosaurus*. (MAK 991008)

Characters: centrally situated and almost vertical dorsal process of the maxilla; jaw articulation only slightly below level of maxillary tooth row; coronoid eminence low; teeth spatulate & coarsely serrated

Links: DinoData Classification Massospondylidae; MASSOSPONDYLIDAE (German); Re: Phytodinosauria status; Massospondylids; MASSOSPONDYLIDS; Massospondylus page in The Natural History Museum's Dino Directory; Massospondylus- Enchanted Learning Software (also in Spanish); MASSOSPONDYLUS (Portuguese).

References: Galton (1990); Paul (1988). ATW020914.

***Yunnanosaurus*:** *Y. huangi* Young 1942.



Range: Early Jurassic (Hettangian to Pliensbachian) of China

Phylogeny: Prosauropoda **:::::** Massospondylidae + *.

Characters: ~7m; self-sharpening, spoon shaped teeth; facultative quadruped? .

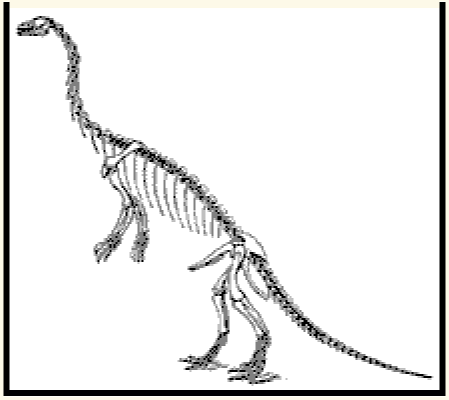
Introduction: This genus is still found even at the very end of the Early Jurassic. No Yunnanosaurs are found elsewhere in the world, so there may have been geographical or other environmental barriers to their migration.

Links: **DinoData Dinosaurs Y017 YUNNANOSAURUS;** Yunnanosaurus -- The Dinosauricon; YUNNANOSAURUS; Yunnanosaurus (Spanish); Yahooligans! Science- Dinosaurs; ??? (Chinese); Paleontology and Geology Glossary- Y; Re- Phytodinosauria status; ?????? -?- (Japanese). ATW030418

"Anchisauria": = "Sauropoda" *sensu* Yates

Range: Late Triassic to Late Cretaceous

Phylogeny: Sauropodomorpha **:::** Prosauropoda + * **:** *Anchisaurus* + (Melanorosauridae + Sauropoda)



Characters: **$** wrinkled tooth enamel; **$** Deep U-shaped fossa on ventral surface of the braincase, between the basal tubers.

Nore: The term "Anchisauria" is used for this clade, to avoid confusion with "Sauropoda" as conventionally defined (beginning with *Antetonitrus*)

References: Yates & Kitching (2003); Yates, A. M. (2004).

MAK050117

References: Galton (1990), Yates & Kitching (2003).

Riojasaurus: *Riojasaurus*

Range: upT of SAm.

Phylogeny: Prosauropoda **:::** Plateosauridae + *.

Characters: Large size (6 to 10 meters); Obligatory quadrapedal

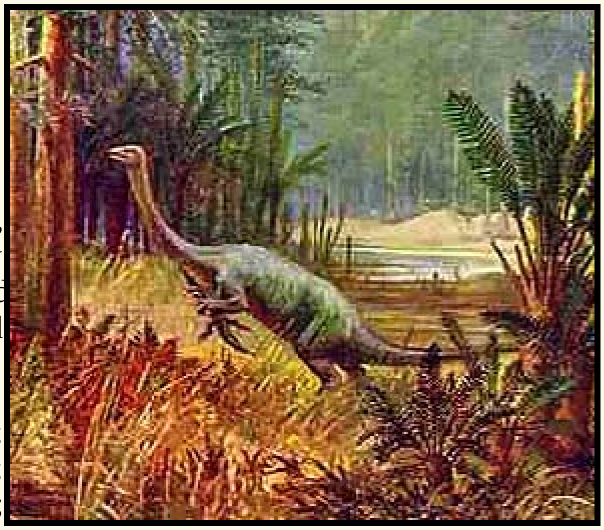
Comments: I have followed Adam Yates in placement of this genus, but further study may reveal it to go elesewhere

Links: Riojasaurus.

References: Yates & Kitching (2003); (cladogram)

MAK050117

Anchisaurus: *A. major* Marsh 1889.



Range: Early Jurassic of North AmericaAm.

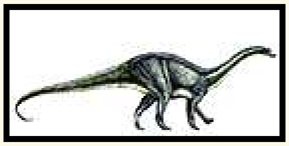
Phylogeny: "Anchisauria" **:** (Melanorosauridae + Sauropoda) + *.

Characters: 2-2.5 m & 40-50 kg; relatively large head; numerous blunt, foliate, se , procumbent (?) teeth; short jaw; jaw articulation below upper tooth row (scissor-like bite); large orbit; digits 5/5 with curved manus 1 with large claw; facultatively bipedal(?); traditionally supposed to have been omnivorous, but this is doubtful.

Links: DinoData: Anchisaurus; Anchisaurus -- The Dinosauricon; Internet Familia: Anchisaurus (Spanish); justin2; Anchisaurus; Anchisaurus (Dutch); Anchisaurus (Italian); Prosaurópodos (Spanish); The Natural History Museum's Dino Directory (with yet another ludicrous attempt to sell old third-rate art as science -- Paleo velvet Elvises); Anchisaurus Printout - ZoomDinosaurs.com; Triassic Period; PANGEA; Anchisaurus; Anchisaurus (Spanish, with lots of information); Paleontology and Geology Glossary; Dinosaurier Interesse.de - Suker- Anchisaurus (German); ANCHISAURUS; Dino Land Travels Database Dinosaur State Park- Anchisaurus Model; ANCHISAURUS THE SAUROPOD.

References: VanHeerden (1997). ATW021210.

Melanorosauridae: *Melanorosaurus*, *Camelotia*, *Blikanosaurus*?, - here defined as ***Melanorosaurus*** > ***Antetonitrus***



Range: upT of Afr, SAm, & Engl.

Phylogeny: Anchisauria **:::** Sauropoda + *

Characters: Large advanced basal forms. Manus may be better adapted to weight-bearing.

Comments: *Riojasaurus* is now considered a Prosauropod, and only distantly related to *Melanorosaurus*. It is not known if the remaining members form a natural group or not. MAK050117

Links: Melanorosauridae; .

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checked ATW040114, last modified MAK050117

Sauropodomorpha: Sauropoda

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      `--Sauropoda
         |--Vulcanodontidae
         `--+--Barapasaurus
            `--Eusauropoda
               |--Mamenchisauridae
               `--+--Cetiosauridae
                  `--+--Haplocanthosaurus
                     `--+--Jobaria
                        `--Neosauropoda
                           |--Diplodocomorpha
                           |  |-
-Rebbachisauridae
                           |  `--Diplodocidae
                           `--Macronaria
                              |-
-Brachiosauridae
                              `-
-Somphospondylii
                                 |-
-Euhelopodidae
                                 `-
-Titanosauria
                                    |-
-Nemegtosauridae
                                    `-
-Titanosauridae
```

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2. Cetiosauridae **X**
3. Eusauropoda **X**
4. *Haplocanthosaurus* **X**
5. *Jobaria* **X**
6. Mamaenchisauridae **X**
7. Neosauropoda **X**
8. Sauropoda **X**
9. Vulcanodontidae **X**

Descriptions

Sauropoda:

Range: upT-upK.

Phylogeny: Sauropodomorpha: Prosauropoda + * **:** Vulacanodontidae + Eusauropoda.

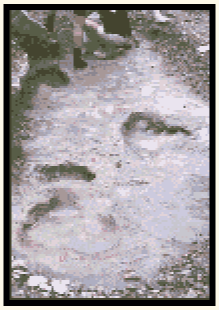
Introduction: The sauropods are the gigantic long-necked plant-eating dinosaurs, and include such well-known names as *Apatosaurus* ("*Brontosaurus*"), *Brachiosaurus*, *Cetiosaurus*, and *Diplodocus*, as well as numerous other species and genera. They were the largest of all land animals, and among the most successful and long-lived of the dinosaurs. The earliest known species, the small *Vulcanodon* (6 1/2 metres) dates back to the Sinemurian epoch, while the latest include a number of species such as the small*Titanosaurus indicus* and *Hypselosaurus priscus* (lengths about 12 metres), and the large *Alamosaurus sanjuanensis* (20 metres), were still flourishing right up until the terminal Cretaceous extinction. It was at one time thought (on the basis of the North American fossil record) that the sauropods became rare after the Late Jurassic, but in most parts of the world they continued as a common element of the megafauna until the very end of the Cretaceous. Throughout their long history they continued to evolve and branch out new species and families. There are at least three peaks of sauropod diversity in the Late Jurassic, late Early Cretaceous and latest Cretaceous, corresponding to high sea levels and increased speciation resulting from geographical isolation.

Sauropods were long believed to be semi-aquatic swamp wallowers, relying on the bouyancy of water to support their massive bodies. But analysis of their skeletons, in comparison with those of large terrestrial and semi-aquatic animals, and of sedimentation where their fossils have been found, show that sauropods were fully terrestrial:

> "The deep thorax of sauropods is an adaption to problems of terrestrial weight-bearing. Sauropod foot and limb structure is generally comparable to elephants...(S)edimentological evidence does not suport immersion in deep lakes as....frequently pictured..."

[Walter Coombs, p.1]

Not only were sauropods as terrestrial as elephants, but fossil trackways indicate that they lived in herds, again like elephants today. It must have been a truely awesome sight to watch a herd of brontosaurs crossing a Mesozoic floodplain; evoking the same sense of awe, and puniness in one's own being in comparison, as one would feel when observing whales close up.



The Sauropoda include the largest animals ever to walk on land. These gigantic herbivores reaches lengths of 15 to 25 metres or more (the very largest may have reached 45 metres) and weights of 15 to 30 or even 50 or 60 tonnes. Previous estimates of 87 to 150 tonne animals are unrealistic and physiologically impossible. No sauropod ever equalled in size the greatest of the baleen whales.

Sauropods were superbly adapted creatures, the Mesozoic equivalent of the elephant. They had an advanced (not a lizard-like) metabolism, inhabited every continent and continued to evolve and diversify right up until the terminal Mesozoic extinction. It has been suggested that they were cold-blooded like conventional reptiles; that they could not possibly have been endothermic, because they were too big to eat enough food to fuel their bodies. This argument falls apart when you realise most weight estimates have been overstated. An analysis of the load-bearing capacity of*Giraffatitan ("Brachiosaurus") brancai* limb bones show that this creature could only have weighed 15 tonnes, not the 50 to 80 tonnes that had previously been estimated Russell *et al.* (1980). Combine that with a huge stomach full of gastric stones (giving a food-grinding ability greater than any elephant's) and a gut full of symbiotic bacteria, and the possibility they were at least partially endothermic is not too unreasonable. Whether they had the full endothermy of birds, mammals, or small theropod dinosaurs is another question. The most likely explanation is that (and this would be true of most large dinosaurs) they started out as active fully endothermic youngsters and settled down into a gigantothermic metabolism as they approached adult size.

There are currently eight valid families of sauropods: Vulcanodontidae, Cetiosauridae, Brachiosauridae, Camarasauridae, Diplodocidae, Euhelopodidae, Dicraeosauridae and Titanosauridae. However, this is certainly an underdestimate of the true diversity of these amazing beasts. Ironically, despite their great size (which would one would think would enable more frequent preservation of remains) the fossil record is quite poor, perhaps due to the large skeletons being skattered before sediment settles to cover them. Most sauropod remains are actually scattered and isolated bones and teeth.

Characters: Very large (7-40 m), quadrupedal herbivorous forms; small head; blunt teeth; nares located high up on the skulls close to orbits; very long neck; long tail; caudal transverse processes dorsoventrally expanded [S+05]; erect, graviportal elephant-like limbs; digits 5/5; some with partial body armor.

Links: DinoData: Sauropoda; Sauropoda; sauropoda cladogram; Basal Sauropoda; Sauropods - Paleontology and Geology Glossary; ?????? Sauropoda; Witmer's Lab Dinosaur Skull Collection: Sauropoda; Literature - Sauropoda; The Natural History Museum's Dino Directory; Sauropodomorpha; sauropoda.

References: Russell *et al.* (1980); Salgado *et al*. (2005) [S+05].

Vulcanodontidae: *Chinshakiangosaurus, Kunmingosaurus, Ohmdenosaurus, Vulcanodon, Zhigongosaurus.* Very early sauropods.

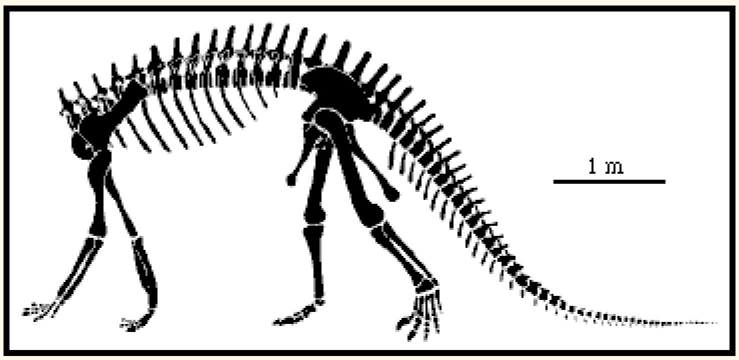
Range: lwJ (& upT?) of Afr & China(?).

Phylogeny: Sauropoda **:** (*Barapasaurus* + Eusauropoda) + *.

Introduction: *Vulcanodon karibaensis* Raath 1972
Vulcanodon beds, Mashonaland North, Zimbabwe
Partial skeleton 6 meters long, missing neck and head
Estimated total length around 8 metres; Weight several tonnes
Lifestyle: Very large terrestrial herbivore
Age: Sinemurian

Vulcanodon is the most primitive known sauropod dinosaur, and retains a number of prosauropod features. Yet some of the characteristics of the skeleton, such as the pubis, are anatomically more advanced than in larger and later sauropods like Barapasaurus. This is a good example of what is called "mosaic" evolution, the presence of both primitive and advanced characteristics within transitional organisms (Archaeopteryx is a good example of this, displaying both theropod ("prmitive") and bird ('advanced") characteristics.)

Somewhat contradictory dates have been given for the "Vulcanodon Beds". Although reported from the earliest Jurassic, close to the Triassic boundary (i.e. early Hettangian), pollen analysis indicates a date no older than the Sinemurian, and possibly younger. Olsen & Sues (1986). I have tentatively dated Vulcanodon as Sinemurian. In any case it seems that the Vulcanodontids and their descendents quickly supplanted the Plateosaurs as large terrestrial herbivores, although smaller prosauropods continued up until the Toarcian.



Kunmingosaurus wudingensis Zhao, 1985
nearly complete skeleton
Overall length: 6 metres

Chinshakiangosaurus zhongheensis Yeh, 1975
fragmentary skeleton
Overall length: ?12 - ?13 metres

Reference is made to a sauropod dinosaur from the Wudin basin in Yunnan, China. Although the horizon is thought equivalent to the adjacent famous prosauropod-dominated Lower Lufeng formation (Hettangian), there is no evidence for sauropods in the Lufeng beds [A.L.Sun and K.H.Cui, "The Lower Lufeng Saurischian fauna", p.278, and Peter M. Galton, "Herbivorous adaptions of dinosaurs, p.208; in *The Beginning of the Age of Dinosaurs*, ed. K.Padian] and it is likely that *Kunmingosaurus* and *Chinshakiangosaurus* comes from a later period, perhaps close in time to *Vulcanodon*. A Sinemurian age is tentatively suggested.

Ohmdenosaurus liasicus Wild, 1978
Posidonienschiefer, Baden-Wurttemberg, Germany
Age: Middle Toarcian
Limb bone
Estimated overall length: 4 metres
This very small, primitive sauropod is known only from a single limb bone, once thought to belong to a plesiosaur. Although classified under the family Vulcanodontidae it may instead belong to a distinct group, which might be called family Ohmdenosauridae. It had no clear descendents, and may have been one of the many types of dinosaur that were wiped out by the terminal Toarcian extinction event. (MAK 991228)

Characters: 5-10 m long, 2m at shoulder. Moderately long neck; 3 or 4 sacrals; unspecialized pelvis, with somewhat prosauropod-like "apron" (actually plesiomorphic per Upchurch (1995)); pleurocoels absent; femur retains inner trochanter; reduced metatarsal V (a prosauropod character); columnar limbs; gastroliths known.

Links: **DinoData: Vulcanodontidae;** dml dinov; sauropoda; Lecture 12 - Early Jurassic.

References: Galton (1986); Olsen & Sues (1986); Sun & Cui (1986); Upchurch (1995), Upchurch (1998).

Note: This is almost certainly *not* a clade. However, following the suggestion of Upchurch (1998), this group is retained to describe the earliest (probably late Triassic) sauropod radiation. *Kotasaurus*, from the Jurassic of India, may represent an even more primitive type. At the moment, *Vulcanodon* consists of a pelvic region, some forelimb bones, and some other odd bits. *Barapasaurus*, which is separately listed below, is some very partial and disarticulated pieces of several individuals. The Chinese species are even scrappier. Thus, it is hard to say who really belongs with whom at the moment.

Image: sculpture of *Vulcanodon* © Tridimont and reproduced by permission. 000517

***Barapasaurus*:** may include, or anchor a family including, *Kotasaurus*.

Range: Early Jurassic of India

Phylogeny: Sauropoda **::** Eusauropoda + *.

Introduction: *Barapasaurus tagorei* Jain, Kutty, Roy-Chowdhury, & Chatterjee, 1975
Kota Formation, Andhra Pradesh, India
Length: 14.5 to 18 metres; Weight: 13 to 25 tonnes
Remains of 6 partial skeletons (missing skull & feet)
Toarcian

The first of the really big sauropods, *Barapasaurus* equalled in size the giants of the later Jurassic. In structure, however, it was much more primitive, resembling *Vulcanodon* in many features of the skeleton. As befits its transitional nature, it is sometimes included under the Vulcanodontidae, sometimes under theCetiosauridae, and sometimes in its own family. *Barapasaurus* is another example of "mosaic evolution" among transitional forms. According to the Argentine palaeontologist Jose Bonaparte the dorsal vertebrae of *Barapasaurus* are of the standard Cetiosaur grade, with a tall neural arch and zygapophyses far above the neural canal; much more advanced the vertebrae of *Vulcanodon* Bonaparte (1986).

Kotasaurus yamanpalliensis Yadagiri, 1988
Kota Formation, Andhra Pradesh, India
Length: 6 metres
partial skeletons
Toarcian (MAK 991228)

Eusauropoda:

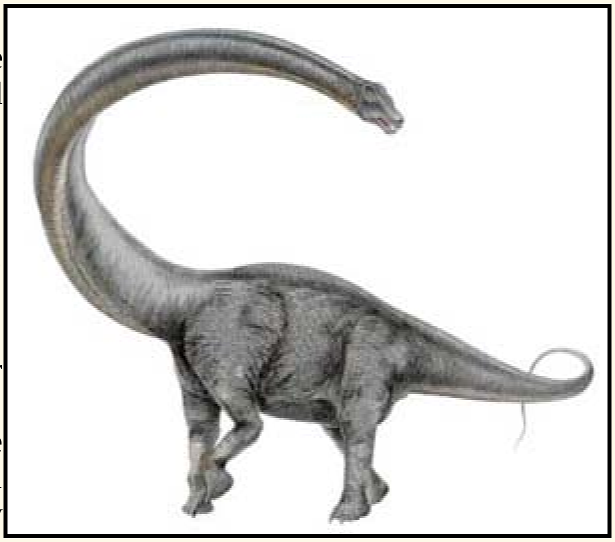
Range: Middle Jurassic to Late Cretaceous.

Phylogeny: Sauropoda ::: *Barapasaurus* + * : Mamenchisauridae + (Cetiosauridae + (*Haplocanthosaurus* + (*Jobaria* + Neosauropoda))).

Characters: snout with stepped, shelf-like subnarial margin; retraction of external nares; ascending process of maxilla meets lacrimal; external mandibular fenestra extends below orbits; short skull roof and temporal region; anterior part of lower temporal fenestra extends under orbits; **$** loss of denticles on tooth crowns; teeth procumbent; teeth anterior to or below antorbital fenestra; extensive pneumatization of vertebrae; 12+ cervical vertebrae; **$** transverse processes of dorsal vertebrae directed dorsolaterally; forked chevrons (?); graviportal stance, with metacarpals arranged in semicircular collonade; manus phalangeal formula 2-2-2-2-1 or less; pubes short, robust & not twisted;**$** 4th trochanter reduced to low, rounded ridge; metatarsal I short & robust; **$** length of metatarsal V 85% or more length of metatarsal IV; loss of ligament pits (?) on toes; pes IV with 3 phalanges.

Links: Basal Sauropoda; Sauropoda -- The Dinosauricon; Atlasaurus imelakei; The Evolution of Dinosaurs; sauropoda; Re: Triassic Sauropods (Cretaceous ones meanwhile); Sauropodomorpha; Re: Details on Huaibasaurus; SAUROPODOMORPHS (October 1) (**Best on the Web**). ATW020716.

Mamenchisauridae:



(=Euhelpodidae?): *Mamenchisaurus*, *Hudiesaurus*. Unclear whether this group should include more primitive Chinese sauropods (*Shunasaurus*, *Omeisaurus*), but treated here as a separate family.

Range: Late Jurassic of China.

Phylogeny: Eusauropoda **:** (Cetiosauridae + (*Haplocanthosaurus* + (*Jobaria* + Neosauropoda))) + *.

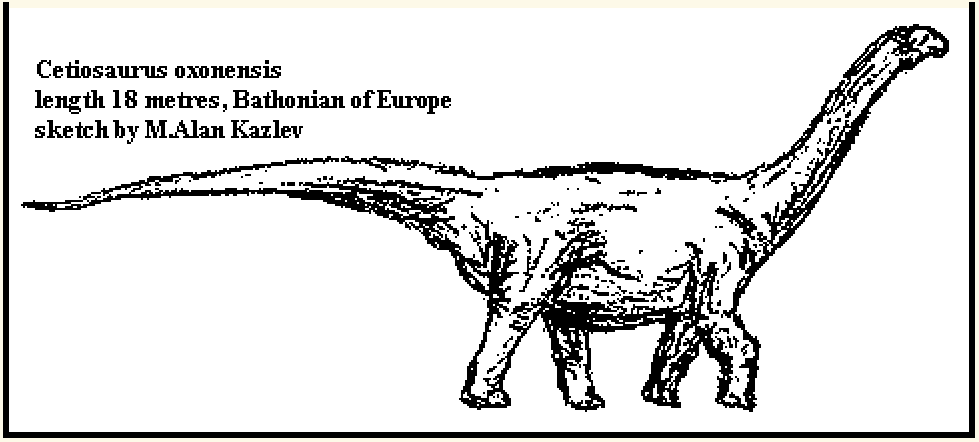
Introduction: This lineage culminates in the 22 meter *Mamenchisaurus*, which has the longest neck of any animal. Mamenchisaurids have been drawn like dinosaurian giraffes, with the head held high in the air. In fact - as with the barosaurs and brachiosaurs - this pose is physiologically impossible. There is no way in which the heart could of pumped blood to the head against the force of gravity. A more reasonable explanation is that the neck was held stiffly in front of the body, and swung from side to side as the creature grazed on ferns and other plants. (MAK 000508)

Characters: Skull taller, blunter than diplodocids; broad se (on both sides), spatulate teeth, not confined to anterior jaw; longest known neck, up to 12 m (of about 22m overall length), with 19 vertebrae (also a dinosaur record); neck vertebrae ventrally braced by elongated, neck supported by interlocked cervical ribs under the cervical vertebrae extending caudally up to 3 vertebrae; vertebrae cleft in pectoral region; vertebrae highly pneumatized; forked tail chevrons (beginning at caudal #12); front and hind limbs almost equal (or hindlimbs longer than forelimbs?); limbs similar to camarasaurids.

Links: **DinoData: Mamenchisaurus**; Re: Euhelopodidae and Mamenchisauridae; Euhelopodidae; Dinosauria Translation and Pronunciation Guide H (entry for *Hudiesaurus*); Mamenchisaurus - Dinosaur - Enchanted Learning Software; DGF, Geological Society of Denmark, Geologisk Tidsskrift Nr. 2, 1996 (see last abstract on page); Mamenchisaurus; FPDM : Mamenchisaurus hochuanensis; Mamenchisaurus; Mamenchisaurus; Untitled Document; Mamenchisaurus (Portuguese); Mamenchissauro (Portuguese); China 2000; Bienvenue chez Nicolas , Futur Paléontologue (French);

Note: As with most dinosaurs, mass estimates for *Mamenchisaurus* have recently been significantly reduced: in this case from 55,000 to perhaps 30,000 kg. (ATW 011219).

Cetiosauridae:



Range: Middle to Late Jurassic.

Phylogeny: Eusauropoda :: *Haplocanthosaurus* + (*Jobaria* + Neosauropoda) + *.

Introduction: This lineage includes some of the most primitive of the great sauropods. Some forms, like *Shunosaurus*, still retained many prosauropod features. Yet even at this early evolutionary stage they had already become specialised, some developing ankylosaurid-like clubbed tails as protection against predators (and maybe also a sexual display device) (MAK 000508)

Characters: Teeth broad; simple vertebral spines on neck and trunk; middle chevrons forked as in Diplodocidae; bony club at end of tail in some species.; fibro-lamellar bone (indicative of fast growth) known from *Cetiosaurus*.

Links: **DinoData: Cetiosauridae**; Sibbick's dinosaur pictures.

***Haplocanthosaurus*:**

Range: Late Jurassic of North America

Phylogeny: Eusauropoda **:::** (*Jobaria* + Neosauropoda) + *.

Introduction:

Haplocanthosaurus priscus Hatcher 1903
(syn H. utterbacki, Haplocanthus)
Morrison Formation; Colorado and Wyoming, United States
Late Kimmeridgian
2 partial skeletons lacking skulls
Length: 13 metres;   Weight about 5 tonnes

This smallish sauropod was unusual in that it was a survivor of the very primitive Cetiosaurid line, existing as a sort of "living fossil" alongside its more advanced descendants. It probably should be grouped with *Cetiosaurus*, which it resembles, in the family Cetiosauridae, although Jose Bonaparte (1986) argues it should be placed in a distinct family because of its unusual and more advanced vertebral structure. Perhaps implausably, Bonaparte classes *Haplocanthosaurus* with *Dicraeosaurus* - which shows a similiar vertebral form but is otherwise a very different type of sauropod - in the Dicraeosauridae. The upper spine of each vertebra was single, not forked as in most sauropods. Lambert (1983). *Haplocanthosaurus* resembled *Brachiosaurus* in its high shoulders, fairly long neck, and short tail, but this was the result of parallel evolution and adaptation to a giraffe-like high-feeding lifestyle, not direct relationship. The back was quite long, containing 14 vertebrae.

Haplocanthosaurus delfsi McIntosh et Williams 1988
Morrison Formation; Colorado, United States
Middle Tithonian
Partial skeleton lacking skull
Length: 21.5 metres;   Weight about 25 tonnes
A huge and rare Haplocanthosaur, the last and one of the largest of the Cetiosaurids. Although "Cetiosaurus" has supposedly been reported from the Early Cretaceous of England, those isolated post-crania would actually belong to other sauropods of that time. It seems that this family, once so successful and widespread, did not survive the mid-Tithonian extinction. (MAK 000218)

References: Bonaparte (1986), Lambert (1983).

Jobaria: 18 m primitive sister taxon of all eusauropods.

Range: lwK of Afr.

Phylogeny: Eusauropoda **:::** Neosauropoda + *. Spoon-shaped teeth; short neck with 12 cervicals; cervical vertebra bearing prezygapophyses with accessory anterior process; cervical ribs 3-6 with accessory anterior spine; dorsal prezygapophyses with broad pendant flange; dorsal neural arches with fossa between para- and diapophyses; U-shaped 1st chevron; mid-caudal chevrons with rugose ridge across distal end of blade.

Links: Project Exploration - Dinosaurs, Education, Exhibits; Project Exploration Presents Jobaria!; Dinosaur News: Jobaria.

References: Sereno (1999); Sereno *et al.* (1999). 010524.

Neosauropoda: Definition: *Saltasaurus* + *Diplodocus*, that is the last common ancestor of titanosaurs and diplodocids and its descendants.

Range: Middle Jurassic to Late Cretaceous.

Phylogeny: Eusauropoda **:::** *Jobaria* + * **:** Diplodocomorpha + Macronaria.

Characters: **$** teeth concentrated at front of jaw; sacral ribs 3-5 fused tightly to *acetabulum* and participating in articular surface [S+05]; **$** pillar-like metacarpals, with elevation of the metacarpus from a plantigrade to digitigrade posture.

Links: neosauropoda cladogram; Untitled Document; The Evolution of Dinosaurs; Wilson & Sereno's Sauropod Phylogeny; Sauropodomorpha (brief discussion); Euhelopodidae (recent changes in the tree); EVOLUTION OF HERBIVORY, NECK ELONGATION, AND LOCOMOTION IN ... (important abstract: Neosauropoda is the end of basic sauropod specialization and beginning into divergence based on either limb [Macronaria] or dental [Diplodocoidea] specialzations) Untitled Document (abstract of Wilson & Sereno, 1998); GEOL 104 Lecture 21-Sauropodomorpha- Size matters (brief discussion).

References: Salgado *et al*. (2005) [S+05]. ATW051102.

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checked ATW051228

Sauropoda: Diplodocomorpha (or Diplodocoidea)

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      `--Sauropoda
         |--Cetiosauridae
         `--Neosauropoda
            |--Diplodocomorpha
            |  |--Cetiosauriscus
            |  `--+--Rebbachisauridae
            |     |  |--Nigersaurus
            |     |  `--Rebbachisaurus
            |     `--Diplodocoidea
            |        |--Diplodocidae
            |        |  |--Apatosaurinae
            |        |  `--Diplodocinae
            |        |     |--Barosaurus
            |        |     `--Diplodocus
            |        `--Dicraeosauridae
            `--Macronaria
               |--Brachiosauridae
               `--Somphospondylii
                  |--Euhelopodidae
                  `--Titanosauria
                     |--Nemegtosauridae
                     `--Titanosauridae
```

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3. *Cetiosauriscus* **X**
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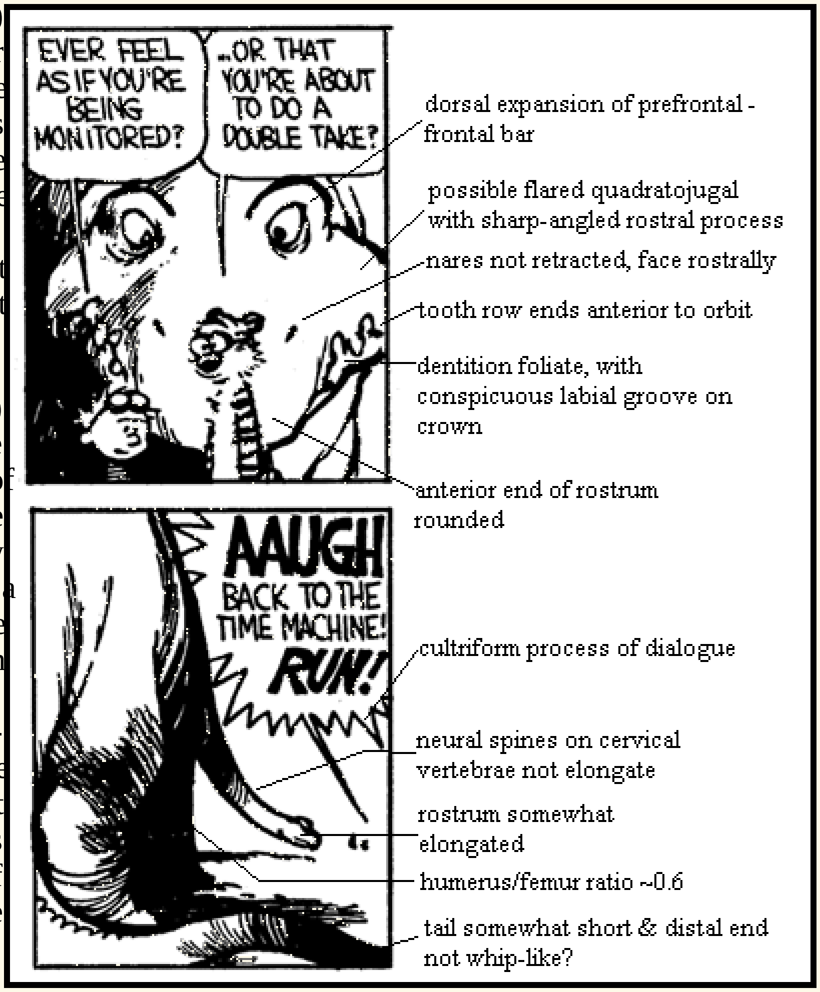
6. Diplodocinae **X**
7. Diplodocoidea **X**
8. Diplodocomorpha **X**
9. *Diplodocus* **X**

10. *Nigersaurus* **X**
11. Rebbachisauridae **X**
12. *Rebbachisaurus* **X**

Rebbachisauridae



The semi-scientific literature (like these Notes) frequently takes pleasure in nit-picking popular depictions of paleontological material. Perhaps a more interesting and useful exercise might be to worry less about why it *isn't* accurate. We might instead assume that it *is* accurate: an accurate representation of some paleocritter unknown to Twenty-First Century science. We might then attempt to determine what it is – or at least what it isn't. Most science, after all, is not about proving good ideas. We can only disprove bad ones.

Consider, for example, the possible (if improbable) sauropod in the figure from Watterson (1989). We might start with the hypothesis that it is some sort of rebbachisaurid. After all, why not? The Rebbachisauridae were founded on a scapula, a few vertebrae in moderately bad shape, and part of a femur. René Lavocat (1954) devoted just over 1 page to these remains in the course of a four-page article on miscellaneous gleanings buried in the deep Sahara. The paper, in turn, was buried in Volume 15 of a 1950-54 series of papers with the stunningly uninformative title: *Questions Diverses de Géologie Générale*. Not surprisingly, Rebbachisauridae has been used as garbage taxon for various bits and pieces of unidentifiable sauropod from the East End of Nowhere for the last 50 years.

So is it a rebbachisaurid? Clearly not. Its dentition doesn't seem to be arranged as a battery. The nares are on the rostrum and face forward, instead of being above the eyes, facing upward. There are no tall spines on the vertebrae, and the front legs are a bit too short.

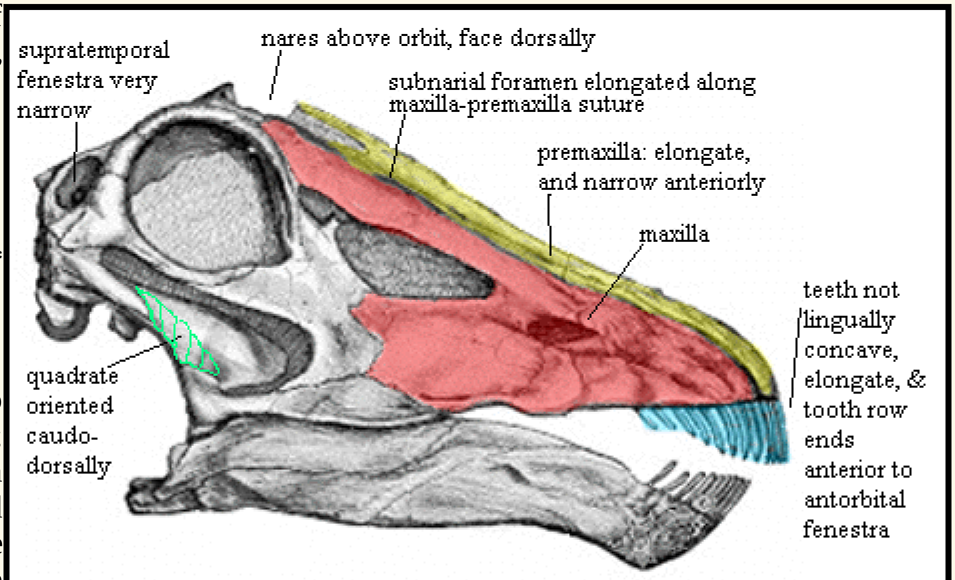
Perhaps a diplodocoid? That would make more sense for North America, but it cannot be. Diplodocoid teeth are even more extreme. The diplodocoid occipital condyle faces ventrally, suggesting that the head was held higher and at an angle to the line of the neck. The rostrum is somewhat elongated, but seems too tall for a diplodocoid.

Is it a diplodocomorph at all? Perhaps a nemegtosaur? The quadratojugal might be right for a nemegtosaur, but the basal diplodocomorph synapomorphies are absent. Again, the foliate, grooved teeth do not meet diplodocomorph specs. The anterior jaw line is unclear, but doesn't seem to be square enough. The nares are wrong, as well.

Reluctantly, we conclude that this interesting specimen falls outside the bounds of the Diplodocomorpha. We will have to look elsewhere for an answer. And, while we're at it, what are those hairy little things making all the noise? ATW030127.

Descriptions

Diplodocomorpha: (= Diplodocoidae of Upchurch (1998) =Diplodocoid**ea**, diplodoc**i**morpha, etc.). *Diplodocus* > *Saltasaurus*.



Diplodocus: skull showing synapomorphies of Diplodocomorpha

Range: Middle Jurassic to Late Cretaceous

Phylogeny: Neosauropoda **:** Macronaria + * **:** *Cetiosauriscus* + (Rebbachisauridae + Diplodocoidea).

Characters: Long, peg-like teeth, limited to anterior jaw; **$** teeth lack lingual concavity; **$** anterior jaw "subrectangular"; dentary with angular "chin", anteriorly directed *basipterygoid processes*; **$** transverse narrowing of the rostral end of the premaxilla & premaxilla elongated posteriorly; **$** elongation of the subnarial foramen along maxilla - premaxilla suture; extreme retraction of the external nares; **$** nares face dorsally, posterior to orbits; **$** no internarial bar; anterior extension of the quadratojugal placed beyond the anterior border of the orbit; **$** supratemporal fenestra width <10% width of occiput; infratemporal fenestra oval or slit shaped; cervical ribs shorter than associated centra (?); very high and undivided neural spine on dorsal vertebrae with a deep pleurocoel on the centrum; tall neural arch in caudals (at least 1.5x height of centra); wing-like transverse processes in anterior caudals; whip-like tails (30 or more elongate boconvex posterior caudals); broad, paddle-like scapular blade; humerus/femur ratio less than 0.70.

Note: The preferred spelling should be "Diplodoc**o**morpha." The taxon Diplodoc**i**morpha Calvo & Salgado 1995 is a different group, defined by them as *Rebbachisaurus tessonei* + Diplodocidae. The citation (we have not read the article) is Calvo, JO & L Salgado (1995), ***Rebbachisaurus tessonei*** *sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae*, **Gaia** 11: 13-33.

Image: original figure ascribed to Marsh, OC (1896), **The Dinosaurs of North America**, with coloring and labels added. I'm unsure whether the element in the original is the quadrate or an internal palatal element, so I have sketched in the outline of the quadrate as shown in figures from other sources.

Links: diplodocimorpha cladogram; Diplodocimorpha (Mikko's Phylogeny); IL Geo Survey Past Dinosaur Questions III; SAMC NEWS 5SAMC NEWS 5 (abstract of important & hard-to-find paper!); Re: Triassic Sauropods (Cretaceous ones meanwhile); Sauropodomorphs (October 1) (**Best on the Web**); IL Geo Survey Past Dinosaur Questions III; diplodocimorpha cladogram; GAIA Vol. 11, December 1995; SAMC NEWS 5SAMC NEWS 5.

References: Upchurch (1998). ATW030617.

Cetiosauriscus:

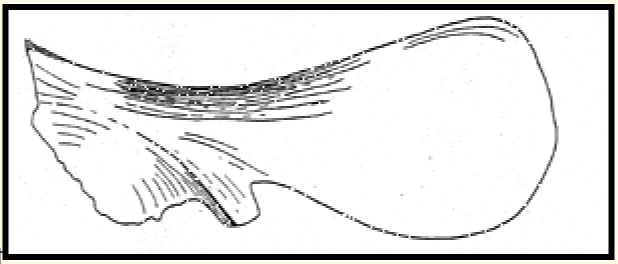
Range: Middle Jurassic of England

Phylogeny: Diplodocomorpha **:** (Rebbachisauridae + Diplodocoidea) + *.

Introduction: *Cetiosauriscus stewarti*, of Callovian age, is found in the Lower Oxford Clay of Cambridgeshire, England. *Cetiosauriscus* is the earliest known of the high-hipped and long-necked diplodocomorphs, representing the second of the two primary sauropod feeding strategies. Whereas the giraffe-like camarasaurs and brachiosaurs used their long forelimbs, high shoulders and and necks to reach into vegetation, the diplodocids relied on a different stratergy. They were built like a suspension bridge, with their great arched backbone and long tails putting their centre of gravity over their long hind legs, thus enabling them to rear on their hind legs, using their tail as a support, and so feed on leaves 15 metres above the ground.

In addition to *C. stewarti*, a "*Cetiosauriscus*" *greppini* (Huene 1922) (syn. *Cetiosaurus, Ornithopsis*) is known from at least 4 partial skeletons without skulls found in the Late Tithonian Unter- Virgula- Schichten of Kanton Bern, Switzerland. These specimens have a humerus measuring about 60 cm, and a femur 70 cm. The overall length about 8.5 metres, the weight about 1 tonne. This was a fairly small form, distinct from and probably not closely related to the gigantic American genera. It may be a relative of the African Tornieria; or an ancestral titanosaurid. During this time, Europe consisted of a number of islands; the small size of *"C." greppini* indicates that this could be an island-dwelling pygmy species (like the dwarf elephants of Pleistocene Malta). The dating of this formation is uncertain, but is tentatively given as Tithonian. (MAK 000218).

Rebbachisauridae: *Agustinia?, Rayosaurus?*



Range: lwK-upK of Afr, SAm, perhaps EEur.

Phylogeny: Diplodocomorpha **::** Diplodocoidea + *: *Nigersaurus* + *Rebbachisaurus*.

Characters: Dental battery similar to hadrosaurs in anterior jaw; short basipterygoid processes (?); nares above orbit; quadratojugal greatly expanded in front of orbit; supratemporal, infratemporal fenestrae slit-like and nearly closed; pocket on posterior surface of quadrate; cervical ribs short but slender; neural spines long ("sail back"), not split; large pleurocoels on all dorsals; anterior caudals amphiplatyan; no forked chevrons; whiplash tail; distal ends of ischia elongated; forelimb/hindlimb 0.80; some with osteoderms with or without spikes (associated with the long neural spines).

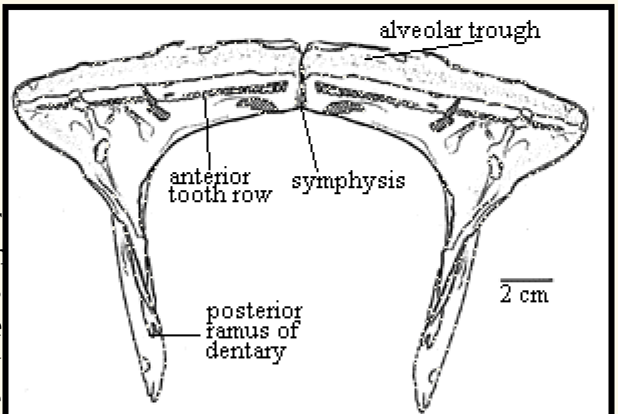
Image: Right scapula of *Rebbachisaurus gerasbae* from Lavocat (1954). The actual length was 117 cm. This is the only figure in Lavocat's very brief description *R. gerasbae*, the type genus and species. Additional material of *R. gerasbae* may have been found in Morocco, but again there is nothing beyond a very short, preliminary report. Monbaron (1978). 010604.

Links: **DinoData: Rayosaurus**; sauropoda; Sauropodomorphs (October 1); Notes on Rebbachisaurs and Tehuelchesaurus (longish); Rayosaurus; EVOLUTION OF HERBIVORY.

Note: much of the description here is based on *Rayosaurus* which is not securely placed in this group.

References: Lavocat (1954); Monbaron (1978); Sereno *et al*. (1999); Watterson (1989).

Nigersaurus:



Nigersaurus: reconstructed lower jaw in dorsal view. Modified from Sereno et al. (1999)

Range: mK of Africa.

Phylogeny: Rebbachisauridae **:** *Rebbachisaurus* + *.

Characters: <15m; teeth small, enamelled on labial side; anterior dental batteries with ~600 teeth; short, very wide & square rostrum (similar to *Antarctosaurus*, a possible Rebbachisaurid from SAm); **$** tooth rows "oriented strictly transversely," forming straight, rake-like line across front of upper and lower jaws; **$** tooth rows extend laterally beyond line of jaw; teeth with enamel much thicker on outer face forming sharp cutting edge; ~7 replacement teeth for each position stacked in dentary & maxilla for total of 600 teeth; tooth row preceded by lip-like trough; lower jaw also extends outward to the sides somewhat like a duckbill; nares retracted as in advanced diplodocoids; **$** elongated, narrow frontal with marked cerebral fossa; neural spines undivided; presacral vertebrae have simple, undivided neural spines with large, paired, sharp-rimmed pneumatic spaces (pleurocoels) under them on the dorsal vertebrae; broad, paddle-shaped scapulae as other rebbachisaurs; **$** prominent rugosity on medial face of base of scapular blade.

Links: **DinoData: Nigersaurus**; Decouverte de dinosaures sauropodes; NEW DESCRIPTIONS 27 mei 2001

(Dutch); Dinosauria Translation and Pronunciation Guide N (entry for *Nigersaurus* -- **Best on the Web**).

References: Sereno *et al.* (1999).

Image: Using the best fit with the figure of Sereno *et al.* (1999), the tooth row was not quite transverse.

Note: Sereno *et al.* (1999) state that the unusual shape of the jaws and numerous teeth suggest *Nigersaurus* browsed on low-lying vegetation. They mention, but do not describe, a titanosaurid from the same location (Tegama group), as well as large hadrosauroids, and *Ouranosaurus*. 010605.

Rebbachisaurus (=*Limaysaurus?*)

Range: mK-upK of Afr & SAm.

Phylogeny: Rebbachisauridae **:** *Nigersaurus* + *.

Characters: ~20m; teeth slightly curved; teeth spoon-shaped, and strongly se ; basipterygoid process oriented anterolaterally (not ventrolaterally); infratemporal fenestra extends to anterior margin of orbit; supratemporal fenestra faces laterally; cervical vertebrae with deep lateral excavation, divided into 2 by accessory lamina; very tall, undivided neural spines on dorsal vertebrae (presumed sailback -- even in the poorly known *R. gerasbae*, one of the neural spines is 145- 150 cm tall while centrum was ~20 cm long.) with deep pleurocoels in centra (two principle pleurocoels in *R. gerasbae*, separated by fairly small layer of bone); hyposphene- hypantrum articulations absent; substantial transverse processes; broad, paddle-like scapular blade, gastroliths.

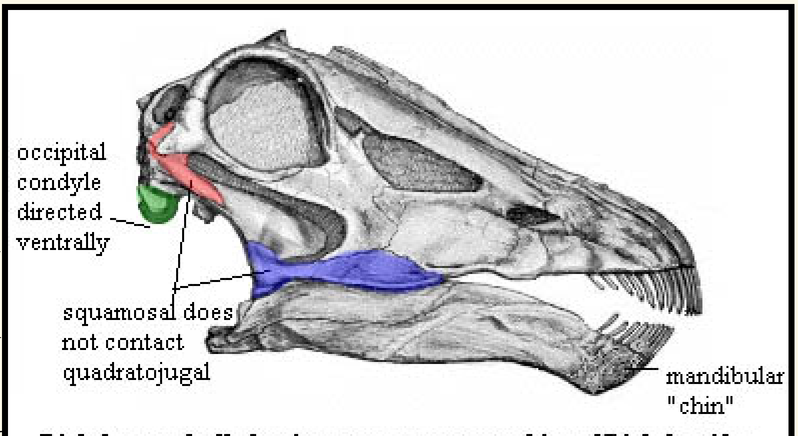
Links: DinoData: Rebbachisaurus; Home Page; Paleontology and Geology Glossary: R; 0253333490.l.gif; GAIA Vol. 11, December 1995; SAMC NEWS 5; Musee dinosaures - sauropodes (French -- with image of the spine mentioned by Lavocat).

References: Lavocat (1954); Upchurch (1998).

Diplodocoidea: *Diplodocus* + *Dicraeosaurus*.

Range: mJ-upK of Afr, NAm., Eur., Asia.

Phylogeny: Diplodocimorpha **::** Rebbachisauridae + * **:** Diplodocidae + Dicraeosauridae.



Diplodocus: skull showing some synapomorphies of Diplodocoidea

Characters: Skull long and low; teeth restricted to very front of mouth and pencil shaped; **$**? mandible forms thin, sharp "chin"; **$** transverse narrowing of the rostral end of the premaxilla [U99]; premaxilla elongated posteriorly; **$** elongation of the subnarial foramen [U99]; **$** extreme retraction of the external nares [U99]; nares joined together at top of skull, above orbits, facing dorsally; narrow crown of skull; lateral temporal fenestrae narrow; **$** squamosal does not contact dorsal process of quadratojugal; **$**? caudal surface of quadrate not excavated; **$** occipital condyle directed ventrally; **$**? cervical vertebrae with concave ventral surfaces; **$**? cervical ribs very short (shorter than centra); **$**? bifurcated neural spines in (at least) posterior cervicals & anterior dorsal vertebrae; **$** anterior caudal centra with *slightly* convex posterior surface (as opposed to deeper convexities in titanosaurs); **$** expanded caudal ribs; most chevrons skid-like; whip-like tail; **$** distal end of ischium dorsoventrally expanded; forelimbs much shorter than hindlimbs; loss of calcaneum from ankle.

Links: The Evolution of Dinosaurs; Sauropodomorpha; Re: Triassic Sauropods (Cretaceous ones meanwhile); The Journal of Vertebrate Paleontology; IL Geo Survey Past Dinosaur Questions III; Ameghiniana Round Up, Pt. II; diplodocoidea; Playing with Wilson and Sereno; The Journal of Vertebrate Paleontology (abstract of Upchurch [1999]); Sauropodomorphs (October 1).

References: Sereno (1999); Upchurch (1998); Upchurch (1999) [U99].

Image: *See* Diplodocomorpha.

Notes: Sereno (1999) asserts a mJ origin for this group. Short forelimbs said by some sources to implicate tripodal "rearing." -- but why should this be? Diplodocoidea, as used here, is equivalent to "Node U" of Upchurch (1998). A number of characters of the tail chevrons from Upchurch (1998) have been omitted as incomprehensible. 010907.

Diplodocidae:

Range: upJ of NAm, Eur.& Afr.

Phylogeny: Diplodocoidea: Dicraeosauridae + * **:** Apatosaurinae + Diplodocinae.

Characters: 40+ m long. Protruding snout; small, peg-shaped teeth confined to anterior jaw; **$** tooth crowns lack grooves on outer face; **$** ectopterygoid processes of pterygoid anterior to lacrimal, reduced and do not project ventrally; **$** jugal forms substantial part of border of antorbital fenestra; **$** rostral & dorsal processes of jugal form angle ~130°; quadrate rostroventrally inclined; external nares opening dorsally; **$** distal ends of paroccipital processes rounded; very long necks; **$** 15 cervical + 10 dorsal (+1 dorsosacral) vertebrae; tall neural spines; spines cleft; 80+ caudal vertebrae with "whiplash" of unornamented long bones at end; proximal caudals with moderately procoelous centra and wing-like transverse processes (fore-and-aft, sled-like chevrons); middle chevrons forked; distal ends of ischia expanded, meeting one another side by side; hindlimbs (much? a bit?) longer than forelimbs; **$** calcaneum absent (but see Untitled Document); pes phalanx II-2 anteroposteriorly compressed; one specimen known with keratinous (?) spines; tripodal stance (2 legs + tail)?

Links: **DD: Diplodocidae**; Walking with Dinosaurs - Fact File: Diplodocus; Paleo Mont Park Diplodocidae; Apatosaurus sp.; Apatosaurus sp.; Apatosaurus sp.; Apatosaurus; Apatosaurus1; The Dinosaur Museum; Britannica.com; Diplodocidae; DIPLODOCIDS; diplodocoidea; DGF, Geological Society of Denmark, Geologisk Tidsskrift Nr. 2, 1996; Biogeographic origin of Diplodocidae;

References: Upchurch (1998).

Image: [1] An old, AMNH-style image of *Diplodocus*, almost as extinct as the sauropod -- but still interesting art and good anatomy. Unlike many newer illustrations, the proportions are correct, even if the posture and locale are unfashionable. **[2]** This taxon includes a number of other forms which are not yet dealt with in **Palaeos**. 010604.

Apatosaurinae: *Apatosaurus*

Range: Late Jurassic of North America

Phylogeny: Diplodocidae **:** Diplodocinae + *.

Inroduction: The apatosaurs constituted one of three distinct evolutionary lines of West Laurasian diplodocids; the other two being the barosaurs and the diplodocii. The apatosaurs are distinguished by their heavy build, relatively shorter but very thick neck, and lightly built forelimbs. Like all the diplodocids, the apatosaurs were huge terrestrial herbivores with a snake-like neck and whiplash tail, who probably fed on lower crown layers of trees and on undergrowth. Species include:

Apatosaurus excelsus (Marsh 1879)
(syn. *Brontosaurus*, *Elosaurus*)
Morrison Formation; Wyoming, Utah, and Oklahoma, United States
Late Kimmeridgian to Early Tithonian
6 partial skeletons without skulls, hundreds of post-cranial elements.
Length: 18 to 21 metres; Weight: 13 to 20 tonnes

Apatosaurus ajax (Marsh 1879)

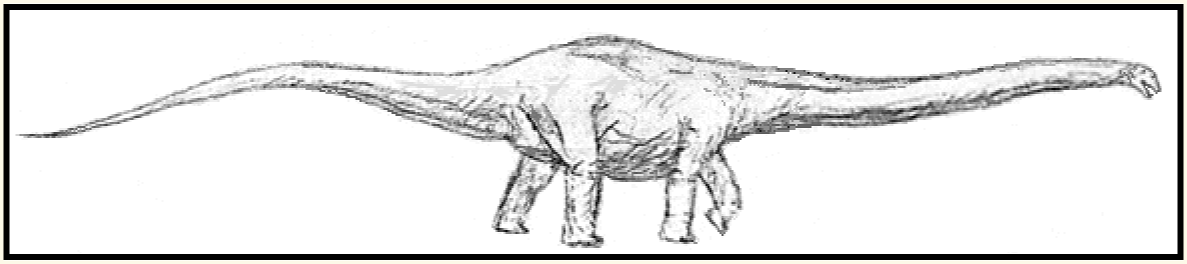
(syn *Atlantosaurus*, *Brontosaurus*)
Morrison Formation; Colorado, United States
Early Tithonian
2 partial skeletons, braincases,
Length: 24 metres, Weight: upto 30 tonnes
The last and largest of all the brontosaurs, this was a huge animal, as big as the bigger brachiosaurids. The humerus or upper arm bone alone measured 2 metres in length, compared with 1.75 metres maximum for A. exelsus. It seems that, as the Morrison ecosystem progressed, there was a tendancy for these giants to evolve into larger and larger forms. The apatosaurs, diplodocines, camarosaurs, brachiosaurs, allosaurs, and stegosaurs all followed this trend, so the early Tithonian dinosaurs were among the most gigantic of these beasts that are known. The same tendancy to increased science also occurs at the very end of the Cretaceous (Campanian-Maastrichtian); in both cases this progession to gigantism was followed by a mass extinction. (MAK 000218)

Diplodocinae:

Range: Late Jurassic of Africa, North America

Phylogeny: Diplodocidae **:** Apatosaurinae + * **:** *Barosaurus* + *Diplodocus*. 020324.

Barosaurus:



Range: Late Jurassic of Africa and North America

Phylogeny: Diplodocinae **:** *Diplodocus* + *.

Introduction:

Barosaurus gracilus Janesch 1961
Middle Saurian Bed, Tendaguru Beds, Mtwara, Tanzania
[Middle or Late Kimmeridgian, Central Gondwana]
Many isolated limb elements; altogether the remains of at least 15 individuals
Overall length about 16 metres; live weight about 4.2 tonnes
B. gracilus is the earliest and smallest of the barosaurs, a line of sauropods which, like the mamemchisaurs, developed extraordinarily long necks. These enabled the beasts to both graze over a wide area of ground or swampland, and feed from the foliage of tree-ferns and cycads. Although the skull is not known, they probably had a delicate *Diplodocus*-like head, with weak peg-like teeth that could only have been useful for stripping leaves or on soft vegetation, and it is less likely that they fed much on the conifer forests that sustained the great brachiosaurs.

Occuring on both sides of the Jurassic Proto-Atlantic seaway, *Barosarus* may have evolved from an ancestral form some time during the late Callovian or early Oxfordian. In the moist Tendaguru rainforest megafauna there was only one evolutionary line of diplodocid, the small African barosaurs. But, in the drier American Morrison megafauna, are found three distinct lines: large barosaurs, *Diplodocus*, and the famous apatosaurs.

Initially, the barosaurs were a relatively unimportant element of the Tendaguru megafauna, making up 10% of identified specimens in the Middle Saurian Bed, and 4% of the actual megafauna biomass. *Barosaurus* is much more common in the succeeding Lower Transitional sands, where it accounts for 50% of identified specimens and 40% of the megafauna biomass. With the eventual dissapearance of the brachiosaurs in this region (possibly due to changing environmental factors) the baraosaurs increased in size and number, and became the dominant element of the Tendaguru fauna.

Barosaurus africanus (Fraas 1908)
(syn. *Gigantosaurus*)
Upper Saurian Bed, Tendaguru, Mtwara, Tanzania
late Kimmeridgian/early Tithonian
More than 3 partial skeletons, a few skull elements, isolated postcrania; altogether the remains of at least 41 individuals

***Barosaurus africanus*: Size of selected skeletal elements**

Size in metres	humerus (upper arm)	ulna (lower arm)	scapula (shoulder balde)	femur (thigh bone)
average sized individual	0.97 m	0.74 m	1.34 m	1.34 m

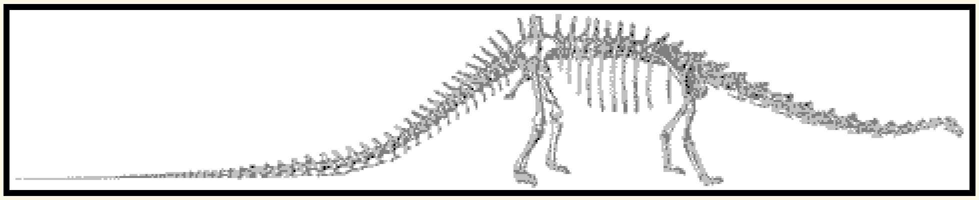
Overall length 20 metres;
Shoulder height about 3 metres; Hip height about 4 metres
Live weight 8.3 tonnes

Strangely, the great *Brachiosaurus brancai*, so common during the earlier Tendaguru, is totally absent in the later fauna. Instead, we find a larger species of *Barosaurus*, and a less abundant newcomer, *Tornieria*. In numbers *Barosaurus africanus* dominates the later Tendaguru fauna the way *Brachiosaurus* dominated the earlier fauna, being more common than *Dicraeosaurus* and *Torniera* put together. But in individual bulk *Barosaurus* is only half the weight of *Brachiosaurus*, and lived a different lifestyle. Whereas *Brachiosaurus* browsed giraffe-fashion from high branches, *Barosaurus* fed on undergrowth and low branches, its enormously elongated snaking neck conveying the head to select vegetation.

Barosaurus lentus Marsh 1890
(syn. *B. affinis*)
Morrison Formation; South Dakota and Utah, United States
Early Tithonian
5 partial skeletons without skulls, isolated limb elements,
Overall length 23 to 27 metres; Weight about 15 tonnes
The American form is the largest of the three *Barosaurus* species; and identical to *Diplodocus* apart from its elongate neck. It has been suggested that it should be included in the latter genus. But the cervicals (neck vertebrae) are 33% longer, distinguishing *Barosaurus* as a distinct type. (MAK 000218).

Links: DinoData Dinosaurs B011 BAROSAURUS; Paleontology and Geology Glossary- Ba; BAROSAURUS; Barosaurus (German); DinoNews.net - Le dinosaure Barosaurus (French); Dino Land Travels Database Carnegie Museum- Barosaurus Bones; Barosaurus Display; Barosaurus Display. 030822.

***Diplodocus*:**



Range: Late Jurassic of North America

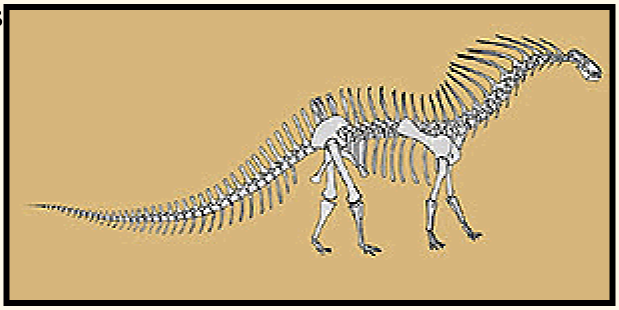
Phylogeny: Diplodocinae **:** *Barosaurus* + *.

Introduction: *Diplodocus longus*
Morrison Formation; Colorado and Utah, United States
Late Kimmeridgian
Length: 25 metres. Weight: 10 tonnes

The earliest American *Diplodocus*, a lineage of huge slender sauropods, it gave rise to *D. carnegii*, which in turn was supplanted by the even bigger *D. ("Amphicoelus") altus*. Bakker (1986).

Diplodocus carnegii Hatcher 1901
Morrison Formation; Wyoming and Utah, United States
Early Tithonian
5 skeletons without skulls, 2 skulls, hundreds of isolated post-cranial elements,
Length: 27 metres, Weight:10 tonnes
The successor and probable descendant of *D. longus*, *Diplodocus carnegii* is a slightly larger form. (MAK 000218)

Dicraeosauridae: *Amargasaurus*, *Dicraeosaurus*. Small sauropods (some not much bigger than a horse)



Range: Late Jurassic to Late Cretaceous of Africa & South America

Phylogeny: Diplodocoidea **:** Diplodocidae + *.

Introduction: *Dicraeosaurus hansemanni* Janensch 1914
Middle Saurian Bed, Tendaguru Beds, Mtwara, Tanzania
Skeleton lacking skull and forelimbs, 2 partial skeltons, altogether postcrania of about a dozen specimens
Overall length about 13.2 metres; weight 3.3 tonnes

***Dicraeosaurus hansemanni*: size of selected skeletal elements**

Size in metres	humerus (upper arm)	ulna (lower arm)	scapula (shoulder balde)	femur (thigh bone)
average sized individual	0.75 m	0.498 m	1.35 m	1.21 m

A relatively small sauropod, *Dicraeosaurus* or "forked lizard" gets its name from the high, forked spines jutting up from the vertebrae. Lambert (1983). These were used to anchor powerful neck and tail muscles. The neck was very short, consisting of only 11 or 12 vertebrae, and the head was - for a sauropod - unusually large in proportion to the body. The forelimbs were very short (humerus to femur ratio 62%) but stoutly built. This was obviously a low-feeder, grazing on the undergrowth and low trees such as cycads. It is also the most primitive of the Diplodocoidea, presumably a late survivor of a line that must have appeared in the late Bathonian, although no traces of these early Dicraeosaurids have been found.

Dicraeosaurus was a common element in the Tendaguru megafauna, making up 22% of identified specimens in the Middle Saurian Bed, but (because of its small size) only 7.5% of the actual megafauna biomass.

Dicraeosaurus sattleri Janensch 1914
Upper Saurian Bed, Tendaguru, Mtwara, Tanzania
late Kimmeridgian/Early Tithonian
2 partial skeltons without skulls; altogether postcrania of about a dozen specimens
Overall length about 8.5 metres; Weight 1.0 tonnes

D. sattleri is considerably smaller than the earlier *D. hansemanni*; with a weight of only a tonne, and a hip height of about 2 metres, it had a body about the size of a large draft horse, with a long tail at one end and a snaky neck at the other. We tend to think of sauropods evolving towards greater and greater size, as with the brachiosaurs and brontosaurs. But *Dicraeosaurus* illustrates the opposite trend, and shows that not all sauropods were huge. This was probably a lively animal, browsing on the undergrowth and the lower branches of the trees of the Tendaguru forest, and sometimes rearing up to reach higher morsels. It was always in danger from the carnivorous *Ceratosaurus*, and may have gained some protection by living in large herds, like wildebeast do today. (MAK 000218)

Characters: muzzle longer; **$** frontals "coalesced" (fused?); nares fully retracted to top of skull; **$** supratemporal fenestrae face laterally; **$** postparietal fenestra present; **$** "leaf-like" dorsolateral process from crista prootica (internal mouse ears?); long, subparallel basipterygoid processes; **$** basipterygoid processes at ~20° angle; **$** deep pit between bases of basipterygoid processes; jaw long & square; neck shorter than diplodocids (~12 vertebrae); **$** pleurocoels lost in cervical vertebrae; cervical ribs short; long bifurcated spines along back from elongated (~4x height of centra) neural spines (esp. *Amargasaurus*); dorsal vertebral pleurocoels reduced or absent; tail long & thin; forelimbs short; .

Note: are the long neural spines really convergent with rebbachisaurs, or is this the primitive condition for diplodocomorphs, convergently lost in some of the larger members of the group? (ATW 010606).

Image: *Amargasaurus*.

Links: **DinoData: Dicraeosaurinae**; AMARGASAURUS - Enchanted Learning Software; Dicraeosaurus (Portuguese); Dicraeosaurudae; Amargasaurus (Dutch); Sauropodomorphs (October 1); DICRAEOSAURIDAE; Amargosaurus, Argentinian but not Titanosaur!.

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checked ATW050910

Sauropoda: Macronaria

Camarasaurs and Brachiosaurs

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      `--Sauropoda
         |--Cetiosauridae
         `--Neosauropoda
            |--Diplodocomorpha
            |  |--Rebbachisauridae
            |  `--Diplodocidae
            `--Macronaria
               |--Camarasauridae
               |  |--Aragosaurus
               |  `--+--Lourinhasaurus
               |     `--Camarasaurus
               `--Titanosauriformes
                  |--Brachiosauridae
                  |  |--Lapparentosaurus
                  |  `--+--Atlasaurus
                  |     `--+--Giraffatitan
                  |        |--Bothriospondylus
                  |        |--Pelorosaurus
                  |        |--Cedarosaurus
                  |        |--Sonorasaurus
                  |        `--+--Sauroposeidon
                  |           `--Brachiosaurus
                  `--Somphospondylii
                     |--Euhelopodidae
                     `--Titanosauria
                        |--Nemegtosauridae
                        `--Titanosauridae
```

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2. *Atlasaurus* X
3. *Bothriospondylus* X
4. Brachiosauridae X
5. *Brachiosaurus* X

6. Camarasauridae X
7. *Camarasaurus* X
8. *Cedarosaurus* X
9. *Giraffatitan* X
10. *Lapparentosaurus* X
11. *Lourinhasaurus* X
12. Macronaria X
13. *Pelorosaurus* X
14. *Sauroposeidon* X
15. *Sonorasaurus* X
16. Titanosauriformes X

Descriptions

Macronaria:

Range: mJ-upK.

Phylogeny: Neosauropoda: Diplodocomorpha + * **:** Camarasauridae + Titanosauriformes.

Introduction: Originally (especially in old books on dinosaurs) the brachiosaurs and camarosaurs were grouped together, with the diplodocids and titanosaurs as a seperate branch. Both brachiosaurs and camarosaurs have long forelimbs, shortish tails, short high skulls, and more and broader teeth. More recently research has shown that the titanosaurs are actually related to the brachiosaurs; the camarasaurs, brachiosaurs, and titanosaurs being collectively referred to as the clade Macronaria. (MAK 001201).

Characters: robust, spoon-shaped teeth; enlarged narial openings (larger than orbits); crests formed by tall nasals; distal shafts of ischia plate-like and nearly coplanar; elongated metacarpals; Gondwanan origin;

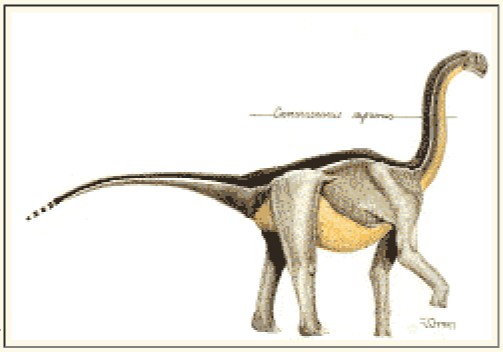
Links: neosauropoda cladogram; macronaria; Untitled Document; ATW010210.

Camarasauridae:

Range: upJ of Eur & NAm, China(?), Aus(??).

Phylogeny: Macronaria :: Titanosauriformes + * : *Aragosaurus* + (*Lourinhasaurus* + *Camarasaurus*)

Introduction: The camarasaurs are the most primitive of the Macronaria. However, they also are specialised in specific ways. The skull is short, blunt and relatively large. The teeth are large and spatulate or spoon-like. The neck very strong but inflexible, and apparently strongly upwardly-directed (an adaptation on browsing on trees, unlike the low-feeding diplodocids and euhelopids). A distinguishing mark is the "bifid" (split or two-branched) neural spines (i.e. the upward part of each vertebra is divided into two), the resulting U-shaped trough perhaps for the location of strong tendons. The forelimbs were not as elongated as in the brachiosaurids. The fore and hind legs are approximately the same length, the hind legs being only slightly longer. The tail is fairly short, relative to diplodocids. These animals appear to have lived in large herds.



Camarosaurus as it may have appeared in life. By Brenner Fishman

Until fairly recently it was stated that *Camarasaurus* evolved from the Chinese *Euhelopus*, but it is more likely that the Chinese forms, with their extraordinarily elongated necks, represented a line of advanced Cetiosaurs.

Despite their unspecialised structure, camarasaurs are not known before the early Kimmeridgian epoch, and it is possible that they evolved either from basal Oxfordian Brachiosaurids, or from early *Jobaria*-like forms. (MAK 001201)

Characters: ~18 m. Skull short, blunt and relatively large; teeth spatulate; teeth (*Camarasaurus*) show heavier wear than *Diplodocus*; short *basipterygoid processes*; jugal excluded from lower margin of skull (?); nares open laterally, just ant of orbits; cervical bracing (in *Camarasaurus*) by cervical ribs extending over 3 vertebrae; cervical vertebrae (12 in *Camarasaurus*) wide and short (neck very strong but inflexible); cervical & trunk vertebrae with extensive pleurocoels; vertical spines with U-shaped cleft (cleft on trunk only?); back horizontal (?); legs > arms, but not as marked as in *Diplodocus*; gastroliths known; most common dinosaur in J Morrison fm., perhaps all NAm.; mass death assemblage known (possible herding).

Links: DinoData: Camarasauridae; Geol 006 Sauropods; DinoData: Camarasaurus; Camarasaurus.

Aragosaurus:

Range: Early Cretaceous of Europe

Phylogeny: Camarasauridae : (*Lourinhasaurus* + *Camarasaurus*) + *.

Introduction: *Aragosaurus ischiaticus* Sanz, Buscalioni, Casanovas, and Santafe, 1987
Age: early Barremian
Place: central Laurasia (Spain)
remains: postcranial elements (forelimb, scapula, partial tail, and partial hip)
Length: 18 metres
Weight: 18 to 25 tonnes

Aragosaurus is very similiar to *Camarasaurus*. *Aragosaurus* is shown here as a primitive camarasaurid; but, in view of its later occurrence, may be a descendent of *Camarasaurus*. It is a very large animal, and shows that camarasaurids, although suffering local extinctions, happened to survive the terminal Jurassic event quite well. (MAK 001201).

Lourinhasaurus:

Range: Late Jurassic of Europe.

Phylogeny: Camarasauridae :: *Camarasaurus* + *.

Introduction: *Lourinhasaurus* (*Camarasaurus*) *alenquerensis* deLapparent & Zbyszewski, 1957.
Horizon: Lourinhã Formation, Provincia do Estremadura and Provincia do Beira Litoral, Portugal
Age: early Kimmeridgian
remains: partial postcrania, tail vertebrae, teeth
estimated length: 17 metres
estimated mass: 15 to 20 tonnes

Previously mistaken for *Apatosaurus*, this giant sauropod was one of the first of the camarasaurids. This species, a robust, average camarasaurid, has recently been placed in a new genus, *Lourinhasaurus*. (MAK 001201).

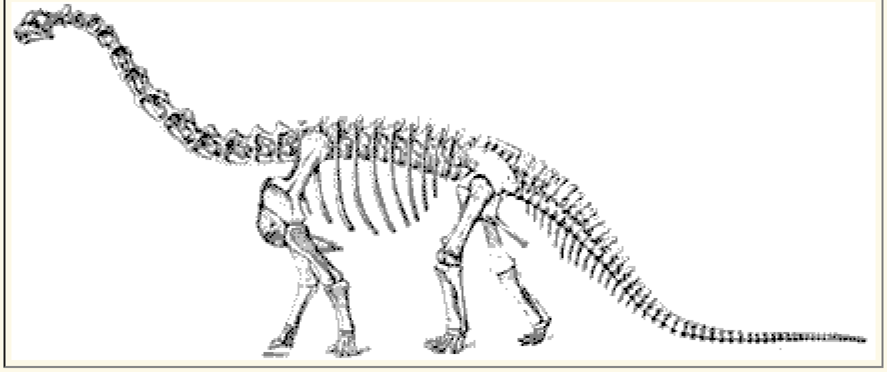
Camarasaurus:

Range: Late Jurassic of North America

Phylogeny: Camarasauridae :: *Lourinhasaurus* + *.

Introduction: *Camarasaurus grandis* (Marsh

1877)
Synonyms: "*Apatosaurus*," *Morosaurus*, *Pleurocoelus*
Horizon: Morrison Formation; Wyoming, Colorado and Montana, United States
Age: Middle Kimmeridgian
Place: western Laurasia



Camarasaurus skeleton, total length 18 metres from the DINOSAURS AND THE HISTORY OF LIFE - GEOLOGY V1001x site.

remains: At least 6 partial skeletons, 2 with skulls; hundreds of postcranial elements
Length: 14 metres
Weight: 10 to 15 tonnes
Comments: a number of juveniles are known

Camarasaurus lentus **(Marsh 1889)**
Synonyms: *Morosaurus, Uintasaurus*
Horizon: Morrison Formation; Wyoming and Utah, United States
Age: Late Kimmeridgian
Place: western Laurasia
remains: 5 skeletons with skulls; hundreds of postcranial elements
Length: 14 metres
Weight: 10 to 15 tonnes
Comments: This animal was extremely common and dominated the megafauna of the region

Camarasaurus supremus **Cope, 1877e**
Horizon: Morrison Formation; Wyoming, Colorado and New Mexico
Age: Early Tithonian
Place: western Laurasia
remains: At least five partial skeletons
Length: 18 metres
Weight: 18 to 25 tonnes
Comments: The last and largest of the American camarasaurs. (MAK 001201)

Titanosauriformes: *Titanosaurus* + *Brachiosaurus* [R&F].

Range: from the Middle? Jurassic worldwide.

Phylogeny: Macronaria : Camarasauridae + * : Brachiosauridae + (Euhelopodidae + Titanosauria).

Characters: dental wear facets sharply inclined with respect to the labio-lingual axis; $ rodlike palatine - maxilla contact [R&F]; anterior dorsal ribs broad & plank-like [VN]; dorsal vertebrae with posterior *centroparapophyseal laminae* [S+05]; medial prespinal lamina in posterior trunk vertebrae; $ simple, undivided chevron blades [R&F]; caudal neural arches, anterior base implanted on centra [S+05]; blades of middle and caudal chevrons curve posteriorly and down [R&F$]; neural arches positioned anteriorly in mid and posterior caudal centra [VN]; distal condyle of metacarpal I undivided [VN]; claw on manual digit I reduced or absent; proximal 1/3rd of femur deflected medially [R&F$]; femur, lateral bulge below lesser trochanter [S+05][3];

Links: Ameghiniana Round Up, Pt. II (and so does Tom Holtz); The Journal of Vertebrate Paleontology; Sauropodomorphs (October 1); Sauropodomorpha; Dinosaur Illustrated Magazine - DIM - number 001, 2001; Untitled Document; Nature Abstract; Phylogenetic Taxonomy of the Sauropoda (not strictly relevent, but interesting); paralititan.pdf; joël donnet Article 157; GEOL 104 Lecture 21- Sauropodomorpha- Size matters.

References: Rogers & Forster (2001) [R&F]; Salgado *et al*. (2005) [S+05]; Smith *et al.* (2001).

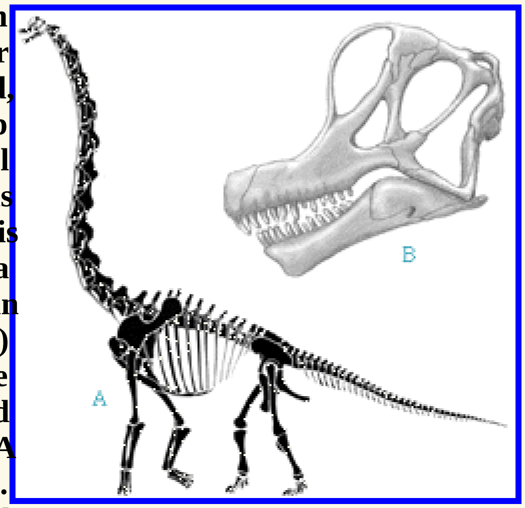
Note: [1] The characters marked "[VN]" show as strong, but not unambiguous, synapomorphies in an analysis I ran of essentially the [R&F] data set. The characters dealing with the ribs and Mt I are reversed in *Rapetosaurus*. The character relating to the caudal centra is reversed in *Alamosaurus*. **[2]** Note the interesting way in which the characters cluster. We might summarize this as: (a) the teeth and palate are redesigned to allow the teeth to shear past each other, (b) the distal forelimbs are simplified, and (c) the posterior balancing system is altered in a way which is not clear, but involves both stance and tail movements. [3] probably the same as the preceeding character. ATW051107.

Brachiosauridae:

Range: mJ-mK of NAm, Eur, Mad & Afr.

Phylogeny: Titanosauriformes : Somphospondylii + *: *Lapparentosaurus* + (*Atlasaurus* + (*Giraffatitan* + *Bothriospondylus* + *Pelorosaurus* + *Cedarosaurus* + *Sonorasaurus* + (*Sauroposeidon* + *Brachiosaurus*))).

Introduction: Together with the camarasaurs and titanosaurs, the brachiosaurs comprise clade Macronaria, one of the two main lineages of advanced sauropods. The brachiosaurs were a family of huge sauropods that includes some of the largest land animals. The brachiosaurs and their cousins, the camarasaurs, were distinguished by having forelimbs as long as or longer than their hind limbs, giving them high shoulders and a sloping back. This, and their long vertical necks, gave them a curiously giraffe-like appearance. They were high-grazers, able to feed on the leaves of trees too high for other sauropods to reach. They relied on sheer size as a defense against predators. The best-known species is the Tanzanian *Giraffatitan* (more commonly known as *Brachiosaurus*), but many other species are also known. The brachiosaurids are the only dinosaurs with forelimbs consistently longer than the hind, hence the name "Brachiosaurus" - arm lizard.



As with the camarasaurs the skull (*right*) is large compared with diplodocomorphs, the teeth long and spatulate (spoon-shaped). The upper front of the lightly-constructed skull (the nasal bones) is highly vaulted, with large, elevated nares (nostril holes) indicating nostrils close to the top of the head. This led to several bizarre theories. One was that the animal hid from predators at the bottom of deep lakes, feeding on water weeds and only poking its "snorkle" through the surface to breath. This is physiologically absurd, as water pressure would make breathing at such a depth impossible. The other theory is that brachiosaurs possessed an elephant-like trunk, as all mammals with trunks (tapirs, elephants, etc) have vaulted elevated nares. However, no reptile is known to have the facial muscles necessary for a trunk, and no indications of scars or blood vessels have been found in any dinosaur indicating a trunk-like organ. A more plausible theory is that the inflated nares were a cooling mechanism. Living during the tropical hothouse conditions of the Jurassic, such enormous animals were in danger of overheating. Blood therefore was conveyed to the top of the head, where it was cooled via heat-exchange and perhaps also membranes of skin (African elephants use their large ears for the same purpose - the frozen remains of woolly mammoths show their ears were a lot smaller).

The neck was long and giraffe-like, with elongated individual vertebrae; the back also sloped in a giraffe-like fashion. These animals were, like the camarasaurs, high browsers, and may indeed have been able to reach even higher branches than the camarasaurids could. Unlike the camarasaurs, the neural spines of brachiosaurids were undivided and small. The neck, although large and stiff, was probably not equipped with the sort of powerful tendons camarasaurs had, and could not have been held as erectly. Most reconstructions are in error in that they show the neck held in a very high, camarasaur-like posture.

The non-zonal fibro-lamellar bone structure indicates fast, uninterrupted growth from the baby to the adult stage, and these animals were perhaps fairly metabolically active (another reason for the vaulted nares as a heat sink.

With average lengths of 18 to 25 metres, and usual adult weights 15 to 45 tonnes (the largest species reaching 30 to 35 meters in length and perhaps 60 to 80 tonnes in weight), the Brachiosaurs were the largest animals of their time. Like the elephants of today, they were lords everything they surveyed. Not even Ceratosaurs,

Allosaurs, or Torvosaurs, the top predators of the Jurassic, would think of taking on a full-grown brachiosaur, any more than a lion would attack an adult elephant.

The phylogeny of brachiosaurids used here is a simplified version of the ones at Mikko's phylogeny site and Justin Tweet's Thescelosaurus! pages. I have also made the completely arbitrary assumption that the three species of Morrison Camarasaurs which suceed each other chronologically are also an evolutionary succession (a chronospecies so to speak). There are of course many more species than those listed in this diagram, but most of them are of questionable relationships.(MAK 010929)

Characters: Mass 20-90 T; if erect neck, 13 m; skull large and moderately long; teeth long & spatulate; vaulted nasal; large, elevated nares; neck vertically oriented (?); long neck with long individual vertebrae; long cervical ribs; neural spines undivided and usually small, especially in sacral region; deep pleurocoels in dorsal vertebrae; long slender dorsal ribs; tail short with simple chevrons; vertebral count 13+(11or 12)+5. forelimb at least as long as leg; metacarpals long; claw on manus I reduced or absent; center of gravity fairly far forward, so rearing unlikely (? controversial); non-zonal fibro-lamellar bone common (fast, uninterrupted growth).

Links: DinoData: Brachiosauridae; InfoBase: Setback pictures; WENCH - Dream star's Brachiosaurus; Brachiosaurus; DINOBASE, Sibbick's dinosaur pictures; Brachiosaurids; brachiosauridae; Brachiosaurus-Enchanted Learning Software; Brachiosaurus: The Natural History Museum's Dino Directory; BBC Online - Walking with Dinosaurs - Fact Files; Sauropodomorpha; Dino Land Paleontology Interviews: Matt Wedel; texas dinosaurs; Brachiosaurus (many links); Lecture 14 - Late Jurassic: Morrison, Tendaguru; Brachiosauridae; Brachiosaurus; Brachiosaurus; Brachiosaurus; Prehistoric World Images - Brachiosaurus brancai - dinosaur art; BRACHIOSAURUS; Brachiosaurus by Kaiypodo; art.com - Brachiosaurus Dinosaurs Animals Posters/prints; DinoMania! - Le Brachiosaurus; Brachiosaurus. ATW021013.

***Lapparentosaurus*:**

Range: Middle Jurassic of Madagascar.

Phylogeny: Brachiosauridae : (*Atlasaurus* + (*Giraffatitan* + *Bothriospondylus* + *Pelorosaurus* + *Cedarosaurus* + *Sonorasaurus* + (*Sauroposeidon* + *Brachiosaurus*))) + *.

Lapparentosaurus madagascariensis Bonaparte, 1986b
Horizon: Isalo Formation, Majungar, Madagascar
Age: Bathonian
Place: central Gondwana
Length: 15 to 20 metres
Based on juvenile remains previously referred to the genus Bothriospondylus, this early species appears to be very similiar to, and perhaps a direct ancestor of Brachiosaurus. Like the approximately contemporary Atlasaurus, this is a Gondwanan form, and it is possible that the Brachiosaurs evolved in central Gondwana; China being dominated by Shunosaurine and Europe by Cetiosaurine Cetiosaurids. (MAK 010929)

Atlasaurus: A. imelakei Monbaron et al., 1999

Range: Middle Jurassic (Bathonian - Callovian) of Africa (Morocco)

Phylogeny: Brachiosauridae :: (Giraffatitan + Bothriospondylus + Pelorosaurus + Cedarosaurus + Sonorasaurus + (Sauroposeidon + Brachiosaurus)) + *.

Atlasaurus imelakei Monbaron, Russell, and Taquet, 1999
Horizon:Guettious Sandstones, Beni Mellal, Morocco
Age: late Bathonian
Place:(northern central Gondwana)
Humerus 1.37 metres; femur 1.60 metres [Steel, p.64]
Overall length about: 13 to 14 meters
Comments: Originally called "Cetiosaurus" mogrebiensis, Atlasaurus imelakei is one of the earliest and most primitive of the brachiosaurids. (MAK 010929).

Characters: skull large relative to Brachiosaurus [M+99]; $ supratemporal fenestra twice as wide as long & not visible in lateral perspective [M+99]; $ paroccipital processes extend horizontally at nearly right angles to long axis of skull [M+99]; basipterygoid process longer than other brachiosaurids [M+99]; $ mandibular symphysis and dentary very shallow [M+99]; dentary straight, not curving toward symphysis [M+99]; neck shorter than in Brachiosaurus [M+99]; 13+ cervical vertebrae [M+99]; cervical rib shafts slender and project beneath centra of following vertebrae [M+99]; probably 12 dorsal vertebrae [M+99]; ribs suggest narrower chest and body than in Brachiosaurus [M+99]; 5 sacral vertebrae, with sacrum not narrowing posteriorly (narrows in Brachiosaurus) [M+99]; tail long [M+99]; humerus 65 % of estimated length of dorsal series [M+99]; forelimbs unusually long [M+99]; $ ulna length > tibia length by about 115 % (?!) [M+99].

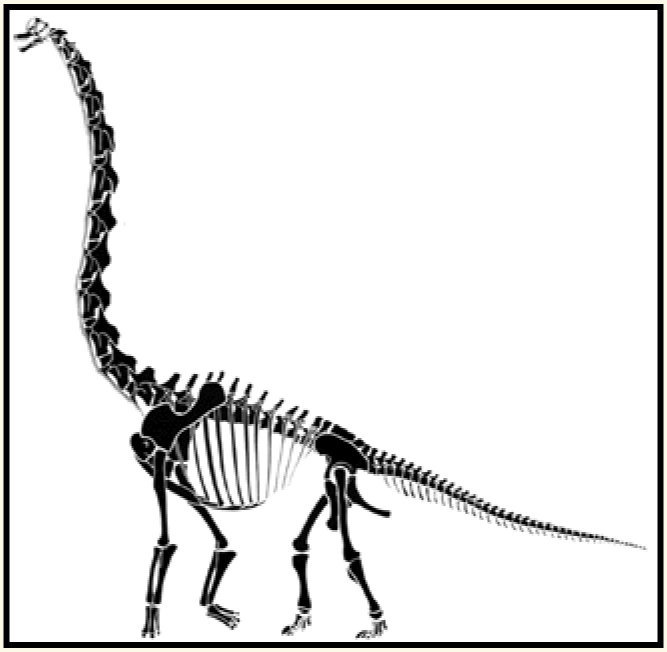
References: Monbaron et al. (1999) [M+99].

***Giraffatitan*:**

Range: Late Jurassic of Africa.

Phylogeny: Brachiosauridae ::: *Bothriospondylus* + *Pelorosaurus* + *Cedarosaurus* + *Sonorasaurus* + (*Sauroposeidon* + *Brachiosaurus*) + *.

Giraffatitan ("Brachiosaurus") brancai Janensch, 1914
Synonyms: Brachiosaurus brancai Janensch, 1914, Brachiosaurus fraasi Janensch, 1914
Horizon: Lower and Middle Saurian Bed, Tendaguru Beds, Mtwara, Tanzania
Age: Early to Middle Kimmeridgian
Place: Central Gondwana
remains: 5 partial skeltons, more than 3 skulls; altogether postcranial elements of at least 34 individuals



size of selected skeletal elements

Size in metres	humerus (upper arm)	ulna (lower arm)	scapula (shoulder balde)	femur (thigh bone)
Fair-sized individual	1.60 m	1.01 m	1.45 m	1.55 m
Large individual [in Berlin Museum]	2.13 m	1.28 m	2 m	

Left, a sketch of the famous Berlin Museum Brachiosaur; this is the tallest skeleton ever mounted. It is actually a composite of a number of specimens. Note - the position of the neck in this sketch is very unrealistic, the neck would actually have been held at a 45° angle

image from Prof. Paul Olsen's Dinosaurs and the history of life - Geology V1001x site

Overall Size of Complete Animal

overall size (metres)	Overall Length	Shoulder Height	Head Height	Estimated weight (tonnes)
Fair-sized individual	18 m			14.9 t
Large individual [in Berlin Museum]	22.2 m	6.0 m	14.0 m	31.5 t
Very large individual [partial skeleton]	25.0 m	6.79 m	18 m	45 t

Comments: Originally considered to be a species of *Brachiosaurus*, *Giraffatitan* is now generally placed in its own genus, although it may or may not be a subgenus of*Brachiosaurus*. It differs from the American *Brachiosaurus altithorax* in its more gracile build and different form of neck vertebrae. Most representations of *Brachiosaurus* are actually based on this species, which is known from more -- and more complete -- remains than any other brachiosaurid. It is a long-armed taxon based on a partial postcranium, and larger individuals are known. The skull has an unusually tall rounded crest containing the nostrils.

The *Giraffatitan* brachiosaurs were gigantic terrestrial herbivores, "giraffe-elephants" adapted to feeding on the crowns of trees. They dominated the Tendaguru megafauna, making up about 27% of all large animals (in terms of numbers of individuals identified in the Middle Saurian Bed), but in terms of actual biomass that figure would be closer to 78%. The large numbers would seem to indicate herding behaviour (like camarasaurs in the Morrison) The whole fauna could be rightfully called a Brachiosaur fauna. The only other identified sauropods were the small dicraeosaurs and *Barosaurus*, both in the vicinity of three to four and a half tonnes, and grasers upon low-lying and (in the case of Barosaurus) medium-height vegetation. (MAK 010929).

***Bothriospondylus*:**

Range: Late Jurassic of Europe and England.

Phylogeny: Brachiosauridae ::: *Giraffatitan* + *Pelorosaurus* + *Cedarosaurus* + *Sonorasaurus* + (*Sauroposeidon* + *Brachiosaurus*) + *.

***Bothriospondylus suffosus* Owen, 1875**
Age: late Oxfordian-early Kimmeridgian
Place: European Islands (England and ?France)
Remains: back and hip verebrae
Length: 17.5 meters
Weight: around 17 tonnes, or possibly less
Comments: Not particularly well known, this sauropod appears to be closely related to Brachiosaurus. (MAK 010929).

Pelorosaurus: P. conybearei Mantell, 1850 [nomen dubium]; P. becklessi Mantell, 1852 [nomen dubium]; "Cetiosaurus" humerocristatus Hulke, 1874 [nomen dubium]; "Dinodocus" mackesoni Owen, 1884; "Ornithopsis" leedsii Hulke, 1887 [nomen dubium].

Range: Early Cretaceous of Europe (UK and Portugal) & North America(?).

Phylogeny: Brachiosauridae ::: Giraffatitan + Bothriospondylus + Cedarosaurus + Sonorasaurus + (Sauroposeidon + Brachiosaurus) + *.

Characters: ~24m; humerus slim and fairly straight, with proximal expansion & well developed deltopectoral crest; another armored form?

Pelorosaurus conybearei Mantell, 1850
Synonyms: Pelerosaurus, Pelosaurus, Pelrorosaurus, Polorosaurus, Telorosaurus
Age: Barremian
Place: European Islands (England), Central Laurasia
Comments: known from assorted postcrania, and skin-impressions showing small, hexagon-like tubercles, Pelorosaurus a poorly known, fairly typical brachiosaurid, somewhat smaller than its Jurassic counterparts. A number of specimens assigned to this genus have been placed elsewhere, or are considered too fragmentary to identify properly. (MAK 010929).

Links: DinoData PELOROSAURUS; Pelorosaurus Fact Sheet - EnchantedLearning.com; PELOROSAURUS; earlyimage; Pelorosaurus sp (French); Synonyms of the species Pelorosaurus conybaerei; Nadine Solf's Dinosaurier-Datenbank (German); On the presence of a sauropod dinosaur (Saurischia) in the Albian ...; . ATW030516.

Cedarosaurus:

Range: Early Cretaceous of North America.

Phylogeny: Brachiosauridae ::: Giraffatitan + Bothriospondylus + Pelorosaurus + Sonorasaurus + (Sauroposeidon + Brachiosaurus) + *.

Cedarosaurus weiskopfae Tidwell, Carpenter, and Brooks, 1999
Horizon: Yellow Cat member of the Cedar Mountain Formation, Utah
Age: Barremian
Place: Western Laurasia (Utah); Cashenranchian Fauna
Remains: partial skeleton.
Comments: Some material referred to Pleurocoelus (but not the type material) may belong here. "Pleurocoelus" (Hollow Side) is a name given to a number of smallish (8 or 10 meters) early Cretaceous American brachiosaurs known from the Arundal formation of Maryland. Astrodon (Star Tooth) is a synonym. Pleurocoelus altus was once thought to be the adult form of P. nanus, but more recently is has been suggested as an entirely different sauropod. The proportionately large pleurocoels of the Arundel type material is likely to be a juvenile trait; juvenile Camarasaurus material was once identified as Pleurocoelus because of the very large pleurocoels. It is likely that, like so many partial dinosaur remains, Pleurocoelus may eventually turn out to be invalid, i.e. nomen dubum (that is, it is sauropod and apparently brachiosaur but not complete enough to diagnose further) and may be assigned other genera. To confuse matters even further, it has recently been suggested that Cedarosaurus and some of the Pleurocoelus material is not even brachiosaurian, but titanosaur instead. (MAK 010929).

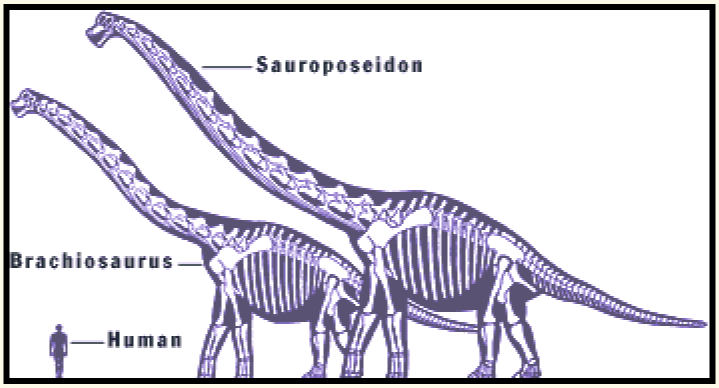
Sonorasaurus:

Range: middle Cretaceous of North America

Phylogeny: Brachiosauridae ::: Giraffatitan + Bothriospondylus + Pelorosaurus + Cedarosaurus + (Sauroposeidon + Brachiosaurus) + *.

Sonorasaurus thompsoni Ratkevich, 1998
Age: latest Albian
Place: Western Laurasia (Arizona); Cashenranchian Fauna
remains: skull and partial skeleton
Length: length 14? to 17? meters
Comments: A "pygmy" brachiosaurid, this animal nevertheless shows strong similarities with its larger Jurassic cousins. (MAK 010929).

Sauroposeidon:



Range: middle Cretaceous of North America.

Phylogeny: Brachiosauridae :::: Brachiosaurus + *.

Sauroposeidon proteles Wedel, Cifelli, and Sanders, 2000
Age: late Aptian-early Albian
Place: Western Laurasia (Oklahoma); Cashenranchian Fauna
Remains: rib, cervical vertebrae
Length: 30 to 35 metres
Weight: around 60 to 80 tonnes
Comments: Currently holding the status of the largest dinosaur ever (although the late Cretaceous titanosaur Argentinosaurus was certainly just as large), this enormous creature is known from four tree-trunk sized cervicals, and had the longest neck of any known animal, possibly twelve meters in length. It could have stood up to 18 meters tall. The drawing shows a comparison with a "standard" Brachiosaurus. (MAK 010929).

Brachiosaurus:

Range: Late Jurassic of Europe & North America

Phylogeny: Brachiosauridae :::: Sauroposeidon + *.

Brachiosaurus atalaiensis Lapparent & Zbyszewski, 1957

Horizon: Unnamed unit, Provincia do Estremadura, Portugal
Age: Middle Kimmeridgian
Place: European Islands (Portugal)
Comments: The huge B. atalaiensis was probably a descendent of the earlier Kimmeridgian "Ornithopsis" leedsi. Like the contemporary Tendaguru Brachiosaurus (Giraffititan) brancai this was a slender animal.

Brachiosaurus altithorax Riggs, 1903a
Horizon: Upper Morrison formation, Colorado and Utah
Age: Early Tithonian
Place: western Laurasia
Remains: two partial skeletons, also an old skull has recently been shown to belong to this species.
Length: 22 to 27 metres or more
Weight: 25 to 45 or 50 tonnes
Comments: A more heavily built species than the slightly earlier Giraffatitan, this species is similar, but less well known. Most restorations are actually based on Giraffatitan. This was one of the largest animals ever to live. The so-called "Ultrasaurus" and "Supersaurus" are actually based on partial remains of giant Brachiosaurs (in the case of Supersaurus mixed up with other species). B. altithorax did not seem to be as common as G. brancai, which may indicate a siolitary behaviour, in contrast to the herding Giraffititan. Alternatively, the rarety may be dues to local preservation and environmental factors; perhaps altithorax frequented areas taht were not conducive to fossilisation. (MAK 010929).

Links:DinoData Dinosaurs B042 BRACHIOSAURUS; Brachiosaurus- Enchanted Learning Software (as usual, excellent treatment disguised as a kid site); Brachiosaurus (list of links); Brachiosaurus (very basic); Brachiosaurus (OK); BBC - Walking with Dinosaurs - Fact Files (discussion); Dinosaur database - Brachiosaurus (Danish); BRACHIOSAURUS (basic data, but also references); Prehistoric World Images - Brachiosaurus brancai - dinosaur art (image); Dinos' Home Page - Brachiosaurus (Portuguese; basic discussion); Brachiosaurus and Ceratosaurus - Art.com, posters, prints and ... (one of my favorite posters); National Museum of Natural History - Dinosaur Exhibits (detail of humerus); DinoMania! - Le Brachiosaurus (French, links to good discussion). ATW021226.

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checked ATW051228

Sauropoda: Titanosauria (Somphospondylii)

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      `--Sauropoda
         |--Cetiosauridae
         `--Neosauropoda
            |--Diplodocomorpha
            |  |--Rebbachisauridae
            |  `--Diplodocidae
            `--Macronaria
               |--Brachiosauridae
               `--Somphospondylii
                  |--Chubutisaurus
                  |--Aegyptosaurus
                  |--Paralititan
                  |--Venenosaurus
                  |--Euhelopodidae
                  `--Titanosauria
                     |--Andesaurus
                     |--Argentinasaurus
                     `--Titanosauridae
                        |--Nemegtosauridae
                        `--Saltasaurinae
```

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3. *Argentinasaurus* X
4. *Chubutisaurus* X
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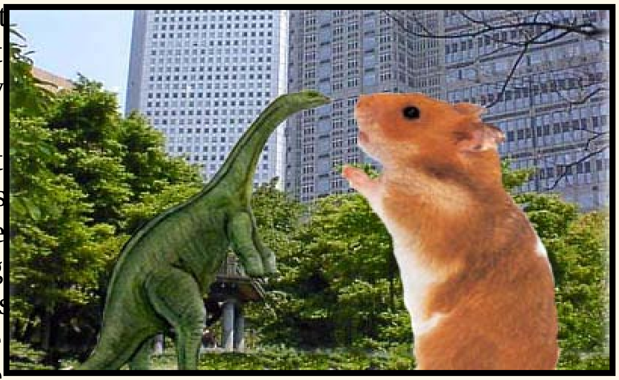
6. *Paralititan* X
7. Somphospondylii X
8. Titanosauria X
9. *Venenosaurus* X

Titanosauria



What can we say about the largest animals ever to walk the Earth? It seems almost disrespectful to devote the essay to technical trivia about anatomy or cladistics. It would be trite to list their statistics, as if they were football players or potential investments. All of this is important, but the truth is that we really don't understand much about what it means. These are creatures who may have pushed the possible limits of the tetrapod design -- whose mass might exceeded ours in the same proportion that we outmass a hamster. Hamsters on the order of 100 kg are somewhat thin on the ground. We cannot simply scale up animals by three orders of magnitude and expect them to work. **[1]** It may be worth reviewing some of the problems involved, since these are precisely the critical issues of sauropod biology.

One of the chief problems is simply breathing. The trachea is very long, and presumably as wide as it can be to minimize turbulence and frictional resistance to air flow against the walls of the trachea. This means that the trachea itself represents a rather large volume of "dead space." Significant gas exchange cannot occur in this volume for two reasons. First, this space is filled with deoxygenated air from the animal's last exhalation. Second, the surface area per unit volume of air is low, so that physiologically significant gas exchange cannot occur. Sucking this deoxygenated air back into the lungs on inhalation reduces the oxygen available for absorbtion. Yet, because of the length of the neck, the total lung volume may not be much bigger than the dead space. How can we get fresh air into the lungs without creating huge and impractical lungs? How do we pump that much air through the trachea in the first place? As Paladino *et al.* (1997: 498-98) state, "The allometrically predicted tidal volume [the volume of air in a breath] for an *Apatosaurus* ... would only be about 19 liters ... . This amount would be totally insufficient and would not even move enough air to replace the dead space volumes ... ." Giraffes have a similar problem. See Re: How do girraffes breathe?? However, unlike a giraffe, a sauropod has no diaphragm. Breathing in reptiles is generally accomplished either by sloshing the liver back and forth to force air in and out of the lung, or by squeezing the ribs to accomplish the same result. I am told by Usually Reliable Sources that sauropods probably lacked the equipment to do either of these things well.

Second, assuming that the sauropods had engineered around this problem, how did they deliver the oxygenated blood to the brain? The act of raising the head would very likely cause a catastrophic loss of blood pressure to the brain. Worse, pumping blood against gravity to the brain would require very considerable pressure. Not only does this demand a massive heart, but the pressure would be high enough to cause serious loss of fluid across permeable capillary beds, especially in the lungs. Reid (1997).

Third, how did they move around? The traditional view of sauropods was that they were barely able to sustain their own weight and therefore lived in swamps. Bakker (1986) and others pointed out that this was very unlikely for any number of reasons. Not the least of these was that sauropods *were* heavy, with relatively small feet for their size. Accordingly, they would have stuck fast in a swamp. Bakker argues that, in fact, sauropods probably avoided marshy areas as much as possible. The reasoning seems impeccable. Unfortunately, sauropods keep turning up in places whch appear suspiciously swamp-like. Generally, the paleoecology of fossil sites is vague enough that the precise context is unclear. Recently, however, Smith *et al.* (2001) dug up one of the largest sauropods of all, *Paralititan*, from what they carefully determined were the fine-grained sediments of a very low energy tidal flat facies covered with mangroves -- in other words, a mangrove swamp. **[2]** As anyone who has spent significant time in mangrove swamps can attest, it is rather easy for human beings to get mired in this environment, much less an 80 ton *Paralititan.* Yet, the animal seems to have walked out there on its own. Perhaps this was simply a mistake which caused its death. The senior author of the paper seems to think otherwise. Re: Paralititan (mangrove swamps).

Finally, how did titanosaurs protect themselves from predation? As much as we like to imagine sauropods stamping their feet and lashing their tails to drive off the vicious theropod predators, the scenario is unlikely for a simple reason. The conduction velocity of ordinary motor neurons, even in mammals, is on the order of 20 m/sec. By the time a 30m titanosaur perceived the threat, determined its probable intentions, and began to lash out in the proper direction, 2-3 seconds might have passed. Although few predators would want to take on a rampaging sauropod, however uncoordinated, it is difficult to see how this would discourage an agile predator from taking a quick snack and departing -- leaving the trampling titanosaur to its tantrum.

This is by no means an exhaustive list of sauropod problems. However, it is not necessary to rely on gravitational anomalies or similar nonsense to resolve these particular issues. In fact, they may all have have been handled with a single adaptation -- the generous application of air sacs. The presence of numerous pleurocoels in sauropod bones is well documented and uncontroversial. Large, avian-style respiratory air sacs are speculative, but entirely reasonable. At least, they are frequently invoked. In addition, a third type of air sac is known from a group of modern dinosaurs, the Anhimidae or Screamers. These rather weird, primitive South American birds are ducks of a sort. In addition to other odd characteristics, the anhimids have a layer of air-filled tissue between the skin and the body wall – something like the plastic bubble wrap used to ship glassware.

We may imagine a large sauropod with all three types of pneumatization. If respiratory air sacs were present, the respiration problem is solvable because the animal could adopt one-way breathing as in birds. Birds do not take air directly into their lungs. Rather, fresh air is shunted off to the air sacs, then fed into the lung from the back as the stale air exits via the trachea. The dead space issue evaporates because air flow is only one way. The blood pressure problem remains significant, but could at least be simplified by a system of pneumatic locks preventing rapid changes in blood pressure. Some have suggested active pneumatic pumping of blood. This requires an unprecedented evolutionary novelty, but cannot be eliminated as a possibility. Mobility and mechanical problems are much easier to address if titanosaurs were lighter than their size would suggest. By way of example, if we model a sauropod body as something between a cylinder and a sphere with (in either case) a diameter of 200 cm, then a very low density, air-filled layer of about 25 cm under the skin would reduce mass by as much as 40-50% over the equivalent volume of normal tissue, even without accounting for respiratory air sac volume. This same layer would provide protection against any serious wound from the "one free bite" which the sauropod's slow reaction might give a fast-moving predator.

All this, of course, is simply speculation; but something was clearly rather special about sauropod anatomy. Not only has no other group of terrestrial tetrapods come close to their size, but the uniformity of the sauropod body plan over 120 My suggests that there was not much room for variation on some special basic theme. Perhaps our 100 ton hamster was not so far off after all, if they were active, but puffed up like scaly zepplins. So much for the dignity of the titanosaurs ... (ATW 010911)

[1] In the image, *Alamosaurus* meets a 100,000 kg hamster. The location is, of course, Tokyo -- the traditional venue for such encounters.

[2] Part of the quarry lies in a tidal channel, raising the possibility that the animal followed the presumably firmer footing in the channel to reach the flat. But this simply revives the idea of a semi-aquatic habit which appeared to have been discredited. In the image, a fairly small specimen of *Argentinasaurus* is placed in a (modern) mangrove swamp. Back to the swamps -- *again*?

Descriptions

Somphospondylii: *Euhelopus* + *Saltasaurus*, Rogers & Forster (2001). But used here as the stem group *Saltasaurus* > *Brachiosaurus*, *i.e.*, to include Titanosauria and Macronarians *incertae sedis* other than brachiosaurids. This latter use be more appropriate if Macronaria is treated as a node, the crown group *Brachiosaurus* + *Saltasaurus*; but the Rogers & Forster usage is more appropriate if Macronaria is the stem group *Saltasaurus* > *Diplodocus*.

Range: Middle Jurassic to Late Cretaceous.

Phylogeny: Macronaria: Brachiosauridae + * **:** *Chubutisaurus* + *Aegyptosaurus* + *Paralititan* + *Venenosaurus* + Euhelopodidae + Titanosauria

References: Rogers & Forster (2001). (ATW 020325).

***Chubutisaurus*:** *C. insignis* delCoro, 1974.

Range: middle Cretaceous of South America (southern Argentina)

Phylogeny: Somphospondylii **:** *Aegyptosaurus* + *Paralititan* + *Venenosaurus* + Euhelopodidae + Titanosauria + *.

Characters: 20+ m; vertebrae with large pneumatic spaces; tail short; forelimbs shorter than the hindlimbs.

***Chubutisaurus insignis* Corro, 1974**
Age: *Albian*
Place: *West Gondwana (Argentina)*
Remains: *two partial skeletons*
Length: *23 meters*
Weight: *30 tonnes?*
Comments: *A number of middle Cretacous forms previously considered to be brachiosaurs now seem to be titanosaurs. Although they do not have the distinct characteristics of the family Titanosauridae, they are certainly representative uncles and aunts; earlier forms continuing to exist alongside their more recent relatives. Chubutisaurus is typical of this group. Previously considered among the brachiosaurs, this huge animal seems to be a representative basal (ancestral) type, closely related to the Titanosauridae. (MAK 011115)*

Links: DinoData CHUBUTISAURUS; CHUBUTISAURUS; Yahooligans! Science- Dinosaurs; Paleontology and Geology Glossary- Ch; Argentina On View - News and Press; Chubutese dinosaurs. ATW040207.

***Aegyptosaurus*:**

Range: Early Cretaceous of Africa

*Phylogeny: Somphospondylii : Chubutisaurus + Paralititan + Venenosaurus + Euhelopodidae + Titanosauria + *.*

***Aegyptosaurus baharijensis* Stromer, 1932**
Horizon: *Continental Intercalaire*
Age: *Cenomanian*
Place: *north-central Gondwana (Egypt)*
Length:*Length: 15m*
Remains: *Remains: leg bones, fragmentary vertebrae (destroyed in WW2)*
Comments: *An early representative of the Titanosaur group. Its relationship to later members is not known. (MAK 011115)*

***Paralititan*:**

Range: Early Cretaceous of Africa

*Phylogeny: Somphospondylii : Chubutisaurus + Aegyptosaurus + Venenosaurus + Euhelopodidae + Titanosauria + *.*

***Paralititan stromeri* J. B. Smith, Lamanna, Lacovara, Dodson, J. R. Smith, Poole, Giegengack, and Attia, 2001**
Horizon: *Baharija Formation of Egypt*
Age: *early Cenomanian*
Place: *north-central Gondwana (Egypt)*
Remains: *postcranial material including a humerus, shoulder girdle, and tail vertebrae*
Length: *30 meters*
Weight: *upto 70 tonnes*
Comments: *A huge animal, Paralititan apparently lived in a swampy mangrove environment. It is not clear how it avoided becoming mired. (MAK 011115)*

***Venenosaurus*:**

Range: middle Cretaceous of North America

Phylogeny: Somphospondylii : Chubutisaurus + Aegyptosaurus + Paralititan + Euhelopodidae + Titanosauria + *.

Venenosaurus dicrocei Tidwell, Carpenter & Meyer, 2001
Horizon: Poison Strip member of the Cedar Mountain Formation, Utah
Age: Aptian/Albian
Place: Western Laurasia (Utah); Cashenranchian Fauna
Remains: adult: partial skeleton, including limb elements and tail vertebrae. Juvenile material probably of the same species.
Comments: May be closely related to Cedarosaurus, if so, the latter is not a brachiosaur, but a titanosaur. (MAK 011115).

Euhelopodidae: *Euhelopus, Klamelisaurus*. As with Mamenchisaurids, unclear whether this group should include more than *Euhelopus*.

Range: Middle Jurassic to Early Cretaceous(?) of China, and perhaps Australia & South America.

Phylogeny: Somphospondylii **:** *Chubutisaurus* + *Aegyptosaurus* + *Paralititan* + *Venenosaurus* + Titanosauria + *.

Characters: Short steep-snouted squarish skull; peg-like (or "spoon-like"?) teeth similar to diplodocids, but larger and not restricted to anterior jaw; nares on top of skull; long neck with 19? (17?) vertebrae; skid-like chevrons; forelegs as long as hindlimbs.

Links: **DinoData: Euhelopus**; Dann's Dinosaur Info: Rhoetosaurus; Dinobase, DINOSAUR CARDS; Dinosaur Families - Enchanted Learning Software; Euhelopus; euhelopodidae (**Best on the Web**); Untitled Document; Euhelopodidae.

Note: Probably only *Euhelopus* belongs here. Other Euhelopidids, if that's applicable any more, are probably closer to *Mamenchisaurus.* 010904.

Titanosauria: To be consistent, Titanosauria really ought to be *Saltasaurus* + *Nemegtosaurus* or something of that sort. However, the Nemegtosauridae are not sufficiently well known or well-defined, so the term is used in a non-cladistic way to include all "traditional" titanosaurs.

Range: Late Jurassic to Late Cretaceous of South America, Europe, Africa, North America & Australia?

Phylogeny: Somphospondylii **:** *Chubutisaurus* + *Aegyptosaurus* + *Paralititan* + *Venenosaurus* + Euhelopodidae + *:

Introduction: While other sauropod groups died out during the late Jurassic or Middle Cretaceous, the titanosaurs continued roight until the end of the period. And not only continued, but flourished. They have been found almost worldwide; only central to northern North America western "Asiamerica" was probably free of them (I wouldnt be surprised if - on the weight of purely biogeographical reasons - the strangely primitive Australian Austrosaurs turn out to be abberent titanosaurs; after all, titanosaurs were common everywhere else in Gondwana)

All titanosaurs were rather primitive and unspecialised sauropods, for a long time considered on the basis of their peglike teeth and badly reconstructed skulls, to be cousins of the diplodocids. It is now known that they are related rather to brachiosaurs and camarosaurs, being grouped with them in the clade *Macronaria*. They ranged in size from realtively small sauropods to some the hugest animals that ever walked on land. (MAK 011115).

Characters: large to gigantic herbivores; very small, peg-like slender teeth; supratemporal fenestrae transversely oriented [R&F]; supratemporal fenestrae narrowed [VN]; quadrate hollow, with excavation posterior [R&F]; distal end of paroccipital process slender and elongated (reversed in *Quaesitosaurus*) [VN]; vertebrae with uncleft spines; cervical vertebrae elongate with shallow lateral pleurocoels [R&F]; cervical pleurocoels simple and undivided (reversed in *Saltasaurus*) [VN]; cervical and anterior dorsal spines single and without median tubercle (several reversals) [VN]; at least 10 dorsal vertebrae [S+05]; pleurocoels usually eliptical, with well-developed system of internal divisions [S+05]; anterior and mid dorsal spines posteriorly inclined; [VN]; dorsal vertebrae with accessory posterior *spinodiapophyseal laminae* [S+05**$**]; dorsal vertebrae with posterior *centroparapophyseal lamina* [S+05**$**]; **$** hyposphene-hypantrum articulation in posterior trunk vertebrae [R&F]; presacrals fiilled with spongy bone; 6 sacrals

[S+05]; second sacral rib directed anterolaterally & distally expanded [S+05]; **$** < 35 caudal vertebrae [R&F]; caudal vertebrae of spongy bone [R&F**$**]; **$** anterior caudals strongly procoelous having "ball and socket" articular faces; chevrons simple; distal caudal vertebrae reduced in number and not elongated [VN]; caudal vertebrae, neural arches with well-developed *prespinal laminae* [S+05]; caudal vertebrae, neural spine vertically oriented [S+05]; scapular glenoid medially inclined; anterior limbs at least as long as posterior limbs; semilunar sternal plates; coracoid long compared to sternal articulation of coracoid [VN]; prominent deltopectoral crest on humerus [VN]; ulna stout [VN]; **$** olecranon process of ulna projects above proximal articulation [R&F]; **$** distal width of radius twice width at midshaft [R&F]; elongate metacarpals [R&F]; claw on manual digit I absent; expanded, sacrum tilted antero-dorsally; semicircular preacetabular process of ilium [R&F]; ilium, pre- and postacetabular processes expanded laterally [S+05]; ischium length/pubis length = 0.90 or less [R&F**$**]; elongate pubis [R&F]; femur usually anteroposteriorly compressed [S+05]; distal end of femur may be expanded transversely; tibia, distal portion expands transversely [S+05]; fibula outer surface convex & inner surface slightly concave [S+05]; astragalus tall & transversely thin [S+05]; diverse dermal armor with plates and small ossicles.

Note: The characters marked "[VN]" show as synapomorphies in an analysis I ran of essentially the [R&F] data set. ATW010907.

Links: **DinoData: Titanosauridae**; titanosaurid megatracksite; Terrestrial trans-Tethyan dispersals (only marginally relevant, but interesting); The Journal of Vertebrate Paleontology; Nature Science Update; Abstract; g00n3a3.pdf; paralititan.pdf; What groups of dinosaurs existed- (brief paragraph);

References: Bakker (1986); Paladino *et al.* (1997); Reid (1997); Rogers & Forster (2001) [R&F]; Salgado *et al.* (2005) [S+05]; Smith *et al.* (2001).

***Andesaurus*:**

Range: middle Cretaceous of South America.

Phylogeny: Titanosauria **:** *Argentinasaurus* + Titanosauridae + *.

Andesaurus delgadoi* *Calvo and Bonaparte, 1991
Horizon: *Rio Limay Formation of Neuquen Province, Argentina*
Age: *Albian*
Place: *west Gondwana (Argentina)*
Remains: *postcrania*
Length: *40 meters?*
Weight: *80 tonnes?*
Comments: *This gigantic primitive titanosaur shows some resemblance to Argentinasaurus, and shares a similar vertebral structure. Andesaurus is the standard-bearer of paraphyletic, or maybe even polyphletic, group of mostly gigantic proto-titanosaurids sometimes referred to as "Andesauridae." The family was named by Jose Bonaparte, the great Argentine paleontologist, and includes the genera Phuwiangosaurus, Andesaurus, Argentinasaurus, Malawisaurus, and perhaps Iuticosaurus (formerly Titanosaurus valdensis Huene - DinoData page). Many workers now consider Andesauridae an invalid taxon and its representative forms as simply generic early/basal titanosaurids. In any case, these animals belong at the base of the titanosaurid tree, intermediate between contemporary forms like Chubutisaurus and more advanced titanosaurs. Inasmuch as true titanosaurids seem to have evolved as early as the Late Jurassic, that means that the "Andesauridae" also extend back equally as far, and continued alongside thier descendents for some 50 million years. (MAK 011115).*

Characters: dorsal vertebrae with hyposphene- hypantrum articulation; caudal centra amphicoelous, with ? laminated spines.

Links: DinoData Andesaurus; ANDESAURUS (basic data and reference); Andesaurus (Spanish: similar, with a bit more detail); Argentina On View. ATW030709.

Argentinasaurus:

Range: Early Cretaceous of South America.

Phylogeny: ***Titanosauria*** ***:*** ***Andesaurus*** **+** ***Titanosauridae*** **+ *.**

Argentinosaurus huinculensi ***Bonaparte & Coria, 1993***
Horizon: ***Rio Limay Formation of Neuquen Province, Argentina***
Age: ***Cenomanian***
Place: ***west Gondwana (Argentina)***
Remains: ***postcrania***
Length: ***length around 35 to 45 meters***
Weight: ***weight upto 80 tonnes***
Comments: ***possibly the largest known dinosaur. It may be related to Andesaurus. In any case it lived in the same geographic region at much the same time. (MAK 011115).***

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checked ATW050910

Sauropoda: Titanosauridae

Abbreviated Dendrogram

```
DINOSAURIA
|
SAUROPODOMORPHA
|--Prosauropoda
`--Sauropoda
   |--Cetiosauridae
   `--Neosauropoda
      |--Diplodocomorpha
      |  |--Rebbachisauridae
      |  `--Diplodocidae
      `--Macronaria
         |--Brachiosauridae
         `--Somphospondylii
            |--Euhelopodidae
            `--Titanosauria
               |--Nemegtosauridae
               `--Titanosauridae
                  |--Ampelosaurus
                  |--Epachtosaurus
                  |--Janenschia
                  |--Magyarosaurus
                  |--Nemegtosauridae
                  |  |--Quaesitosaurus
                  |  `--+--Rapetosaurus
                  |     `--Nemegtosaurus
                  `--Saltasaurinae
                     |--Alamosaurus
                     |--+--Titanosaurus
                     |  `--Jainosaurus
                     `--+--Neuquensaurus
                        `--Saltasaurus
```

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2. *Ampelosaurus* X
3. *Epachtosaurus* X
4. *Jainosaurus* X
5. *Janenschia* X
6. *Magyarosaurus* X
7. Nemegtosauridae X
8. *Nemegtosaurus* X
9. *Neuquensaurus* X
10. *Quaesitosaurus* X
11. *Rapetosaurus* X

12. Saltasaurinae X
13. *Saltasaurus* X
14. Titanosauridae X
15. *Titanosaurus* X

Descriptions

Titanosauridae: Since Titanosaurus is a somewhat vague genus, and is currently in disfavor as an anchor taxon, "Titanosauridae" is not much used in the literature. While no one is looking, we have absconded with this label and used for an equally vague group consisting of all "traditional" titanosaurians more derived than the most basal genera.

Range: Late Jurassic to Late Cretaceous

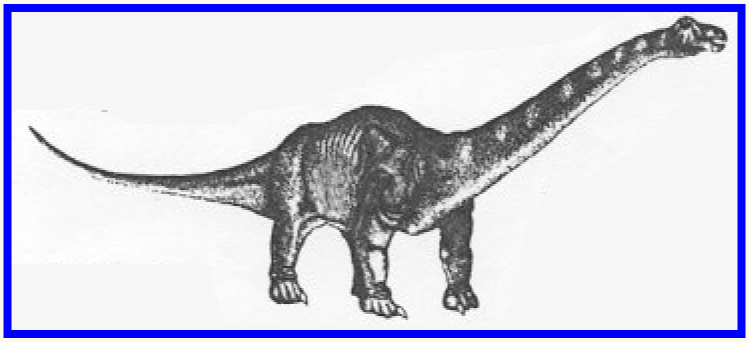
Phylogeny: Titanosauria : Andesaurus + Argentinasaurus + * : Ampelosaurus + Epachtosaurus + Janenschia + Magyarosaurus + Nemegtosauridae + Saltasaurinae.

Introduction: This is one of the largest families of dinosaurs. Because Titanosaurus is based on poor materials, it has been suggested that the name be changed to Saltasauridae. Titanosaurids are mostly known from the Cretaceous of Gondwana, especially South America, but they were also representative of India, Madagascar, and even Europe. While some were as huge in size as their name indicates, many were of moderate proportions, and there were also dwarf forms that seem to have been island-dwellers. Many titanosaurids are rather poorly known, and it is not unlikely that - as is usually the case - a lot of the taxa based on fragmentary material will turn out to be invalid. It used to be thought that the Titanosauridae were cousins to the diplodocids. More recent studies reveal that titanosaurid skulls were not diplodocid-like (as restored by von Huene, an early but influential worker in this field) nor extremely flat (as has also been suggested), but were instead similiar to Camarasaurus and Brachiosaurus, although not as high (see illustration of Rapetosaurus). The way in which the teeth mesh together is different from that of other sauropod groups, especially diplodocoids. The head is surprisingly small, even by sauropod standards (say around 30 cm for a 14.5 meter long animal).

A vast nesting colony of titanosaurids has been discovered in Argentina recently, with some fossilised embryos showing skin impressions, and another such possible colony was uncovered in Spain. The embryo skin impressions indicate (according to the placement of these scales) that these titanosaurs would not have sported the keratinous dorsal spikes found associated with a diplodocid specimen. *See* Czerkas (1997). Neither were the juveniles feathered.

The existence of nesting grounds indicates that these were social animals, perhaps congregating and nesting in large heards. Possibly the safety of numbers protected them from the carnivorous abelisaurs that were well placed to be their main predator. (MAK 011115)

Ampelosaurus: A. atacis Le Loeuf 1995.



Range: Late Cretaceous (Maastrichtian) of Europe (France)

Phylogeny: Titanosauridae : Epachtosaurus + Janenschia + Magyarosaurus + Nemegtosauridae + Saltasaurinae + *.

Characters: teeth slightly spatulate; neural arches bent posteriorly; armored, with several diffrent types of armor (plates, spines, etc.).

Ampelosaurus atacis Le Loeuff, 1995
Horizon: Aude Valley, Esperaza, France
Age: early Maastrichtian

Place: *European islands (France) (Central Laurasia)*
Remains: *several individuals; most of a skeleton, at least 20 different specimens in all*
Length: *15 meters*
Comments: *A primitive titanosaurid known from good material. A number of types of armor have been found with it, indicating that primitive as well as advanced titanosaurs possessed bony plates in the skin.*

Links: Dinosaur hunting in the South of France; DinoData Dinosaurs A100 AMPELOSAURUS; DinoMania! - Le dinosaure Ampelosaurus (French); Ampelosaurus atacis; MUSEE.DINOSAURES - AMPELOSAURUS; AMPELOSAURUS; Ampelosaurus atacis; Paleontology and Geology Glossary; GLOSSAIRE. MAK 011115, ATW020818.

Epachtosaurus:

Range: Late Cretaceous of South America

*Phylogeny: Titanosauridae : Ampelosaurus + Janenschia + Magyarosaurus + Nemegtosauridae + Saltasaurinae + *.*

Epachtosaurus sciuttoi *Powell, 1990*
Age: *Campanian-Maastrichtian*
Place: *west Gondwana (Argentina)*
Remains: *postcrania*
Length: *15-20 meters*
Comments: *a primitive late surviving form, this species seems to lack the typical titanosaur osteoderms. Originally thought to be Cenomanian (mid Cretaceous, it appears to be later Cretaceous instead, making it a sort of "living fossil" existing alongside more advanced saltosaurid titanosaurs. (MAK 011115).*

Janenschia:

Range: Late Jurassic of Africa

*Phylogeny: Titanosauridae : Ampelosaurus + Epachtosaurus + Magyarosaurus + Nemegtosauridae + Saltasaurinae + *.*

Janenschia robusta *(Fraas, 1908)*
Horizon: *Upper "Saurian beds" Tendaguru, Tanzania*
Age: *Late Kimmeridgian*
Place: *central Gondwana*
Remains: *limb and vertebaral elements*
Length: *24 meters*
Weight: *30 tonnes*
Comments: *this wastebasket taxon is composed of all sauropods that couldn't be placed in the other Tendaguru sauropod taxa (including some genuine Titanosaurids that are the earliest representatives of the group). Also previously known as Gigantosaurus. (MAK 011115).*

Magyarosaurus: von Huene 1932. M. dacus Nopcsa 1915, M. transylvanicus von Huene 1932 (probably a synonym).

Range: Late Cretaceous (Maastrichtian) of Eastern Europe

*Phylogeny: Titanosauridae : Ampelosaurus + Epachtosaurus + Janenschia + Nemegtosauridae + Saltasaurinae + *.*

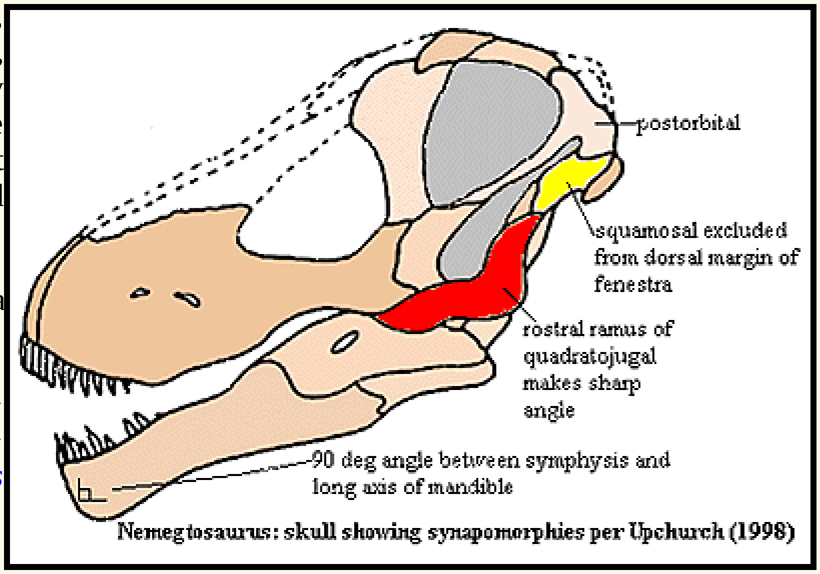
Magyarosaurus dacus *Huene, 1932*
Synonym: *Titanosaurus dacus Nopcsa, 1915*
Horizon: *Sinpetru Beds, Hunedoara, Romania*
Age: *late Maastrichtian*
Place: *European islands (Romania) (Central Laurasia)*
Remains: *isolated postcranial material of at least 10 individuals*
Length: *5.25 meters*
Weight: *600 kg*

***Comments:* the smallest known adult sauropod, this little animal would seem to have been an island dweller. Often limitations of food, and absence of large predators, on islands result in previously large animals evolving into smaller forms (like the dwarf elephant (Elephas falconeri) of Pleistocene Malta). As the remains include both robust and slender humeri, it is likely that these are from several different species of dwarf sauropods. (MAK 011115).**

***Note:* Recent evidence indicates that Magyarosaurus may have been another armored titanosaur.**

***Links:* DinoData Dinosaurs M012 MAGYAROSAURUS; MAGYAROSAURUS; Paleontology and Geology Glossary-Ma; New evidence of armoured titanosaurids; Dinopedia ATW030427.**

Nemegtosauridae: *Antarctosaurus*, *Malawisaurus*, *Nemegtosaurus*, *Phuwiangosaurus*, *Quaesitosaurus*, *Rapetosaurus*. This group is used without a name by [R&F]. Since it incorporates all the members of the Nemegtosauridae Barrett & Upchurch (1995), I use that name as a matter of convenience. In this sense, it would be defined as *Nemegtosaurus* > *Saltasaurus*.



Nemegtosaurus: skull showing synapomorphies per Upchurch (1998)

Range: Early to Late Cretaceous of Asia, Africa, India & Madegascar

Phylogeny: Titanosauridae : *Ampelosaurus* + *Epachtosaurus* + *Janenschia* + *Magyarosaurus* + Saltasaurinae + * **:** *Quaesitosaurus* + (*Nemegtosaurus* + *Rapetosaurus*).

Introduction: Modestly-sized specialised sauropods from the Late Cretaceous of western Asiamerica. Originally believed to be aberrant dicraeosauran diplodocids, they are now considered aberrent titanosaurs. Most likely through geographic isolation these animals evolved in their own way. Their main predators were Tyrannosaurids. *Rapetosaurus* from Madagascar may belong to the same group, although the geographic distance makes me think it actually belongs to a different subfamily (perhaps one indigenous to Madagascar, at that time, like now, an island and hence with its own unique fauna).

Characters: Lightly built, elongate skull; slender, peg-like teeth at front of jaws; tooth row perpendicular to line of dentary; wear facets on teeth with angle <30º from long axis of teeth; **$** long axis of mandibular symphysis makes 90º angle with long axis of mandible; dentary rami are parallel; dentary length almost same as length of cranium; coronoid present; *basipterygoid process* directed ventrally; **$** basipterygoid process length at least 4x basal diameter [R&F]; basipterygoid processes angled ~45° to skull roof (also in some diplodocoids) [VN]; preantorbital fenestra absent; maxilla & premaxilla relatively tall & robust in lateral view; retroarticular process absent; nasal does not contact maxilla; **$** frontals fused at midline [R&F]; anterior process of quadratojugal deflected anteriorly; **$** sharp change in angle of rostral ramus of quadratojugal; **$** parietal does not contribute to posttemporal fenestra [R&F]; squamosal reaches quadratojugal; **$** squamosal excluded from lateral temporal fenestra; quadrate inclined anteriorly (possible taphonomic artifact); quadrate with deeply invaginated posterior fossa [VN]; **$** occiput long, with paroccipital processes directed posterolaterally [R&F]; midcervical centra long (as compared to saltosaurines) [VN].

Links: DinoData: Nemegtosaurus; Untitled Document; Nemegtosaurus; Sauropodomorphs (October 1); Dinosaur Illustrated Magazine - DIM - number 0: Editorial, November 17/1998; Opisthocoelicaudia.

References: Rogers & Forster (2001) [R&F]; Upchurch (1995); Upchurch (1998).

Note: [1] often classified as aberrant, basal titanosaurs -- as opposed to aberrant, basal diplodocimorphs. The question was apparently addressed at length and resolved in favor of the diplodocimorph connection in Upchurch (1999). Only two months later (8/01) *Nemegtosaurus* appears to be back among the titanosaurs [R&F]. The August, 2001 Dinosaur Mailing List contains a good deal of relevant, high quality discussion. **[2]** The characters marked "[VN]" show as synapomorphies in an analysis I ran of essentially the [R&F] data set. 010905.

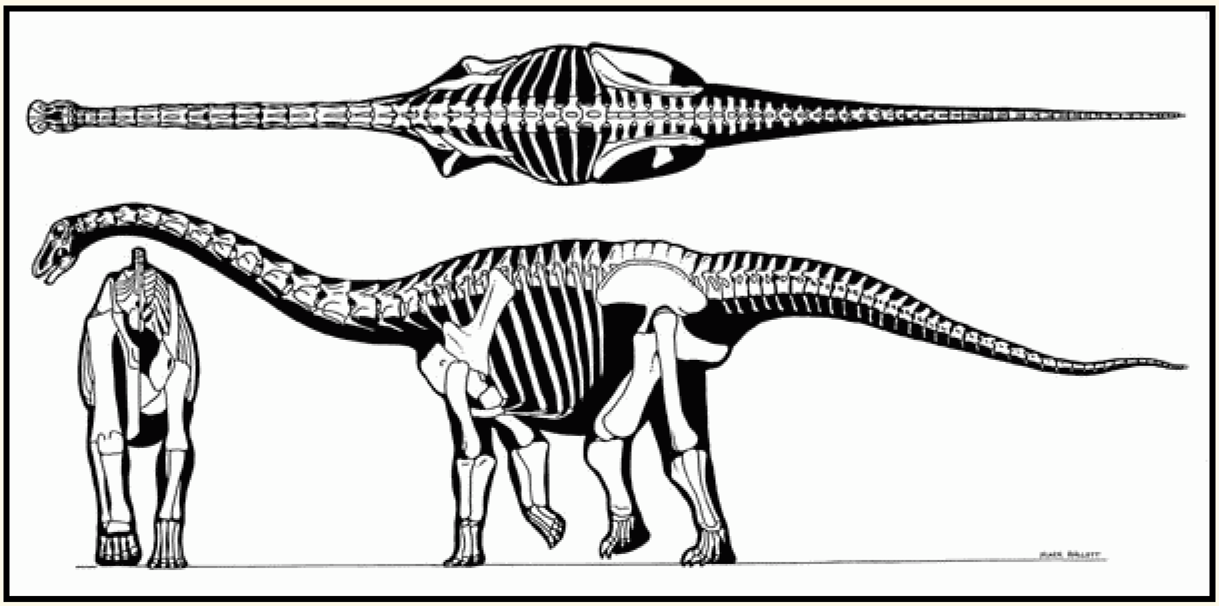
***Quaesitosaurus*:**

Range: Late Cretaceous of Asia

Phylogeny: Nemegtosauridae **:** (*Nemegtosaurus* + *Rapetosaurus*) + *.

***Quaesitosaurus orientalis* Kurzanov and Bannikov, 1983**
***Horizon:* "Barungoyotskaya" Formation of Omnogov, Mongolia**
***Age:* early Campanian**
***Place:* eastern Asiamerica (Mongolia)**
***Remains:* partial skull**
***Comments:* A close relative of Nemegtosaurus mongoliensis, it lived in the same locality but several millions of years earlier, possibly an ancestral form. This species might be a species of Nemegtosaurus, rather than a distinct genus. (MAK 011115).**

***Rapetosaurus*:**



Reconstruction of the skeleton of Rapetosaurus, with body outline. Image © Mark Hallett/State University of New York (SUNY) at Stony Brook.

***Range:* Late Cretaceous of Madagascar.**

***Phylogeny:* Nemegtosauridae :: Nemegtosaurus + *.**

***Rapetosaurus krausei* Rogers and Forster, 2001**
***Horizon:* Maevarano Formation of Madagascar**
***Age:* early-mid Maastrichtian**
***Place:* Madagascar, Gondwana**
***Remains:* skull and most of skeleton**
***Length:* 15 meters**
***Comments:* "the most complete titanosaur yet discovered, provides a view of titanosaur anatomy from head to tail. A total-evidence phylogenetic analysis supports a close relationship between brachiosaurids and titanosaurs (Titanosauriformes). The inclusion of cranial data from Rapetosaurus also lays to rest questions concerning the phylogeny of the enigmatic Mongolian genera Nemegtosaurus and Quaesitosaurus. In spite of their elongated, diplodocoid-like skulls, all three taxa are now firmly nested within Titanosauria." [RF01] (MAK 011115).**

Characters: [1] expanded antorbital fenestra extends over tooth row; preantorbital fenestra positioned posterior to antorbital fenestra; subnarial foramen anteriorly positioned and dorsoventrally elongate; jugal process of maxilla posterodorsally elongate and narrow; frontals with median dome; quadrate with V-shaped quadratojugal articulation; supraoccipital with two anteriorly directed median parietal processes; pterygoid with extremely shallow basipterygoid articulation and dorsoventrally expanded anterior process; basipterygoid processes diverge only at distal extremes; dentary with 11 alveoli that extend two-thirds the length of the element; gracile cylindrical teeth with high-angle planar wear facets; 16 cervical vertebrae with constricted neural canals and continuous pre- and postspinal coels devoid of pre- or postspinal laminae; cervicalneural spines with proximal bifurcation and three pneumatized coels bounded by discrete laminae; 11 dorsal vertebrae with deep lateral pleurocoels; dorsal neural spines with strong pre- and postspinal laminae in deeply excavated anterior and posterior coels; dorsals with median interpre- and interpostzygapophyseal laminae; middle and posterior dorsals with divided spinodiapophyseal lamina; six sacral centra with deep lateral pleurocoels; all caudal centra procoelous with convex ventral margin lacking excavation; anterior caudal centra broad transversely and anteroposteriorly compressed; middle-posterior caudal centra with constant length:width ratio; anterior-middle caudal neural spines with spinoprezygapophyseal, prespinal and postspinal laminae on rectangular and anteriorly positioned neural arches; chevrons throughout 80% of tail; iliac peduncle of ischium comprises one-quarter of acetabulum; ischial peduncle of ilium low and poorly developed; pubis more than twice as long as ischium; scapula and coracoid with equal glenoid contribution; scapular blade not distally expanded; humerus/femur length quotient 0.80; radius and ulna with oblique interosseus ridges.

Notes: [1] These characters quoted directly from Micky Mortimer's summary in Rapetosaurus stuff.

Links: DinoData Dinosaurs R037 RAPETOSAURUS krausei; Paleontology News - Rapetosaurus; NSF - OLPA - PR 01-61: NEW LONG-NECKED DINOSAUR DISCOVERED IN MADAGASCAR; DinoNews.net - Le dinosaure Rapetosaurus; ラペトサウルス-rapetosaurus; Dinosaur Count Up! The Newest Dinosaurs and all the rest - ...; Dinosaur museum.

References: Rogers & Forster (2001) [RF01]. ATW031004.

Nemegtosaurus: N. mongoliensis Nowinski, 1971; N. pachi Dong, 1977.

Range: Late Cretaceous (?Campanian to Maastrichtian) of Asia

*Phylogeny: Nemegtosauridae :: Rapetosaurus + *.*

***Nemegtosaurus mongoliensis** Nowinski, 1971*
Synonym: Opisthocoelicaudia skarzynskii Borsuk-Biallynicka, 1977
***Horizon:** Nemegt Formation of Omnogov, Mongolia*
***Age:** early Maastrichtian*
***Place:** eastern Asiamerica (Mongolia)*
***Remains:** partial skull; skeleton*
***Length:** 12 meters*
***Weight:** 7 tonnes*

***Comments:** based on a partial skull with some features similar to both Brachiosaurus and Diplodocus, Nemegtosaurus was for a long time associated with the latter (specifically under the Dicraeosaurs), in part because of poor reconstruction. There followed some indecisiveness among dinosaurologists as to whether Nemegtosaurus should be considered an aberrant titanosaur or an aberrant diplodocimorph. The discovery of Rapetosaurus finally showed without a doubt Nemegtosaurus' titanosaurid affinities. But Nemegtosaurus's problems did not end there. Early on, a headless skeleton found nearby was named Opisthocoelicaudia skarzynskii and classified as a camarasaurid. This was during the period in which Nemegtosaurus was thought to be a Dicraeosaur. It was then suggested that the skull and skeleton belong to the same animal. However, while the skull is now safely ensconed among the Nemegtosauridae, the skeleton is still often included with the saltasaurinae (I am not sure, not having the journal at hand, but I think the reference here may be Upchurch). Following the dictum of the Franciscan monk William of Occam (c. 1280/5-1349) that entia non sunt multiplicanda praeter necessitatem (No more things should be presumed to exist than are absolutely necessary) I would rather retain the Nemegtosaurus head firmly on the Opisthocoelicaudia body. (MAK 011115).*

Characters: ~12m; maxilla & premaxilla relatively tall & robust in lateral view; floor of external nares formed by flat to concave dorsal edges of maxilla & premaxilla; preantorbital fenestra absent; unusually large eyes; basipterygoid process directed ventrally; jaw length almost equal to skull length; dentary rami parallel; dentary symphysis perpendicular to tooth row; coronoid present; surangular foramen present; retroarticular process absent; teeth pencil-like, long & cylindrical; wear facets at <30° to axis of tooth.

Links: DinoData NEMEGTOSAURUS; Paleontology and Geology Glossary N; Nemegtosaurus; Yahooligans! Science- Dinosaurs; Dinosaur Illustrated Magazine - DIM - number 001, 2001; Opisthocoelicaudia. ATW030608.

Saltasaurinae: Presumably *Saltasaurus* > *Nemegtosaurus*.

Range: Late Cretaceous of South America & Africa.

Phylogeny: Titanosauridae **:** *Ampelosaurus* + *Epachtosaurus* + *Janenschia* + *Magyarosaurus* + Nemegtosauridae + * **:** *Alamosaurus* + (*Titanosaurus* + *Jainosaurus*) + (*Saltasaurus* + *Neuquensaurus*).

Introduction: The Saltasaurs, here taken to include the Saltasaurs and Alamosaurs - i.e. the "crown titanosaurids" - were advanced latest Cretaceous forms were apparently limited to west Gondwana and south-west Asiamerica. These were stocky animals of medium to very large size. When these armor nodules were first found they were assumed to belong to ankylosaurians. In fact, no ankylosaur is known from South America (west Gondwana). however, primitive abarrent ankylosaurs did inhabit Australia (south-east Gondwana) . For a while the Saltasaurs were the only sauropod known to have armour plates in the skin (osteoderms), but it has recently been found that other (possibly most, although not all) titanosaurids, and possibly some other sauropod lineages, were also so equipped. (MAK 011115)

Characters: dorsal transverse processes are directed strongly dorsolaterally [? reversal]; cervical postzygapophyses extend posteriorly beyond centrum [S+05**$**]; **$** first caudal centrum with biconvex articulating surfaces [R&F]; number of caudal vertebrae with transverse processes reduced (<10) [? unambiguous]; anterior and middle caudal centra, ventral longitudinal hollow present [VN]; caudal centra, longitudinal depression with median longitudinal ridge [S+05]; caudal vertebrae, arch and transverse processes "spongy" with uniformly distributed (air?) cells [S+05**$**]; caudal vertebrae, neural spines with strong posterior slant, beginning with caudal 2 [S+05**$**]; middle and posterior caudal centra, anterior articular face shape procoelous (cone-shaped) [VN]; scapular blade, orientation: forming a 45 degree angle with coracoid articulation [R&F**$**]; scapular blade, shape: acromial edge not expanded [? reversal]; coracoid, anteroventral margin shape: rectangular [VN]; humeral proximolateral corner, shape: square (1) [VN]; **$** deltopectoral crest reduced [R&F]; humeral distal condyles, articular surface shape: expanded onto anterior portion of humeral shaft (1) [VN]; metacarpals long [VN]; Mt I longer than Mt IV [VN]; manus digits II & III lack ossified phalanges; ischial blade length much shorter than pubic blade [VN]; ischial blade with no emargination distal to pubic peduncle [VN]; tibia distal breadth more than twice midshaft breadth [VN].

References: Rogers & Forster (2001) [R&F]; Salgado *et al*. (2005) [S+05]. .

Notes: [1] The characters marked "[VN]" show as (not necessarily unambiguous) synapomorphies in an analysis I ran of essentially the [R&F] data set on PHYLIP. **[2]** Its hard to tell exactly what, but there is clearly something significant going on here relating to the forelimbs and hip. These could simply be size-related, but the distal forelimb changes suggest a fundamental change in the manner of walking. ATW051024.

Alamosaurus**:**

Range: Late Cretaceous of North America

Phylogeny: Saltasaurinae **:** (*Titanosaurus* + *Jainosaurus*) + (*Saltasaurus* + *Neuquensaurus*) + *.

Alamosaurus sanjuanensis* *Gilmore, 1922
Horizon:* *Upper Kirtland Shale, New Mexico; Javelina and El Picacho Formations, Texas; North Horn Formation, Utah
Age:* *late Maastrichtian
Place:* *southeast Asiamerica
Remains:* *partial postcranial skeleton, isolated postcrania
Length:* *21 meters
Weight:* *20 tonnes

***Comments:* these huge advanced titanosaurs migrated north across a land-bridge and invaded southwest Asiamerica, where they were preyed on by Tyrannosaurus (and you think you've got troubles...). This genus was larger but more lightly built than Saltasaurus. Also, unlike its South American cousins, it seems to have lacked large osteoderms. No armor has ever been found for this species. *Trivia note:* This evocatively named genus is not named after the Alamo, a some may think, but was originally described from the "Ojo Alamo Sandstone," strata now assigned to the Kirtland Shale (the "Ojo Alamo Formation" is currently used for Paleocene deposits). This in turn is named after a trading post in New Mexico -- Ojo Alamo -- where it was first found. The trading post in turn was named after a large cottonwood tree, called alamo in Spanish, that grew next to the spring nearby (info from Alamosaurus!, and Dinosauria Translation and Pronunciation Guide A (Ben Creisler) (MAK 011115).**

Links: DinoData: Alamosaurus; Alamosaurus; TMMSH - Exhibits - Scratching the Surface - Alamosaurus; Alamosaurus -- The Dinosauricon; Alamosaurus (Dutch); ALAMOSAURUS; Alamosaurus page in The Natural History Museum's Dino Directory; CNNfyi.com - Fossil feuding - June 12, 2000; Giant Dinosaur Found In Texas.

Titanosaurus:

Range: Late Cretaceous of India

Phylogeny: Saltasaurinae :: Jainosaurus + *.

***Titanosaurus indicus* Lydekker, 1877**
***Horizon:* Lameta Formation, Madhya Pradesh, Maharashta, and Aviyalur Group, Tamil Nadi, India**
***Age:* mid-late Maastrichtian**
***Place:* Indian subcontinent**
***Remains:* partial postcrania (tail vertebrae, femur)**
***Length:* 19 meters**
***Weight:* 14.7 tonnes**
***Comments:* The femur is much more slender than those of Saltasaurus and Alamosaurus, indicating a more lightly built animal. Otherwise this is a poorly known form, which served as the basis of the family Titanosauridae. Not surprisingly, some workers wish to change the name to Saltasauridae, as Saltosaurus is much better known. As with Megalosaurus and Megalosauridae, I am in favour of keeping the old name; call me sentimental. MAK**

Titanosaurus colberti Jain and Bandyopadhyay, 1997
Horizon: Lameta beds of India
Age: mid-late Maastrichtian
Place: Indian subcontinent
Remains: most of a postcranial skeleton
Comments: better material than *T. indicus* (MAK 011115).

***Jainosaurus*:**

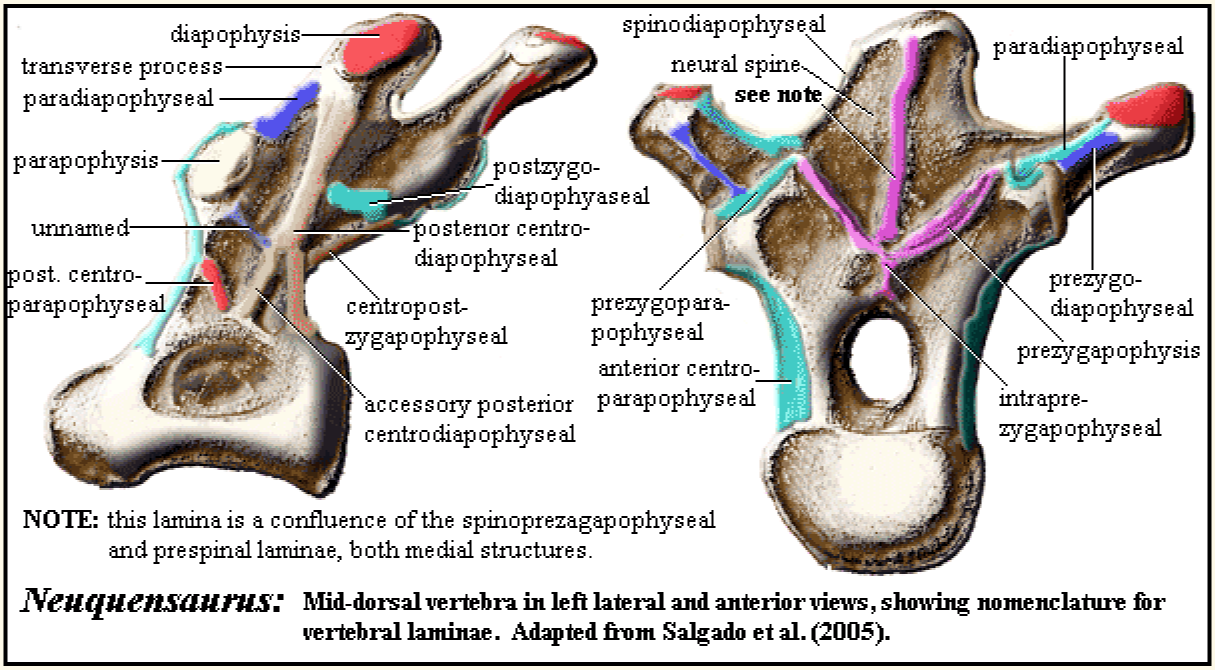
Range: Late Cretaceous of India

Phylogeny: Saltasaurinae **::** *Titanosaurus* + *.

***Jainosaurus septentrionalis* Hunt, Lockley, Lucas, and Meyer, 1995**
***synonym:* Antarctosaurus septentrionalis Huene and Matley, 1933**
***Horizon:* Lameta Formation, Madhya Pradesh, Maharashta, India**
***Age:* mid-late Maastrichtian**
***Place:* Indian subcontinent**
***Remains:* basicranium and partial postcranial skeleton**
***Comments:* probably should be included under the genus Titanosaurus. MAK 011115.**

***Neuquensaurus*: Powell 1992. N. ("Titanosaurus") australis Lydekker 1893.**

***Range:* Late Cretaceous (Early Campanian to Early Maastrichtian) of South America (Brazil, Argentina). Ancleto and Allen Fms. of the Neuqén Basin.**



Neuquensaurus: **Mid-dorsal vertebra in left lateral and anterior views, showing nomenclature for vertebral laminae. Adapted from Salgado et al. (2005).**

***Phylogeny:* Saltasaurinae :: Saltasaurus + *. [S+05]**

***Characters:* 10-12 m? 7m?; cervical vertebrae short & wide, strongly opisthocoelous [S+05]; cervicals with prezygapophyses widely splayed out from centrum, with triangular articulations, somewhat anteriorly convex [S+05]; cervical postzygapophyses extend posteriorly beyond centrum [S+05]; cervical neural spine terminating in hemispherical protuberance [S+05]; 10 opisthocoelous dorsal vertebrae [S+05]; dorsal centra short, with reduced pleurocoels containing well-developed internal partitions [S+05]; dorsal centra with slight ventral keel dividing 2**

concavities [S+05]; dorsal 1 lacking centroprezygapophyseal & centropostzygapophyseal laminae [S+05$]; dorsal neural spines initially inclined posteriorly, becoming more dorsal, but with distal posterior bend [S+05]; dorsal vertebrae with confluent prespinal and spinoprezygapophyseal laminae and well-developed posterior spinodiapophyseal laminae [S+05]; dorsals with accessory posterior spinodiapophyseal laminae [S+05]; 6 well-consolidated sacral vertebrae [S+05]; 7th sacral vertebra biconvex, not fully integrated [S+05$]; sacrals 3-5 with narrow centra [S+05$]; sacral rib 3 directed posterolaterally, almost reaching pubic peduncle [S+05]; sacral ribs 3-5 fused tightly to acetabulum and participating in articular surface [S+05]; 7th sacral ribs laterally directed, distally expanded & articulate with postacetabular ilia [S+05]; caudal vertebrae low [S+05]; caudal vertebral centra strongly procoelous, with lateral wall minimally exposed in ventral view, and concave ventral surface [S+05$]; caudal prezygapophyses short [S+05]; first caudal centrum short, with concave ventral & lateral sides [S+05]; middle & posterior caudal centra with wide, deeply excavated ventral surface and marginal ridges merging with articular facets of hemapophyses [S+05$]; sternal plates with very prominent ventral crests [S+05]; scapula with prominent medial muscle attachment scar near anterodorsal border [S+05]; limb bones short & more gracile than Saltasaurus [S+05]; humerus short & proximally expanded [S+05]; humerus deltopectoral crest developed to mid-shaft [S+05]; radius with sigmoid outline [S+05]; metacarpals short & robust [S+05]; ilium with laterally expanded anterior and posterior processes, anterior process shorter than in Saltasaurus [S+05]; ilium, pubic peduncle long and posteroventrally directed, with triangular distal surface [S+05]; ischium flat & short, with well-developed iliac peduncle [S+05]; femur anteroposteriorly compressed [S+05]; femur, medial condyle higher (= shorter/more proximal?) than lateral condyle [S+05]; tibial-femoral articulation rather flat [S+05]; tibia, cnemial crest very pronounced in anterior view [S+05]; tibia, distal portion expands transversely [S+05]; fibula relatively gracile and expanded at both ends [S+05]; fibula outer surface convex & inner surface slightly concave [S+05]; fibula with simple, well-developed lateral tuberosity & bent shaft [S+05$]; astragalus tall & transversely thin [S+05]; ossified calcaneum absent [S+05]; MtIII triangular in proximal view [S+05]; thick body armour in the shape of bony plates and bumps across its back.

Links: DinoData Dinosaurs N019 NEUQUENSAURUS; NEUQUENSAURUS; Neuquensaurus (Spanish); Los dinosaurios (Spanish).

References: Salgado et al. (2005) [S+05]. ATW051024.

Saltasaurus:

Range: Late Cretaceous of South America

Phylogeny: Saltasaurinae **::** *Neuquensaurus* + *.

Saltasaurus loricatus *Bonaparte and Powell, 1980*
Horizon: *Lecho formation of Salta, Argentina; also known from Uruguay*
Age: *early Maastrichtian*
Place: *South America*
Remains: *remains of several individuals.*
Length: *12 meters*
Weight: *7 tonnes*

Characters: scapula with prominent medial muscle attachment scar near anterodorsal border [S+05]; limb bones more robust than Neuquensaurus [S+05]; ilium with laterally expanded anterior process, longer than in Neuquensaurus [S+05]; femur anteroposteriorly compressed [S+05]; femur, medial condyle higher (= shorter/more proximal?) than lateral condyle [S+05]. ATW051024.

Comments: *This rather small sauropod caused a stir in the paleontological world when it was discovered to possess body armor (up until then all sauropods were believed to be smooth-skinned and rather defenseless). Since then, other titanosaurs have been found that are similarly equipped. Dermal scutes are present in many sauropods, and in diplodocomorphs they take the form of a crest along of the back. But, in many titanosaurids, these spines developed into, or were replaced by, armoured scutes. There is no compelling evidence that the scutes formed a dorsal carapace. In his doctoral dissertation, Jaime Powell (the co-discoverer of this species) arranged them along the back in two parallel rows in Saltasaurus. MAK 2002.*

References: Salgado et al. (2005) [S+05]. ATW051024.

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Sauropodomorpha Dendrogram

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
|--Prosauropoda
`--Sauropoda
   |--Cetiosauridae
   `--Neosauropoda
      |--Diplodocomorpha
      |  |--Rebbachisauridae
      |  `--Diplodocidae
      `--Macronaria
         |--Brachiosauridae
         `--Somphospondylii
            |--Euhelopodidae
            `--Titanosauria
               |--Nemegtosauridae
               `--Saltasaurinae
```

Contents

```
DINOSAURIA
|
SAUROPODOMORPHA X Th, MH
|--Thecodontosaurus •X
`--+--Efraasia •X
   `--+--Prosauropoda X
      |  |--Riojasaurus •X
      |  `--+--Plateosauridae •X
      |     `--+--Massospondylidae •X
      |        `--Yunnanosaurus •X
      `--Sauropoda X Th, MH
         |--Anchisaurus •X
         `--+--Melanorosauridae •X
            `--+--Vulcanodontidae •X
               `--+--Barapasaurus •X
                  `--Eusauropoda X
                     |--Mamenchisauridae •X MH
                     `--+--Cetiosauridae •X
                        `--+--Haplocanthosaurus •X
                           `--+--Jobaria •X
                              `--Neosauropoda X
                                 |--Diplodocomorpha X  MH
                                 |  |--Cetiosauriscus
                                 |  `--+--Rebbachisauridae X
                                 |     |  |--Nigersaurus •X
                                 |     |  `--Rebbachisaurus •X
                                 |     `--Diplodocoidea X Th
                                 |        |--Diplodocidae X MH
                                 |        |  |--Apatosaurinae •X
                                 |        |  `--Diplodocinae X
                                 |        |     |--Barosaurus •X
                                 |        |     `--Diplodocus •X
                                 |        `--Dicraeosauridae •X
                                 `--Macronaria X  Th, MH
                                    |--Camarasauridae X Th
```

```
 |     |--Aragosaurus •X
 |     `--+--Lourinhasaurus •X
 |        `--Camarasaurus •X
 `--Titanosauriformes X
    |--Brachiosauridae X, Th, MH
    |  |--Lapparentosaurus •X
    |  `--+--Atlasaurus •X
    |     `--+--Giraffatitan •X
    |        |--Bothriospondylus •X
    |        |--Pelorosaurus •X
    |        |--Cedarosaurus •X
    |        |--Sonorasaurus •X
    |        `--+--Sauroposeidon •X
    |           `--Brachiosaurus •X
    `--Somphospondylii X
       |--Chubutisaurus •X
       |--Aegyptosaurus •X
       |--Paralititan •X
       |--Venenosaurus •X
       |--Euhelopodidae •X Th, MH
       `--Titanosauria •X, , MH, Th
          |--Andesaurus •X
          |--Argentinasaurus •X
          `--Titanosauridae X
             |--Ampelosaurus •X
             |--Epachthosaurus •X
             |--Janenschia •X
             |--Magyarosaurus •X
             |--Nemegtosauridae X
             |  |--Quaesitosaurus •X
             |  `--+--Rapetosaurus •X
             |     `--Nemegtosaurus •X
             `--Saltasaurinae X
                |--Alamosaurus •X
                |--+--Titanosaurus •X
                |  `--Jainosaurus •X
                `--+--Neuquensaurus •X
                   `--Saltasaurus •X
```

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Sauropodomorpha References

Abbreviated Dendrogram

```
DINOSAURIA
|--ORNITHISCHIA
`--+--THEROPODA
   |
   `--SAUROPODOMORPHA
      |--Prosauropoda
      |  |--Plateosauridae
      |  `--Melanorosauridae
      `--Sauropoda
         |--Cetiosauridae
         `--Neosauropoda
            |--Diplodocomorpha
            |  |--Rebbachisauridae
            |  `--Diplodocidae
            `--Macronaria
               |--Brachiosauridae
               `--Titanosauria
```

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